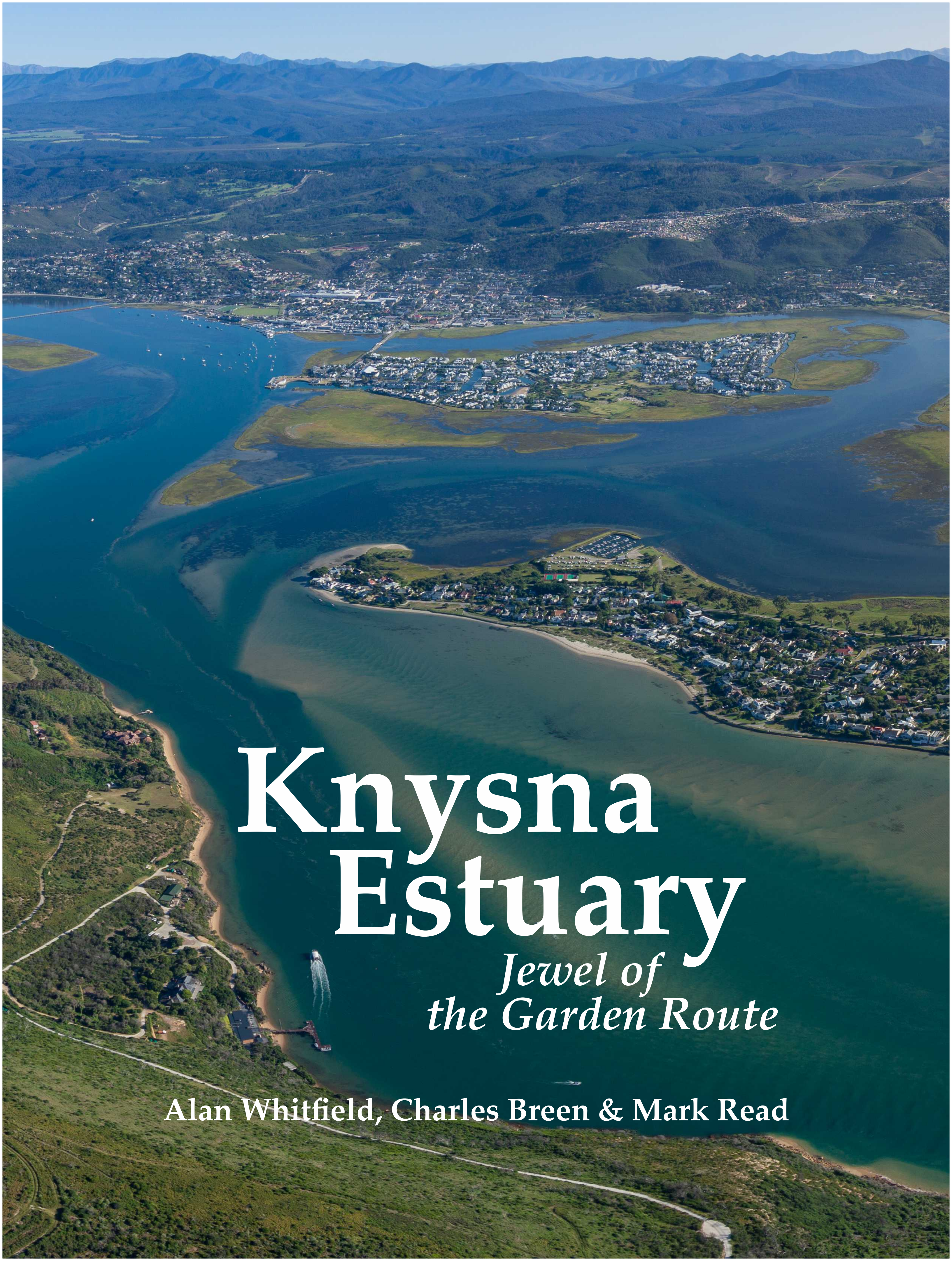

Knysna Estuary

Jewel of the Garden Route

Alan Whitfield, Charles Breen & Mark Read

Knysna Estuary

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Evening view over the Knysna Lagoon towards the Outeniqua Mountains in the distant background
(Photograph: © Markus Hallberg)

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Dedication

This book is dedicated to the late Professor Brian Allanson, who retired as Chair of the Zoology Department and Dean of Science at Rhodes University in 1988, and built his retirement home in Steenbok Crescent on Leisure Isle. Brian was one of the key drivers behind the launch of the Knysna Basin Project (KBP) in 1995 and the establishment of a research laboratory that supported the aims and objectives of this project. As Director of the KBP, he was also responsible for the compilation of a dedicated volume in the Transactions of the Royal Society of South Africa, covering various scientific aspects of the Knysna Estuary. These papers have formed important reference works for the chapters presented in this book and taken our ecological understanding of the estuary to new levels. In this regard we thank Brian for his dedicated service in promoting research and supporting wise estuarine management, based primarily on scientific facts rather than opinion or conjecture. It is therefore most appropriate that the proceeds from the sale of this book will be donated to the KBP to help further Brian's dream of a healthy Knysna system for both the aquatic biota and people of this Garden Route gem.

Foreword

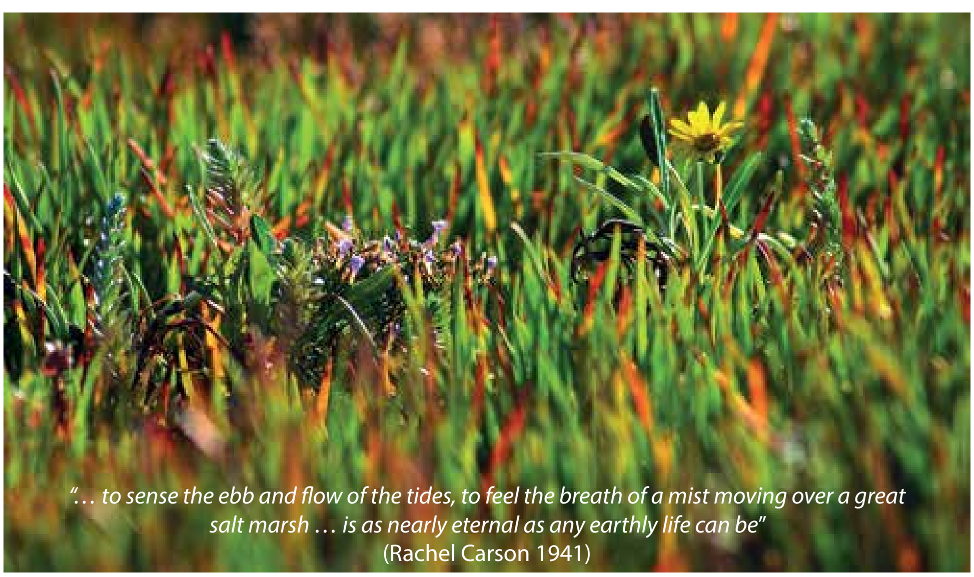
Knysna Estuary — It's hard to avoid superlatives: South Africa's most biologically diverse estuary; the most important for conservation; jewel; rich in history and prehistory; exquisitely beautiful; heaven on earth.

Three things set this book apart. First, the scope spans from the deep-time origins of the system to the modern world. It opens with five chapters that introduce the system, deal with early human use, palaeontology, physical development and nature, and its role as the meeting place between river and sea. Pivotal is the fact that towering on either side of the mouth are the twin rocky headlands that stabilise the estuary, so that much of it is dominated by tidal exchange. Second, the estuary has a rich scientific literature; but these papers are not accessible to the average person, so this synthesis is welcome. The book is written by renowned experts but in a communicative style that will be a joy for all to read. Thirdly, it is liberally illustrated, increasing the pleasure of the read and capturing its beauty and wonder. Four chapters deal with the plants and algae, invertebrates, the fishes and the water birds, and the book then concludes with the effects of climate change, the complexities of management, and the way forward.

My personal treasured memories of Knysna include spending the coldest night imaginable sampling for fish in inky snow-sprinkled darkness, having shots fired overhead from a 12-bore by JLB Smith when I had the temerity to sample 'his' eastern banks, multiple glorious sunrises dappling the lagoon, and the discovery of species as yet unknown to science.

It's a delight of a book: I read it from cover to cover, learnt a great deal, and cherished it for both content and design. It's a book to be devoured and then returned to time and time again to absorb its multifaceted coverage and details.

George Branch



"… to sense the ebb and flow of the tides, to feel the breath of a mist moving over a great salt marsh … is as nearly eternal as any earthly life can be"
(Rachel Carson 1941)

Preface

The genesis of *Knysna Estuary—Jewel of the Garden Route* happened three years ago midway through a stroll along the edge of the eelgrass beds fringing the quiet northeastern side of Leisure Isle. I was ruminating about a vociferous braai-side debate the previous evening when topics concerning the much loved Knysna Estuary (or lagoon as it's more popularly called) had been aired. Should outboard motor power be limited? Does the fish catch bag limit affect the realities of contemporary fish populations? Is the partially treated sewerage water in the Ashmead Channel being sufficiently flushed by tidal movement? What effect will rising sea levels have on the estuary? These are amongst the plethora of questions asked and argued endlessly by people who have fallen under the spell of perhaps South Africa's most beautiful stretch of water. So many questions and no reliable in-depth source of information to address them.

Just then I spied a lone figure collecting mud prawns from an area within the bait reserve and I set off to remonstrate with the fellow who was clearly no sport fisherman, merely attempting to feed his family with a fresh grunter. What followed was that I received, by way of an erudite lecture, an insight that the establishment of the critical invertebrate bait reserves had happened many years ago, and the demarcation of these areas therefore needed to be urgently interrogated to make them more meaningful to contemporary South Africans from both a conservation and human utilization perspective.

For me the switch flipped at that point—it was obvious that a broadly informative and scientifically reliable reference book on the ecology and natural history of the Knysna Estuary was required. This book needed to be clearly presented and illustrated such that any member of the public could appreciate the issues and possible solutions for future management of the estuary. I also realized that this was an impossible task for an enthusiastic amateur naturalist such as myself to undertake. Fortunately, Charles Breen and Alan Whitfield took up the challenge and the result is a volume that will take its place amongst the finest publications dealing with South African nature and biodiversity. It is my fervent hope that this book becomes a much-used friend by all who seek to deepen their knowledge about our wondrous Knysna Estuary.

Mark Read

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At the outset we thank the 33 authors who have helped create a book packed with important and useful information on the structure, functioning, evolution and management of the Knysna Estuary. Just as important in this endeavour is the generosity of our 20 sponsors (listed above), without whose support this volume would not have been possible. Finally, the dedication of our typesetter and graphics artist, Susan Abraham, is highlighted for her skills and attention to detail in creating the final layout for this book.

Alan Whitfield
Charles Breen
Mark Read

Author Contact Information

Adams, Janine (Prof) – DSI/NRF Shallow Water Ecosystems Research Chair, Nelson Mandela University, Port Elizabeth/Gqeberha, South Africa (email: janine.adams@mandela.ac.za)

Allan, David (Mr) – Durban Natural Science Museum, eThekwini Municipality, Durban (email: davidallan@telkomsa.net)

Barnes, Richard (Prof) – Department of Zoology, Rhodes University, Grahamstown/Makhanda, South Africa (email: rsb1001@cam.ac.uk)

Breen, Charles (Prof) – Knysna Basin Project, Knysna, South Africa (email: breenc39@gmail.com)

Cawthra, Hayley (Dr) – African Centre for Coastal Palaeoscience, Nelson Mandela University, Port Elizabeth/Gqeberha, South Africa (email: cawthra.h@gmail.com)

Claassens, Louw (Dr) – Palau International Coral Reef Centre, Koror, Republic of Palau (email: kyss.louw@gmail.com)

Cleghorn, Naomi (Prof) – Department of Sociology & Anthropology, University of Texas at Arlington, Texas, USA (email: Cleghorn@uta.edu)

Cooper, Andrew (Prof) – School of Geography and Environmental Sciences, University of Ulster, Coleraine, UK (email: jag.cooper@ulster.ac.uk)

De Vynck, Jan (Dr) – African Centre for Coastal Palaeoscience, Nelson Mandela University, Port Elizabeth/ Gqeberha 6031, South Africa (email: jandevynck2@gmail.com)

Dixon, Mark (Mr) – African Centre for Coastal Palaeoscience, Nelson Mandela University, Port Elizabeth/Gqeberha 6031, South Africa (email: ghostfishing@strandloperproject.org)

Freitag, Stef (Dr) – South African National Parks (SANParks), Knysna 6570, South Africa (email: stef.freitag@sanparks.org)

Green, Andrew (Prof) – Geological Sciences, University of KwaZulu-Natal, Durban, South Africa (email: greena1@ukzn.ac.za)

Helm, Charles (Dr) – African Centre for Coastal Palaeoscience, Nelson Mandela University, Port Elizabeth/Gqeberha, South Africa (email: helm.c.w@gmail.com)

Hodgson, Alan (Prof) – Department of Zoology, Rhodes University, Grahamstown/Makhanda, South Africa (email: a.hodgson@ru.ac.za)

Human, Lucienne (Dr) – South African Environmental Observation Network (SAEON) Elwandle Node, Port Elizabeth/Gqeberha, South Africa (email: lr.human@saeon.nrf.ac.za)

James, Nicola (Prof) – South African Institute for Aquatic Biodiversity (SAIAB), Port Elizabeth/Gqeberha, South Africa (email: NC.James@saiab.nrf.ac.za)

Lamberth, Stephen (Dr) – Department of Forestry, Fisheries and Environment (DFFE), South Africa (email: SLamberth@dffe.gov.za)

Largier, John (Prof) – Bodega Marine Laboratory, Coastal & Marine Sciences Institute, University of California Davis, Bodega Bay, USA (email: jlargier@ucdavis.edu)

Nurse, Pat (Mrs) – Lakes Bird Club, Knysna, South Africa (email: jgn@lantic.net)

Read, Mark (Mr) – Everard Read Group of Galleries, Johannesburg, South Africa (email: mark@everard.co.za)

Roux, Dirk (Dr) – South African National Parks (SANParks), Garden Route and Frontier Research Unit, South Africa (email: dirk.roux@sanparks.org)

Russell, Ian (Dr) – South African National Parks (SANParks), Garden Route and Frontier Research Unit, South Africa (email: ian.russell@sanparks.org)

Smith, Kyle (Mr) – Scientific Services, South African National Parks, Sedgefield, South Africa (email: martin.smith@sanparks.org)

Stear, Willo (Dr) – African Centre for Coastal Palaeoscience, Nelson Mandela University, Port Elizabeth/Gqeberha, South Africa (email: willostear@gmail.com)

Taplin, Megan (Ms) – South African National Parks (SANParks), Knysna, South Africa (email: megan.taplin@sanparks.org)

Thesen, Guy (Mr) – African Centre for Coastal Palaeoscience, Nelson Mandela University, Port Elizabeth/Gqeberha, South Africa (email: gthesen@gmail.com)

Turpie, Jane (Dr) – Anchor Environmental, Tokai, Cape Town, South Africa (email: jane@anchorenvironmental.co.za)

Van Berkel, Fred (Dr) – African Centre for Coastal Palaeoscience, Nelson Mandela University, Port Elizabeth/Gqeberha, South Africa (email: fn.vanberkel@gmail.com)

Van Niekerk, Lara (Prof) – Council for Scientific and Industrial Research (CSIR), Stellenbosch, South Africa (email: LvNieker@csir.co.za)

Wasserman, Johan (Mr) – DSI/NRF Shallow Water Ecosystems Research Chair, Nelson Mandela University, Port Elizabeth/Gqeberha, South Africa (email: johanwasserman@gmail.com)

Watt, Lorna (Mrs) – Lakes Bird Club, Knysna, South Africa (email: lornawatt@telkomsa.net)

Whitfield, Alan (Prof) – South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown/Makhanda, South Africa (email: A.Whitfield@saiab.nrf.ac.za)

Wooldridge, Tris (Prof) – Department of Zoology, Nelson Mandela University, Port Elizabeth/Gqeberha, South Africa (email: Tris.Wooldridge@mandela.ac.za)

Wurz, Sarah (Prof) – School of Geography, Archaeology and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa (email: Sarah.Wurz@wits.ac.za)

Contents

Chapter 1 : Introduction

Alan Whitfield & Charles Breen

1.1 Background and aims of this book

The Sonqua meaning of the word Knysna relates to a place of forests and ferns, with the Knysna River having its source in the magnificent Outeniqua (people bearing honey) Mountains. Ancestral hominin association with this region goes back more than a million years, with Earlier, Middle and Later Stone Age tools littering the caves and coastline in the vicinity of the Knysna Estuary. Indeed, early human fossil footprints (90 000 years ago) have been discovered at Brenton-on-Sea (Chapter 3), artefacts dating to more than 250 000 years ago are present on the Western Heads (Chapter 2), and a rich archaeological record shows that the ancestors of modern peoples walked the shores of Knysna long before the historical era. Other early human tracks in coastal rock formations from the region provide evidence of the possible first use of 'shoes' by these ancestral beings (see Chapter 3 for details).

The Knysna Estuary is the only natural estuarine bay (Figure 1.1) on the subcontinent, with both Durban Bay and Richards Bay having been significantly altered from their natural state. The Knysna Estuary is also the most important of South Africa's 290 estuaries in terms of conservation importance[1]. With a deep mouth and strong marine and freshwater influences, rich and diverse plant, invertebrate,

Figure 1.1 South-easterly aerial view of part of the Knysna Estuary (Photograph: © Duran De Villiers).

fish and bird assemblages now occupy the system (Appendix 1). The estuary also has the largest meadows of the endemic eelgrass *Zostera capensis* in southern Africa, which provide a home to both the endangered Knysna seahorse *Hippocampus capensis* and critically endangered false limpet *Siphonaria compressa*.

Just as rarity is one of the most prized qualities of a gemstone, so it is that the unique nature the Knysna Estuary affords it singular importance in the Garden Route and to South Africa. In this book we introduce readers to the multifaceted nature of the Knysna Estuary and how the biotic and abiotic components function together as a system. We are connected to and have responsibility for the future of the Knysna Estuary. It is through our direct and indirect connections with the estuary that value is generated; the flows of goods and services provide the foundations for the economic and social well-being of Knysna and further afield in the Garden Route. The gem is under our care; we are responsible for ensuring that our asset retains its capacity to generate value for future generations.

Apart from acting as the most important estuarine nursery area in the southern Cape for estuary-associated marine fish species such as the Cape stumpnose *Rhabdosargus holubi* and white steenbras *Lithognathus lithognathus*, the system also supports a number of Palaearctic migrant bird species that use the rich food resources of the Knysna Estuary during the Northern Hemisphere winter. The African clawless otter *Aonyx capensis* frequents quieter parts of the system, particularly in the more remote upper reaches and the coastal region around The Heads. Other rare or unique faunal residents/visitors to the Knysna Estuary are highlighted in Appendix 2, with a full biotic list provided in Appendix 1.

This book brings knowledge of the Knysna Estuary together in a format that is useful to as wide a section of society as possible, targeting learners, students, scientists, managers and the general public. Our primary goal is for the wealth of information on the natural history of the Knysna Estuary to contribute towards creating an informed society. In so doing, the book will encourage interest and support for the wise use of the estuary, now and into the future. Furthermore, knowledge of the Knysna system biota and ecological functioning has direct relevance to other South African estuaries since

Figure 1.2 A stream flowing through an ancient temperate forest in the Outeniqua Mountain catchment. Notice the clear, slightly peat-stained water that will eventually enter the Knysna Estuary (Photograph: © Alan Whitfield).

Figure 1.3 During high river flow periods the tannin stained water can penetrate deep into the Knysna Estuary, even as far as the eelgrass (*Zostera capensis*) beds in the middle reaches (Photograph: © Alan Whitfield).

many of these species and processes occur in systems elsewhere around our coast.

The contents of the various chapters are written by experts in their field, most with a strong knowledge and direct research experience of the Knysna system. The aim throughout is to enable and encourage readers to appreciate life within the estuary, understand its structure and functioning, and empower people to communicate its value and conservation importance from an informed position. And, above all, to ensure that we tread lightly, leaving something of great value for others to enjoy.

1.2 Some facts and figures about the Knysna Estuary

The Knysna Estuary is situated on the southern Cape coast and is fed by streams and rivers arising in the Outeniqua Mountains. The major tributaries of the Knysna River are the Bobbejaan, Kruis, Lawnwood, Rooi-Els, Gouna and Steenbras, with the Bigai, Bongani and Salt rivers flowing directly into the Knysna Estuary. Rainfall in these mountains can exceed 900 mm per annum, spread fairly evenly throughout the year. The total catchment area is approximately 526 km^2 and run-off is usually between 70 and 133 million cubic metres per annum but will exceed this range during very dry or very wet years.

Although the stream and river gradients are often steep, erosion on the forested and fynbos covered slopes is minimal, and the flowing waters are usually clear, though tannin-stained (Figures 1.2 and 1.3). This lack of suspended sediments is because the geology of most of the catchment comprises Table Mountain Sandstone which is resistant to water erosion. Soil nutrient levels are low and the leaves of plants in the area have high levels of tannins that leach out into the water when immersed. The pH of the water is low (acidic) but this increases to a pH of 7–8 once it enters the estuary as a result of the marine buffering effect. Weirs and causeways have been built across some of the streams and main river stem in places but no major dams have, as yet, been constructed on the Knysna River.

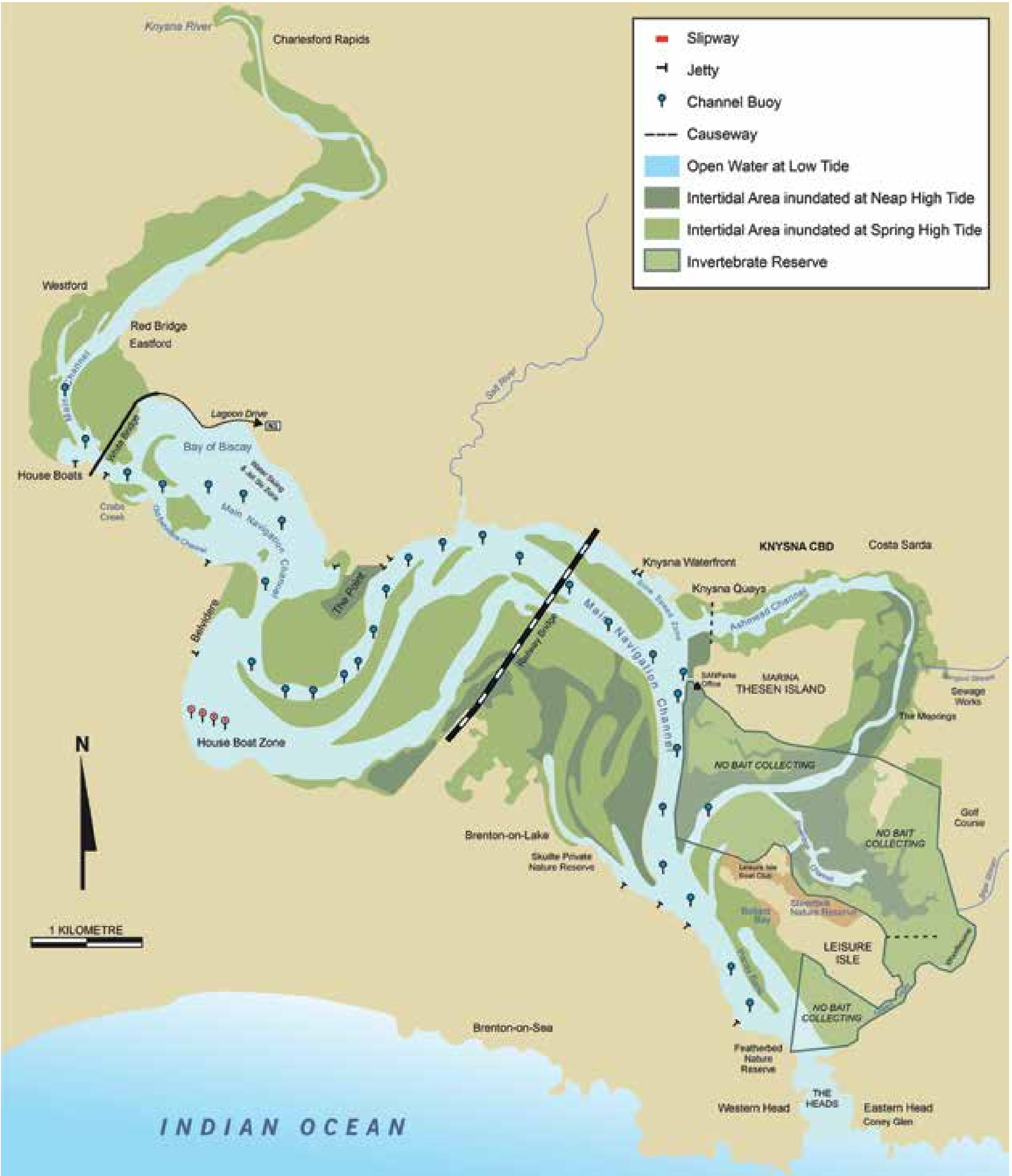

Figure 1.4 Map of the Knysna Estuary showing places referred to by chapters in this book.

Figure 1.5 The rocky shores at Coney Glen adjacent to the mouth limit the input of sand to the Knysna Estuary (Photograph: © Alan Whitfield).

The permanently open Knysna Estuary (Figure 1.4) is about 19 km long, 1633 ha in extent, and gradually broadens to form a lagoon over 3 km wide. Channel depths increase from about 2–3 m in the upper reaches, 3–5 m in the middle reaches, and 5–7 m in the lower reaches. The mouth of the estuary opens between two rocky headlands that prevent longshore drift of coastal dune sand into the lagoon. Depths of up to 16 m have been recorded in places in the mouth channel. The spring tidal range along the south coast is approximately 1.8 m, and although there is some amplitude reduction in the broad Knysna lagoon, this range persists more than half-way up the estuary and is indicative of an excellent connection with the sea.

Two road bridges in the upper half of the estuary and a rail bridge across the middle of the system do have an impact on sedimentary processes, mainly because of the solid embankments which restrict tidal flow, reduce major river flood scouring, and encourage sediment deposition along the adjacent earthen embankments. Whilst the Knysna railway has been non-functional for several decades, and could be removed to facilitate estuarine rehabilitation, the upgrade of the N2 along the north-western shore of the estuary did impact on the functionality of the littoral zone along this section of the system. Fortunately, the state of the littoral zone along the southern parts of the Knysna Estuary is relatively unimpacted and therefore functions normally.

At the Charlesford Rapids, which mark the head of the Knysna Estuary, the water is well stratified with salinities of <1 ppt on the surface and up to 5 ppt at the bottom (seawater salinity = 35 ppt). However, the normal river discharge is insignificant when compared with the tidal exchange at the mouth, so that any salinity stratification downstream of the headwaters rapidly breaks down and surface and bottom salinities of 30 – 35 ppt are usually recorded at the rail-bridge and seaward of this point. Even during flooding of the Knysna River, reduced salinities only prevail in surface waters of the lower reaches and seawater can still penetrate the estuary in bottom waters at high tide.

Water temperatures in the upper reaches of the Knysna Estuary range from a winter minimum of about 13°C to a summer maximum of about 28°C. The stabilising effect of the sea becomes evident in the lower reaches of the estuary, where the annual range is normally 15–23°C. Summer temperatures

Figure 1.6 Clear marine water entering the Knysna Estuary through the mouth on a flood tide (Photograph: © Alan Whitfield).

Figure 1.7 The Woodbourne salt marsh in the south-eastern part of the Knysna Estuary (Photograph: © Alan Whitfield).

in the lower reaches of the Knysna Estuary can decline by up to 10°C during summer due to the inflow of cold upwelled water from the sea. A dense fog often accompanies these upwelling events and is caused by the mixing of warm air from the land with cool air above the cold upwelled water. Because rocky shores dominate on both sides of the entrance to the estuary, the transport of sand into the estuary is constrained.

Nutrient and trace metal concentrations in the Knysna Estuary are typically low. Nitrate nitrogen and soluble reactive phosphorus levels tend to be in the 1–2 μg per litre range, except in regions where processed sewage outfall or localised pollution events occur. Also linked to sewage effluent inputs are depressed dissolved oxygen levels, especially in the Ashmead Channel and the area north of Thesen Island. These conditions have a major negative impact on the invertebrates and fishes within these parts of the estuary. Water clarity (Figure 1.6) suggests that phytoplankton biomass is low but attached macroalgae are widespread, especially in the intertidal and subtidal areas of the estuary. In addition, there are extensive eelgrass (*Zostera capensis*) beds at and below low tide, with oval saltweed *Halophila ovalis* and strap caulerpa *Caulerpa filiformis* often also present in patches at the lowest tide level.

Salt marshes (Figure 1.7 and 1.8) are a major aquatic habitat in the Knysna Estuary and comprise approximately 17% of the total saltmarsh area in the country. This particular habitat is dominated by the cordgrass *Spartina maritima* which is usually situated directly above the upper eelgrass zone and is normally completely inundated during spring high tides. Immediately above the cordgrass zone are bands of the glasswort samphire *Salicornia tegetaria* and arrow grasses T*riglochin buchenaui* and *Triglochin striata* that are also inundated at spring high tides. Above these plants are clumps of saltspurge *Chenolea diffusa*, marsh samphire *Salicornia meyeriana*, hairy plantago *Plantago crassifolia* and sea lavender *Limnolium scabrum* that are never completed inundated, even during spring high tides.

What constitutes an 'estuary' is a contentious matter, and the Knysna system is no exception. According to some scientists only the region north of the N2 White Bridge is an estuary, with the Lagoon and Bay divisions downstream not being classified as estuarine (Figure 1.9). For others, it is the whole system from the Charlesford Rapids to

Figure 1.8 Salt marsh species zonation patterns of cord grass *Spartina maritima* (upper part of picture), glasswort samphire *Salicornia tegetaria* (middle of picture) and saltspurge *Chenolea diffusa* (lower picture) on the north-western shore of the Knysna Estuary (Photograph: © Alan Whitfield).

the mouth that embrace the full extent of the estuary. The idealised definition of an estuary includes three zones; a lower marine one dominated by seawater, a middle region of mixed sea and fresh water, and an upper freshwater dominated section that is still influenced by tidal water movements. In broad terms, the Knysna Estuary conforms to this 'ideal' zonation pattern but, depending upon river flow regime, these reaches or regions can change over a period of days, weeks, months or even years. For example, during prolonged drought periods the lower estuary expands upstream from a salinity perspective, whereas river flooding has the effect of expanding the upper and middle estuary sections downstream. Nevertheless, even during river flood events, the deeper water of the Lagoon and Bay remains marine dominated, with the low salinity riverine influenced surface waters flowing out to sea over the top of the more saline bottom waters. Perhaps the most important criterion is what the plant, invertebrate and fish species are indicating in terms of where the estuary begins and ends—in this regard the biota are suggesting that the estuary extends from the Charlesford Rapids to The Heads.

An indication of the zonation of the various salt marsh species is shown in Figure 1.8. This zonation is not always linear but is normally related to the periods of immersion and therefore the elevation of the ground relative to tidal inundation cycles. In its pristine state the forest edge would probably have abutted onto the upper saltmarsh zone along the northern banks of the estuary but developments have broken that continuity (Figure 1.10). In addition, forest trees in close proximity to the estuary would have been the first to be harvested by early settlers for ship repairs, home construction, etc.

Salt marshes help bind the soil above the mid-tide level and prevent major erosion of the littoral banks during tidal and river flooding events. They also filter the water running off the land and adjacent roads, thus reducing nutrient and organic overloading of estuarine waters. These plants are very effective at locking up carbon from the atmosphere during photosynthesis, thus reducing CO_2

Figure 1.9 Aerial view of the western portion of the Knysna Estuary, with the White Bridge visible in the upper centre of the picture. The lagoon is situated immediately downstream of the White Bridge and the upper estuary above it (Photograph: © Domossa).

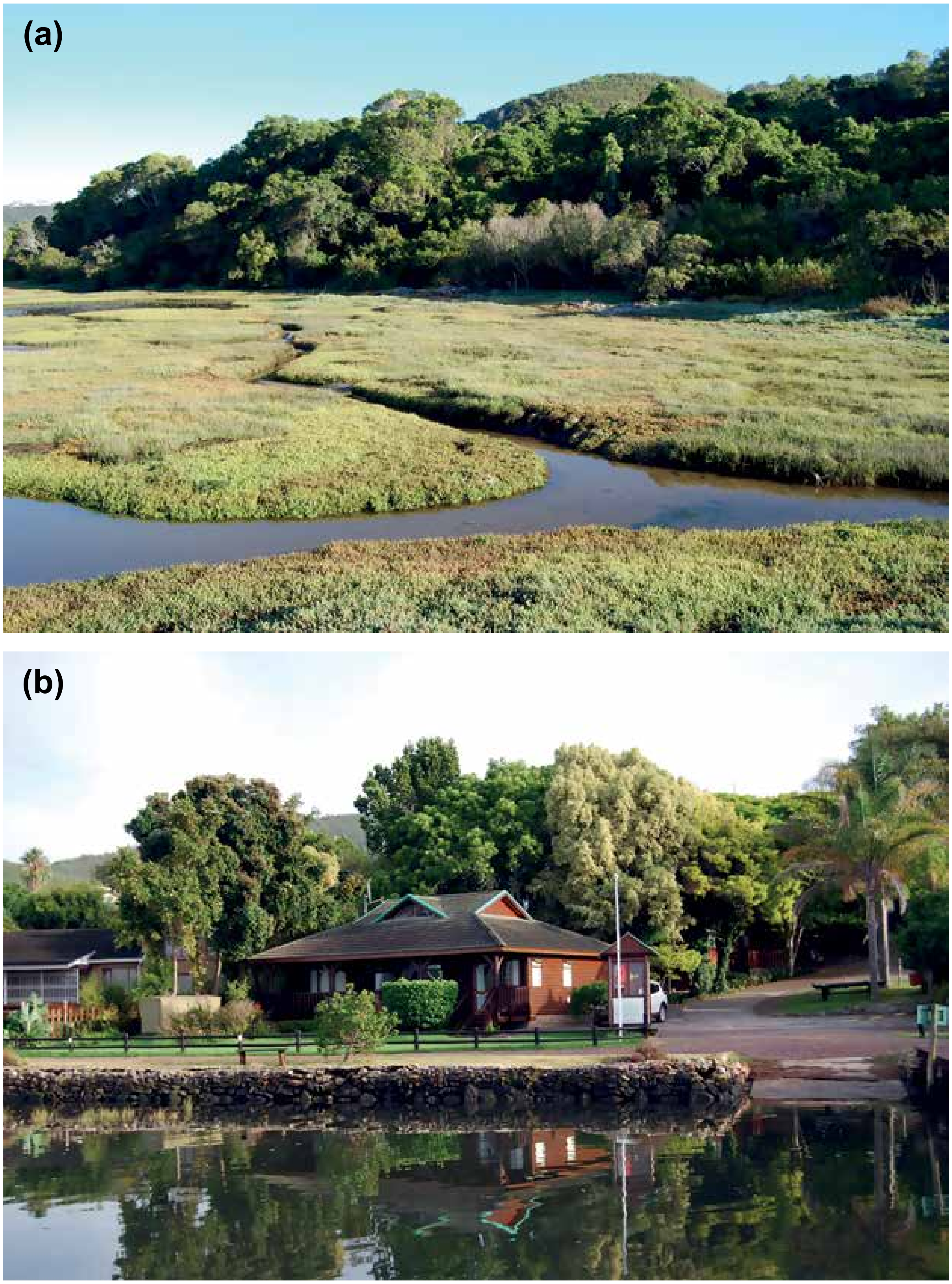

Figure 1.10 Two photographs taken on the north-west side of the Ashmead Channel showing the gradation of salt marshes into the natural forest habitat in (a) and loss of salt marsh and forest in (b) (Photographs: © Alan Whitfield).

levels and aiding our fight against accelerated global warming. Unfortunately, we have lost large areas of Knysna Estuary salt marsh to road, town and home developments (Figure 1.10) but there are sufficient of these marshes, mainly along the southern and eastern parts of the estuary, to provide adequate habitat for saltmarsh associated fauna and sustain food webs within the system.

The intertidal and subtidal rocky areas are colonised by a wide variety of macroalgae and seaweeds, some of which are only visible when SCUBA diving in this region. The saw-edged jelly weed *Gelidium pristoides* is a relatively short tufted purple-coloured seaweed that grows on moist rocks, whilst the sargassum *Sargassum incisifolium* and starred cushion *Lyengaria stellata* can proliferate in rock pools near The Heads. There are also some seaweeds, such as fragile upright codium *Codium fragile* (subspecies *capense*), that are washed into and out of the estuary with the tides but are also known to colonise the Thesen Island boat canals. Other seaweeds such as the delicate pink and feathery *Asparagopsis taxiformis* and iridescent blue *Plocamium corallorhiza* can sometimes be found in clear shallow waters near Leisure Isle at low tide. Large clumps of the red alga *Polysiphonia* sp. can often be seen drifting with the tides, sometimes washing ashore where they become a home for small invertebrates such as isopods.

In recent decades there has been an increase in nutrient pollution, especially from the Knysna Wastewater Treatment Plant (Figure 1.11) into the Ashmead Channel, leading to the proliferation of the sea lettuce *Ulva lactuca*. This invasion has resulted in the loss of eelgrass beds in the above channel and intertidal areas around Thesen Island. The sea lettuce can grow very rapidly under eutrophic conditions and large mats are then washed onto intertidal eelgrass beds, smothering these plants and altering the littoral food web for invertebrates and fishes. When the sea lettuce fronds dry out at the high tide mark, these mats can turn white and closely resemble toilet paper!

The water column in the mouth of the Knysna Estuary is inhabited by coastal marine zooplankton, while further up the system, estuarine species predominate. Benthic invertebrates within the estuary are diverse and abundant, with rich beds of the mudprawn *Upogebia africana* found in muddy areas, and the sandprawn *Kraussillichirus kraussi* and pencil bait *Solen capensis* in sandy areas. The blood worm *Arenicola loveni* used to once be relatively common in the lower reaches of the Knysna Estuary and was important for the aeration of

Figure 1.11 Flow from the Knysna Waste Water Treatment Plant prior to entering the estuary. Notice the foam on top of the water just after it flows over a small concrete culvert sill (Photographs: © Alan Whitfield).

Figure 1.12 A Cape stumpnose *Rhabdosargus holubi* that uses the Knysna Estuary, and particularly the eelgrass beds (*Zostera capensis*), as a primary nursery area (Photograph: © Alan Whitfield).

subsurface sediments by circulating water through its U-shaped burrow. Unfortunately, this invertebrate is now rare due to over-exploitation by anglers seeking to use this worm as fish bait. Another sought after worm by anglers for bait is the ribbon worm *Polybrachyiorhynchus dayi* that has a long branched sticky proboscis that it uses to capture invertebrate prey.

On the sediment surface the most noticeable invertebrate at low tide is the large shaggy sea hare *Bursatella leachii*, which occurs singly or in groups, often in open pools within eelgrass beds. Closer examination of these pools will likely reveal large numbers of the tick shell *Nassarius kraussianus* which prey on small bivalves. The tick shell is, in turn, preyed upon by the mottled necklace shell *Tectonatica tecta*, which creates a small hole through the shell of the gastropod and then consumes the contents. Middle Stone Age people in the area also used these gastropods to create shell bead necklaces by creating a small hole in each *N. kraussianus* shell and then stringing them into a necklace. Swimming about in the vicinity of the eelgrass leaves are often large numbers of isopods *Exosphaeroma hylecoetes*. Also swimming in the lower reaches of the Knysna Estuary, where full seawater salinity usually prevails, are groups of predatory cuttlefish *Sepia vermiculata*.

The fish community within the estuary is dominated numerically by small estuarine resident species, mainly the zooplanktivorous estuarine roundherring *Gilchristella aestuaria* and Cape silverside *Atherina breviceps*. However, from a biomass perspective the marine migrants that use the estuary as a nursery area predominate. These species are derived from two major families, the mullet (Mugilidae) and sea breams (Sparidae). Examples of the mullet include the southern mullet *Chelon richardsonii*, grooved mullet, striped mullet *Chelon tricuspidens*, flathead mullet *Mugil cephalus* and freshwater mullet *Pseudomyxus capensis*. Sea breams include the Cape stumpnose *Rhabdosargus holubi* (Figure 1.12), white stumpnose *Rhabdosargus globiceps*, blacktail *Diplodus capensis* zebra *Diplodus hottentotus* and white steenbras *Lithognathus lithognathus*.

As a tidal estuarine bay, the Knysna Estuary offers wading birds permanent access to intertidal sand and mud flats. The mouths of most estuaries in South Africa are closed to the sea for considerable periods of time each year, thus denying waders access to the rich intertidal invertebrate fauna of these systems. The abundance of small fishes in the shallows also attracts a range of wading piscivores such as little egrets *Egretta garzetta* and grey herons *Ardea cinerea*, with swimming piscivores such as reed cormorants *Phalacrocorax africanus* and white-breasted cormorants *Phalacrocorax carbo* venturing into deeper, more offshore waters. The aerial feeders are dominated by a variety of kingfisher and tern species, with the iconic African fish eagle *Haliaeetus vocifer* an ever present component of Knysna's rich avifauna.

Mammals are also represented in the Knysna Estuary, albeit in low numbers and often in the form of temporary visitors such as the juvenile southern right whale *Eubalaena australis* that died in the lagoon in 2020. Loggerhead turtles *Caretta caretta*, the Cape fur seal *Arctocephalus pusillus* and bottlenose dolphins *Tursiops truncatus* have been recorded visiting the estuary but seldom spend much time in the system (see Appendix 2). There are also elusive, but resident, African clawless otters *Aonyx capensis* in the estuary and along the adjacent coastline but they avoid areas where human disturbance levels are high.

1.3 Important studies on the Knysna Estuary

Much research has been conducted on the Knysna Estuary over the past half century (Figures 1.13 and 1.14). The earliest comprehensive study was that conducted by Professor John Day and his team from the University of Cape Town in the early 1950s[2,3]. However, only a few publications on the zooplankton, fishes or birds of the estuary appeared in the 1900s, with more recent research on these components now summarised in Chapters 7, 8 and 9 of this book.

An extremely valuable synthesis of available information on the Knysna Estuary was conducted by Professor John Grindley, also from the University of Cape Town[4]. The launch of the Knysna Basin Project by Professor Brian Allanson from Rhodes University in the mid-1990s represented the next major step in bringing together research endeavours on the Knysna Estuary and culminated in the production of a special edition of the Transactions of the Royal Society of South Africa. That volume detailed physical and biological research on the estuary and also provided a comprehensive bibliography[5,6,7,8].

In terms of published knowledge of the Knysna Estuary, it would appear that we have a rich database to draw upon for most of the scientific disciplines. Surprisingly, one of the most neglected of these disciplines is the birdlife associated with the estuary. Whilst considerable attention has been focused by ornithologists on the birds of the nearby Wilderness Lakes and Swartvlei[9], little has been paid to the importance of the Knysna Estuary to aquatic associated bird species.

The socio-economic importance of the Knysna Estuary to people in the area has also been addressed in recent decades[10], There is little doubt that the natural attraction of the estuary to both national and international visitors is a cornerstone of the tourism business in the area which is estimated at a value of approximately R1 billion per annum[11]. Non-destructive activities such as swimming, sunbathing, canoeing, sailing, sightseeing and birding are all important options available to these visitors. The large number of recreational anglers and subsistence fishers are also dependent on a healthy estuary maintaining sustainable stocks of both bait organisms and fish stocks that are valued more than R786 000 per annum for the subsistence fishery in this estuary alone. Overall, the wider economic contribution of the Knysna Estuary to the nursery function of fishes and invertebrates amounts to at least R167 million per annum[12].

For much of its history, the Knysna system had no dedicated management authority looking after the conservation and wise utilisation of the estuary. This changed with the appointment of SANParks in 1991 as the designated authority to oversee the conservation and management of the estuary. Currently the Knysna Estuary is formally protected (Figure 1.15) under the National Environmental Management Act: Protected Areas Act and falls under the jurisdiction of the Garden Route National Park. The park is divided into different management sections, and the estuary falls under the Knysna Lakes Section. Although the estuary falls within a national park, access is not restricted and most of the properties adjacent to the estuary are privately owned[13]. Some consequences of this free access are shown in Figure 1.16 where destruction of intertidal eelgrass (*Zostera capensis*) plants by bait harvesting in particular is widespread.

Water and sediment pollution in particular have come under the spotlight in recent decades and there is an increasing realisation that the resources of the estuary are not infinite and need to be carefully managed to facilitate sustainable yields in the future. There is also an increasing awareness, brought about by the occurrence of prolonged droughts on river flow from the catchment, that water is a precious commodity for both people and the ecology of the estuary. Fortunately, the large tidal prism currently overrides the inputs of excessive nutrients and other pollutants on water quality in the estuary[7]. Nevertheless, non-compliant discharges from the Knysna Waste Water Treatment Works pose a major eutrophication threat

Figure 1.13 Botanical researchers from Nelson Mandela University collecting phytoplankton samples in the Knysna Estuary (Photograph: © Alan Whitfield).

Figure 1.14 Ichthyological researchers from Rhodes University and SAIAB sampling fish using a beach seine net in the Knysna Estuary (Photograph: © Alan Hodgson).

Figure 1.15 Signage installed by SANParks at one of the public boat access points to the Knysna Estuary (Photograph: © Alan Whitfield).

Figure 1.16 The consequences of bait extraction and a boat outboard propeller path in a SANParks designated Invertebrate Reserve highlight two human pressures on Knysna Estuary eelgrass beds (Photograph: © Alan Whitfield).

Figure 1.17 A view of Thesen Island across the Ashmead Channel, indicating the close proximity of people and natural habitats associated with the Knysna Estuary, thus emphasizing the need for a socio-ecological approach to the management of the system (Photograph: © Alan Whitfield).

Figure 1.18 The African elephant (*Loxodonta africana*) and hippopotamus (*Hippopotamus amphibius*) would have been residents of the Knysna Estuary area prior to the advent of hunters with rifles almost three centuries ago. Unfortunately, the original wild elephants of the Knysna forests have now dwindled in numbers, almost to a point of no return. Hippo numbers in the pristine Knysna Estuary would have been restricted to a few small pods, primarily due to the limited available grazing in the surrounding area. Hippo bones and teeth have been found adjacent to the Knysna Estuary (Photographs: © Knysna Elephant Park and © Alan Whitfield).

in the lower reaches of the estuary which leads to macroalgal blooms and loss of eelgrass beds in certain areas[13].

1.4 Content covered by this book

The following sections give a 'taste' of the contents covered by this book. The major findings of each chapter were also taken into consideration when compiling the final synthesis on pages 295 – 312. As each chapter unfolded, it soon became apparent that there was a wealth of documentation on various topics relating to the Knysna Estuary. This book, which synthesizes this available information, has been interpreted and conveyed in a format that can be readily understood by all. It also provides ideas on ways forward for a new era of restoration and recovery of the Knysna system, such that future generations will be able to enjoy an increasingly healthy and more natural estuary.

We live in an era when the Knysna system takes the form of an estuarine bay. Twenty thousand years ago the estuary would have been located about 80 km south of Knysna on the then terrestrial Palaeo-Agulhas Plain and what is today known as the marine Agulhas Bank. The exact form that the estuary would have taken 20 000 years ago is unknown—it could have resembled a typical permanently open estuary such as Keurbooms or it may have been represented by an estuarine lake system similar to Swartvlei.

What we do know is that if sea level continues rising over the next 20 000 years due to global warming, then the Knysna Estuary will have a very different form to that which exists today. Under this future scenario, many of the current characteristic features of the estuary, such as Leisure Isle and Thesen Island (Figure 1.17), will all be permanently inundated under several metres of water—but new features will be created as the estuary 'migrates' up into the river catchment.

There is also an understanding that some aspects of the pristine Knysna Estuary are unlikely to be restored. For example, the reintroduction of the African elephant and hippopotamus (Figure 1.18) to the shores of the estuary will, for obvious reasons, never occur. There is also a hope that the original elephants of the Knysna forest will continue to exist—not just as a memory but as a reality!

Early humans and changing landscapes (Chapter 2)

Although little has been published on the deep-time archaeological record of the Knysna area, recent research, early surveys, and local resident knowledge of sites and finds leave little doubt that people have made Knysna home for a very long time. From the hand-axe using human ancestors of more than 300 000 years ago (or more) Knysna has attracted people to the shores of its estuary, river and coastline. A rich diversity of edible plants, animals, freshwater and marine resources made it an ideal place for humans reliant on wild resources. Stone tools, the most enduring 'visiting cards' of the ancients, show evidence of inspiration and ingenuity, changing design and function over time. This, coupled with pigment (ochre) use and other creative activities show that the early Knysna residents were resourceful and creative.

For much of this time, Knysna was an inland locale, a river valley connected through the rocky Knysna Heads to a broad grassland—the Palaeo-Agulhas Plain. Here, some of the earliest modern humans hunted, cooked, made things, and played in the sand (Figure 1.19), leaving the astonishingly preserved footprints discussed in Chapter 3. A recently studied site (KEH Cave 1) faces south toward the ocean. This site records at least 50 000 years of human activity in an ever-changing landscape. People made their home in the cave, lit hearths, cooked meals, and told stories around the fire. Nutrient-rich grasses would have supported large herds of animals. The elevated (> 20 m above sea level) perspective of the cave mouth would have provided an excellent vantage point from which to track both animals and other people.

The ancient people of Knysna also experienced extreme changes in the location of the coast associated with sea level rise. Although this brought coastal resources, particularly marine shellfish, closer to the lagoon, it also meant a significant loss of both hunting territory and the large herds of grazing ungulates. It also seems likely that the loss of the Plain would have brought different human groups closer together, possibly setting up the conditions for competitive interactions.

Tracks cast in stone (Chapter 3)

West of the Knysna Estuary, between Wilderness and Brenton-on-Sea, rock exposures of global importance are found, and a similar phenomenon occurs to the east at Robberg. These aeolianites and cemented foreshore deposits are the remains of Pleistocene dunes and beaches, respectively. Most can be dated to between 70 000 years and 140 000 years. The exposed surfaces have the capacity to record events that transpired on them, sometimes in exquisite detail, and a total of 144 vertebrate tracksites have thus far been identified on this stretch of coast alone.

Figure 1.19 A painting that illustrates life on the Palaeo-Agulhas Plain near Knysna (© Maggie Newman).

Figure 1.20 A fossilised trackway near Gericke's Point of a sand-swimming golden mole that inhabited the dune fields of the Cape south coast during the Pleistocene (scale bars = 10 cm) (Photograph: © Alan Whitfield).

Many of these are in remarkably spectacular, pristine settings, including the Garden Route National Park and Goukamma Nature Reserve.

One example is the profusion of elephant tracksites and the first global record of trunk-drag impressions, as well as the largest fossil tracks ever recorded since the Age of Dinosaurs. A carnivore tracksite provides a rare glimpse of the extinct Cape subspecies of the African lion, and carnivores are also represented by the only examples ever recorded of fossil seal traces. The Pleistocene megafauna of the region is further represented by tracks of rhinoceros and hippopotamus and the extinct long-horned buffalo and giant Cape horse. Crocodile tracks are present, along with the only known crocodile swim traces in Africa. Avian sites feature the tracks of larger-than-expected birds, including flamingos. Smaller creatures are represented by mole rat and golden mole burrows (Figure 1.20). Unusual forms of coprolites (fossilised dung) have been identified.

However, it is the discoveries of hominin tracksites, in what is perhaps the greatest concentration of such sites in the world, which are arguably of the greatest significance. Three sites have been identified, plus a number of possible sites and possible evidence for the first use of footwear, as well as patterns in the sand that our ancestors created.

Finally, if we go back much further in geological time, a small coastal basin opened in the area during Jurassic-Cretaceous times, and filled with sediment. A young resident of Brenton-on-Lake made the discovery of a lifetime when examining these sediments which now fringe the Knysna Estuary: a theropod dinosaur tooth.

Evolution of the Knysna Estuary (Chapter 4)

The present day Knysna estuary has been shaped over the past 120 000 years by major changes in sea level from 8 m higher than present to 120 m lower. The estuary occupied its present position for a short time around 120 000 years ago and once again during the past 7 000 years. In between, it was located on what is now the continental shelf and the area now occupied by the estuary was an upland river channel. Its furthest excursion took place during the Last Glacial Maximum some time just over 20 000 years ago. At that time, the continental shelf was dry land and rivers flowed across it, forming estuaries and lagoons at what is now the edge of

Figure 1.21 View of the lower Knysna Estuary lagoon showing Leisure Isle and Thesen Island that would have been completely inundated during the last major marine interglacial warming period when the sea level was 8 m above present day levels (Photograph: © Domossa).

Figure 1.22 Looking seaward from The Heads during ebb tide shows a strong outflow of estuarine water forming a plume headed offshore (greener colors in foreground and softer blue in background). Due to the narrow mouth outflow from the estuary jets offshore and is not pulled back into the estuary on the subsequent tidal inflow (Photograph: © Myetech).

the continental shelf.

The modern estuary owes its unusually wide channel to the relatively soft and erodible surrounding rocks and coastal sediments landward of the mouth. The tidal inlet between is flanked to landward by a well-developed flood-tide delta of marine sand. In the central part of the estuary are a mosaic of subtidal channels and intertidal flats. These are shaped by a combination of river and tidal flows and are typically composed of fine sandy sediment. The uppermost reaches of the estuary are more fluvially dominated and contain coarse-grained sediments derived from the river catchment, in particular during floods.

Humans have modified the estuary in several ways, by (i) stabilising sections of the shoreline, limiting its future migration and cutting off sediment supply by bank erosion, (ii) building bridge embankments that alter the currents causing both scouring and deposition of sediment, and (iii) dredging of channels for artificial canals that change the tidal flows and overall hydrology of the estuary.

The steep surrounding topography means that even when sea level was 8 m higher during the last interglacial period, the margins of the estuary were not substantially different to the present. The presence, however, of property and infrastructure (Figure 1.21) does pose a challenge for future management of the system, as even small increases in water level do threaten human interests. If this results in an expansion in armouring of the shoreline, this will limit the extent of intertidal habitats, preventing their landward migration and leading to a general deepening of the estuary.

Estuarine hydrodynamics (Chapter 5)

Knysna Estuary is an estuarine bay characterized by clear waters that are regularly exchanged with ocean waters (Figure 1.22). Despite a modest tide range, the extensive tidal area draws in a large volume of seawater, filling the outer estuary up to the railway bridge at spring high tide. While waters are flushed more slowly from the mid-estuary (landward of bridge), water residence time is still limited and low nutrient inputs preclude dense algal blooms, maintaining clear waters. The inner estuary is well flushed by river inflow and the stratified circulation that develops there. While blooms may

Figure 1.23 Some of South Africa's largest salt marshes stretch across the banks of the Knysna Estuary, adding colour to the already picturesque views of the system (Photograph: © Alan Whitfield).

occur naturally in the estuary at times, following pulses of river inflow or high-nutrient seawater inflow, these are isolated events. This is not the case where there is nutrient pollution (e.g. Ashmead Channel). Anthropogenic effects include morphological change that can reduce flushing, and organic pollution that results in green tides and high algal densities not commonly found in Knysna Estuary (i.e. eutrophication).

The strong tidal flows also account for well-developed flood-tide shoals in the outer estuary as well as extensive tidal flats that support seagrass meadows in the mid-estuary. While tidal outflows flush out estuarine waters (Figure 1.22), inflowing waters bring new material from the ocean. Notably, cold, high-nutrient water can fill the outer estuary during summer months when upwelling occurs along the open coastline. The cold water is dense and may intrude sub-surface beyond the railway bridge. Alternately, freshwater inflows can form surface layers that spread across the estuary during periods of high river flow, thus supplying nutrients to the estuary. For much of the time, however, the inner estuary (landward of the N2 bridge) is distinct from the outer estuary—the former characterized by tannin-stained blackwater, and the latter characterized by turquoise-green clear waters. The inner estuary is always low salinity with little influence of ocean waters and switches from being colder than the outer estuary and ocean in winter and warmer at other times. The estuary is well-oxygenated throughout (with the exception of the heavily polluted Ashmead Channel).

Plants and algae of the estuary (Chapter 6)

The Knysna Estuary, with its rich flora, is one of South Africa's most botanically important estuaries. The estuary boasts the largest, most stable beds of the endangered eelgrass *Zostera capensis*, as well as some of the largest salt marshes in the country. Microalgae teem the water column, while seaweeds line the sandy channel bottoms, rocky areas, harbours and marinas. Each of these different types of primary producers play an important role in maintaining the ecological health and functioning of the estuary. Furthermore, they provide important

Figure 1.24 Each square metre of a typical Knysna intertidal seagrass bed, such as this one at Kingfisher Creek on Leisure Isle, can support a total of 4 000 individual animals and 75 different invertebrate species (Photograph: © Richard Barnes).

ecosystem services such as valuable nursery habitats for estuarine fauna, improving water quality by transforming and cycling nutrients, bank stabilization and climate mitigation through carbon storage.

This chapter provides an up-to-date synthesis of botanical research that has been carried out on the Knysna Estuary. The distribution of different plant and algal species in the dynamic estuarine environment is detailed, and insights to the structure and function of primary producer communities are provided. The importance of the plants and algae to the health of the estuary is emphasized through an account of the multiple ecosystem services they provide. Also outlined are pressures that threaten the estuary's primary producers, both at present and looking toward the future. Land needs to be set aside for landward migration of salt marsh (Figure 1.23) in response to sea level rise. Structures acting as a barrier for salt marsh migration should be removed.

Protection of sensitive plant habitats in the Knysna Estuary is essential as there are few opportunities for restoration or recreation of habitat due to coastal squeeze. Other threats are increases in nutrient input that stimulate growth of sea lettuce *Ulva lactuca* leading to smothering of eelgrass, particularly in the Ashmead Channel. This chapter aims to highlight the value of conserving and maintaining the health of Knysna Estuary's flora through proper management actions guided by informed studies.

Benthic and planktonic invertebrates (Chapter 7)

The invertebrate fauna of the Knysna Estuary has been under study since the late 1940s when Professor John Day and his colleagues Naomi Millard and Arthur Harrison visited Knysna from Cape Town several times over a period of four years. Day's team also visited 30 other localities as part of a much wider study of the ecology of South African estuaries, and concluded that of these Knysna "has the richest fauna we have seen", both in terms of individual animals and of numbers of species (Figure 1.24), a distinction that they ascribed to its clear water and deep permanently-open mouth. They recorded over 350 different types of invertebrate on

Figure 1.25 Catch and release fishing, such as the spotted grunter *Pomadasys commersonnii* shown in this picture, is a sustainable form of angling for all fish species targeted in the Knysna and other estuaries in the southern Cape (Photograph: © Leonard Flemming).

and in Knysna's rocky and soft-sediment shores in a 1952 paper[2] that is still consulted today.

Fifty years later the University of Cape Town surveys were repeated[8] by a team led by Professor Brian Allanson of Rhodes University, as part of the Knysna Basin Project which he established in the 1990s, their transects yielding unchanged values of high species richness. It is in part this abundant and diverse invertebrate biodiversity that has, through to the 21st Century, given Knysna the distinction of being the estuary of highest overall conservation importance amongst the 290 possible South African contenders[1].

Building on these earlier surveys, attempts have been made in the last decade to understand the patterns that can be observed in the distribution of invertebrate fauna across the estuary as a whole and to comprehend the processes that have given rise to such patterns. This work has been led by Professor Richard Barnes of Cambridge and Rhodes universities and has resulted in the zoobenthos community of the Knysna Estuary having one of the best studied invertebrate components of any South African system[14]. It is the overall picture that has emerged from these recent studies of the ecology of these invertebrates that is portrayed in Chapter 7.

Fishes of the Knysna Estuary (Chapter 8)

At least 119 fish species have been recorded from the Knysna Estuary. This system is the most important fish nursery area along the southern Cape coast by virtue of its size, permanently open mouth and variety of habitats available for occupation by a wide range of species. The dominant group in terms diversity and biomass are estuary-associated marine fish species, some of which are totally dependent on estuaries for their juvenile life stages. The other major fish component in the Knysna Estuary is an estuarine resident group that are able to conduct their entire life cycle within estuaries. Most of these are small species that reach reproductive maturity within one year and seldom exceed 5 cm in length as adults. They are numerically very abundant and the pelagic shoaling members of this group such as the Cape silverside *Atherina breviceps* and estuarine round-herring *Gilchristella aestuaria* are important 'fodder' fish for large piscivorous predators such as leervis *Lichia amia* and dusky kob *Argyrosomus japonicus*.

This chapter highlights the importance of the Knysna Estuary as a fish nursery area, as well as the food web supporting the fish assemblages in this system. The importance of submerged aquatic plants such as eelgrass *Zostera capensis* is highlighted, together with the rich invertebrate resources for fishes associated with these habitats. Two iconic species are selected for special attention—the first is the white steenbras *Lithognathus lithognathus* which is an important endemic species that is harvested by both recreational and subsistence fishers throughout the Eastern and Western Cape provinces. The second highlighted species is the Knysna seahorse that only occurs in three southern Cape estuaries and is strongly dependent on the Knysna system for its existence. The value of the Knysna Estuary to the recreational and subsistence fisheries is also emphasized and ways are suggested in which sustainable catches can be ensured for the future (Figure 1.25).

Waterbirds of the Knysna Estuary (Chapter 9)

Knysna Estuary is a key estuary in South Africa for waterbirds, primarily due to its large size. Biannual counts over 30 years provide insights into the status of its waterbird populations. Ninety-three waterbird species have been recorded but many are vagrants and the typical community comprises 63 species. Common waterfowl are Egyptian goose, *Anomia achaeus*, Cape shoveler and Cape teal. Of the Palearctic migratory waders, curlew sandpiper, common greenshank, Eurasian whimbrel, grey plover, common ringed plover and marsh sandpiper are common. The most abundant resident charadriiform waders are black-winged stilt, blacksmith lapwing, African oystercatcher, Kittlitz's plover and pied avocet. Kelp gull is the second-most abundant waterbird after curlew sandpiper. Common and swift terns are the most abundant terns. Reed and Cape cormorants are both common with the larger white-breasted cormorant less frequent. Other large common waterbirds include African sacred and hadeda ibises, African spoonbill, little egret and grey heron. The most abundant small waterbirds are pied kingfisher and Cape wagtail.

The average number of waterbirds is higher in

Figure 1.26 The iconic African oystercatcher *Haematopus moquini* is the most emblematic bird of Knysna Estuary which supports a thriving and globally important breeding population of this endemic coastal species (Photograph: © David Allan).

summer (4 338) than winter (2 530), mainly due to influxes of invertebrate-feeding migratory waders and of Egyptian geese. Several other waterbird groups, e.g. resident invertebrate feeders, piscivores and gulls, are more abundant in winter. Waterbirds are distributed fairly evenly across the wetland. The small Woodbourne Pan and, to a lesser extent, the large Rail Bridge-The Heads sections though support disproportionately high densities of birds. Overall waterbird numbers are decreasing, mainly due to large-scale decreases in migratory waders. Other species show increasing trends, e.g. Egyptian goose, African oystercatcher, blacksmith lapwing and African sacred ibis. Some of the most pronounced changes in abundance (both increases and decreases) seem linked to regional and even global causal factors rather than being related to any obvious changes in the ecology of the estuary itself. Knysna Estuary supports globally significant nesting populations of African oystercatcher (Figure 1.26) and Cape cormorant (the latter a Red Data species). It qualifies as both an 'Important Bird and Biodiversity Area' and as a 'Wetland of International Importance' under the Ramsar Convention.

Climate change (Chapter 10)

In the Knysna Estuary, climate change will exacerbate anthropogenic stressors. The estuary will be affected by changing air, river and sea temperatures, with an increase in the occurrence of tropical species such as the mud crab *Scylla serrata*, the peregrine paddler crab *Varuna litterata*, and the mangrove snail *Cerithidea decollata*, indicative of global warming. Along with causing changes in the distribution and abundance of species, global warming interacts with other climate and anthropogenic stressors and negatively impacts species living in the estuary. For example, warmer waters combined with nutrient enrichment can result in nuisance macro- and microalgal blooms, as well as bio-fouling of seagrass in the estuary. Climate change also alters rainfall patterns, with the Knysna region predicted to be drier overall, with an increase in rainfall variability by the end of this century.

Less rainfall will amplify the effects of ongoing and escalating freshwater abstraction, which has already resulted in a reduction in the productive

Figure 1.27 In terms of climate change, salt marshes are the most threatened aquatic plant habitat type in the Knysna Estuary (Photograph: © Duran De Villiers).

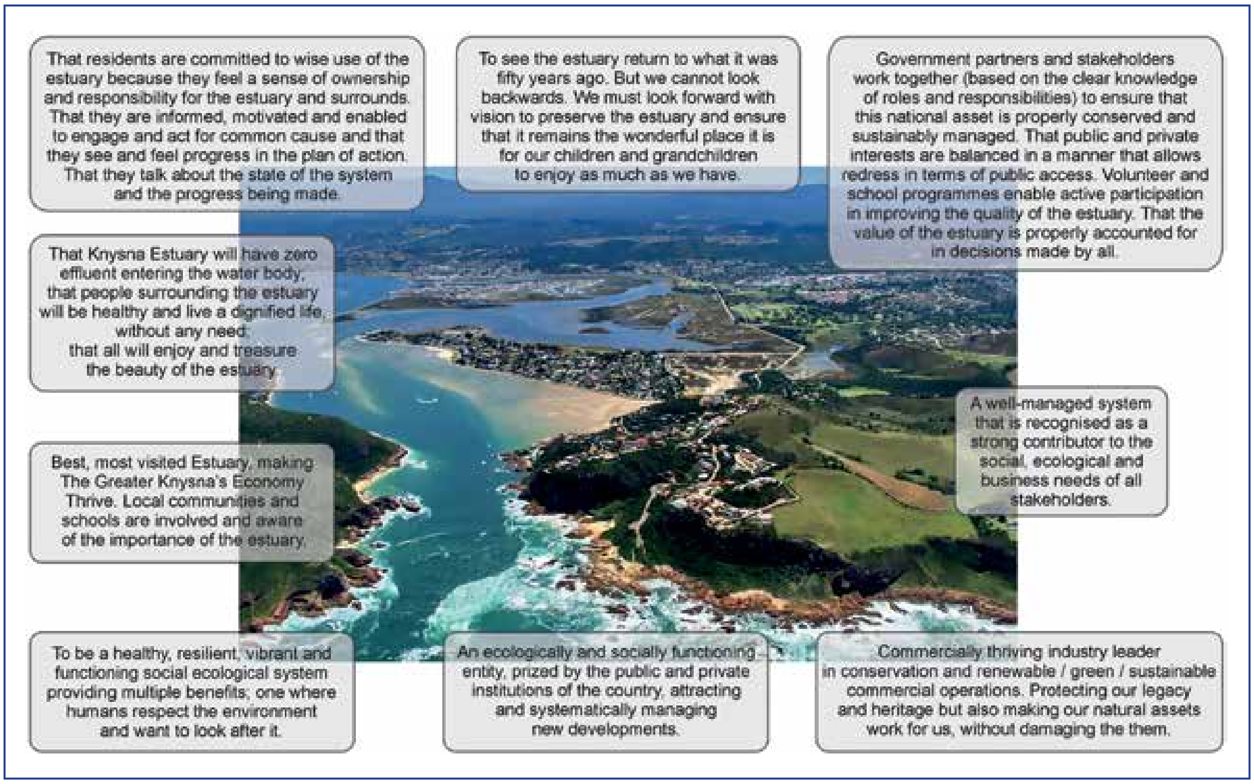

Figure 1.28 Stakeholder dialogue during 2021 co-exploring governance of the Knysna Estuary has revealed a diverse, yet converging and not mutually exclusive, range of dreams for the estuary. It is hoped that ongoing dialogue will engender an ethos of shared responsibility for the management of Knysna Estuary.

upper reaches of the estuary and increasing poor water quality. River flooding can also temporarily result in poor water quality, nutrient enrichment and an increase in sediment loads carried into the estuary.

Of all the climate-induced changes, sea level rise is the greatest threat to salt marsh habitats in estuaries. This threat is particularly dire where sediment accumulation fails to keep pace with sea level rise and development prevents inland migration of salt marsh habitats. Salt marsh habitats in the middle reaches of the Knysna Estuary are the most threatened by sea level rise (Figure 1.27) as they are not keeping pace with present day levels of sea level rise and are surrounded by development. In the future, ocean acidification and an increase in nutrient enrichment in the estuary could also result in an increase in pH variability and acidification in the lower and middle reaches of the estuary, which are strongly marine influenced. Seagrass beds in the lower and middle reaches of the estuary may, however, counteract the effects of ocean acidification (by raising the overall pH of the surrounding water) and serve as ocean acidification refugia for the animals living within them.

Managing Knysna Estuary (Chapter 11)

Knysna Estuary forms part of the Garden Route National Park (GRNP) and hence falls under the jurisdiction of SANParks. However, in contrast to most national parks where access is controlled, the estuary can be viewed as an open access common pool resource that is shared and freely used by many. Common pool resources are vulnerable to overuse and user conflict because it is typically difficult to manage access, users may have diverse interests and values (Figure 1.28), and each user could potentially reduce the ability of others to benefit from the resource. Effective governance and management of common-pool resources is critical to enable sustainable use and promote equitable benefits to users. In Chapter 11 we explore governance principles for common pool resources and propose a framework for applying these to the management of Knysna Estuary.

Three conditions for effective management of common pool resources are: (1) people and the environment are viewed as interdependent components of the resource system; (2) the system is acknowledged as being complex with social and ecological components interacting with each other in evolving ways, leading to unpredictable behaviour and uncertainty; and (3) monitoring of key system components and co-learning among stakeholders are critical for navigating unpredictable change.

Four contexts are relevant to operationalising the above conditions. First, the governance or social context, where diverse stakeholders from multiple levels of government, policy sectors and organisations are connected through relationships and trust to co-learn and collaborate in pursuit of a shared vision. Second, the planning context, referring to the participatory crafting of a vision and objectives to guide the development of management plans. Participatory planning also plays an important role in reconciling diverse stakeholder values and expectations, and shaping relationships and partnerships. Third, the implementation context entails operationalizing the vision and objectives through management actions in conjunction with research and monitoring programs. Fourth, evaluation refers to ongoing assessment of current performance against set objectives as well as co-reflecting with stakeholders on issues such as monitoring results, research findings, management options, and acceptability of outcomes.

The way forward (Chapter 12)

This chapter identifies Knysna Estuary issues and opportunities that will benefit from co-management. To provide the appropriate conditions for co-management, there needs to be a promotion of the value of 'Sense of Place' to both residents and visitors to the estuary. Increased strength of attachment to the estuary, and the services it provides, will lead to environmental stewardship—a key characteristic for the long-term successful management and conservation of the Knysna ecosystem. Stewardship is largely a collaborative endeavour, bringing together multiple stakeholders who may hold quite different attachments and meanings to a system such as the Knysna Estuary. In essence stewardship is driven by a shared desire for sustainability (Figure 1.29).

There are a number of examples in the literature of how collective stewardship capacity can be built and actioned. For example, although much larger and more complex than the Knysna Basin system, the stewardship approach instituted for Puget Sound in the USA is outlined in this chapter in some detail. What the Puget Sound Partnership shows is that such an approach may assist in providing a foundation for developing a Way Ahead or Action Agenda for the Knysna Basin. This way ahead could take the form of a Compact that replaces the 'traditional' approach where only regulatory agencies lead and coordinate efforts to promote estuary management. What is required is a non-regulatory agency, the Knysna Basin Partnership, to be formed through a Compact among interested and affected parties.

To set up a platform for the establishment of a Knysna Basin Partnership it is proposed to initiate a Programme for Climate and Global Change Resilience. In this process it will be necessary to motivate for the Compact that will secure commitment among partners, develop a shared Action Plan, and motivate investment. To this end, interested parties need to promote a Knysna Basin Climate and Global Change Resilience Workshop at which a Compact and Action Plan can be developed.

There are a number of immediate management issues that require attention, e.g. the possible removal of the now defunct railway line that bisects the estuary. Many of these issues have been raised before but still require resolution, and some are new, e.g. removal of vibracrete walls in the vicinity of Brenton-on-Lake that were erected in a failed attempt to stop shoreline erosion. The chapter then concludes with a discussion of the recent Knysna Estuary Management Plan that identifies research priorities to fill important knowledge gaps that will help inform future management of the estuary.

Figure 1.29 SANParks has regular Knysna Estuary Management Plan focus group meetings with stakeholders, including the subsistence fishing representatives shown here (Photograph: © Megan Taplin).

Acknowledgements

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Chapter 2 : Early humans and changing landscapes in the Knysna region of the southern Cape

Naomi Cleghorn & Sarah Wurz

2.1 Introduction

Knysna has attracted people for several hundreds of thousands of, and possibly more than a million years. The biodiverse habitat of the lagoon and associated river system, which sometimes flowed out onto a broad plain beyond the current coastline, had a wide variety of useful resources and must have been a focal point for all of these millennia. Hunter-gatherers would have found a stable and varied source of food staples in this rich environment. Early modern humans and their ancestors left evidence of their lives across this landscape in stone artefacts, the remains of the animals they hunted, the shellfish and fish they consumed, the hearths in which they cooked, and even in the traces of artistic endeavor they left behind. In this chapter, we summarize what is known about these lives and the world in which they lived — a world at times so different from the modern landscape, that a contemporary resident of Knysna might have difficulty recognizing it.

Dramatic sea level changes during the Pleistocene (2.6 million to 11 700 years ago) had a profound impact on the topography, environment, and societies of the southern African coast. A shallow, nearly flat continental shelf stretches out 75 km south of the current coastline at Knysna (Figure 2.1). For much of the last 2.6 million years, this shelf was an exposed grassy plain with broad, meandering rivers that flowed south and, in some places, created wide marshy deltas and estuaries where they met the ocean[1,2]. This is now referred to as the Palaeo-Agulhas Plain[3].

When glaciers expanded to the greatest extent in high latitudes, and sea level was at its lowest, the exposed plain added an area roughly the size of Ireland to the southern African landscape. In other times, the collapse of global ice sheets and warming temperatures raised oceans far above modern sea level. These high sea stands not only inundated Knysna but cut into the sandstone cliffs that now overlook the ocean, creating a series of caves up to about 25 m above modern sea level[4–6]. After the waters receded, these caves sheltered people as they hunted on the expanding plain or collected shellfish along the changing coastline all along the southern coast, including in the area around Knysna.

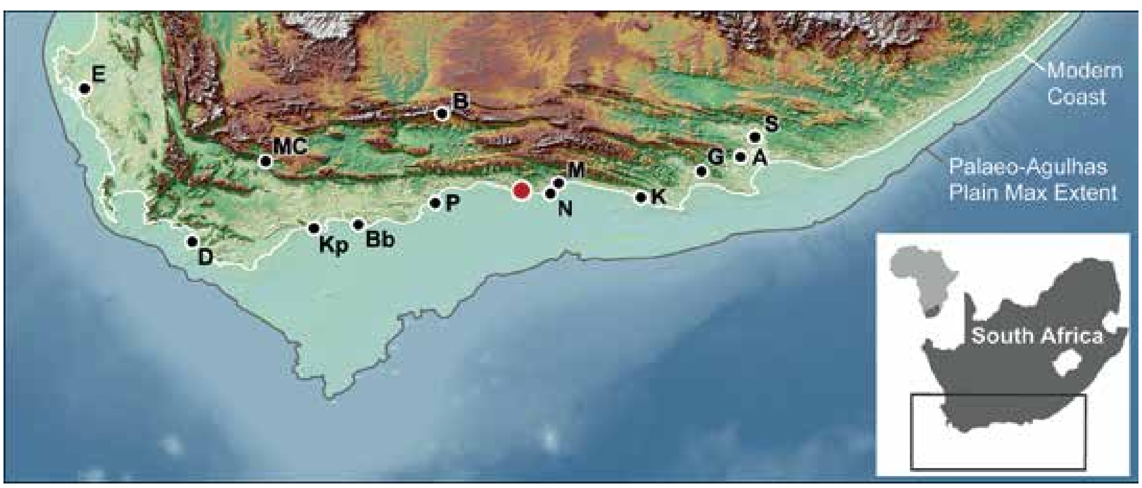

Figure 2.1 Map showing the current southern coastline (white line), the Palaeo-Agulhas Plain at maximum extent (bounded by grey line), and sites discussed in the text. Red dot – Knysna. Site labels: A- Amanzi Springs; Bb – Blombos Cave; B – Boomplaas; D – Die Kelders; E – Elandsfontein; G – Geelhoutboom; K – Klasies River Main Site; Kp – Klipdrift Shelter; M – Matjes River Site; MC – Montagu Cave; N – Nelson Bay Cave; P – Pinnacle Point; S – Sundays River Sites (map created by P. Fahey).

2.2 The Earlier Stone Age: human ancestors at Knysna

The earliest evidence of ancient people in the Knysna area is found across the surrounding coastal plateau — particularly in higher areas surrounding the Knysna Lagoon (as at the top of the Western Heads — see Figure 2.2) and along the top of the coastal escarpment. Large, oval or tear-drop shaped stone tools, colloquially known as "hand-axes" (Figure 2.3), are often found in the sandy sediments of these uplands — particularly appearing during road and construction projects. In some places, there are large concentrations of these tools — many of which appear unbroken. Why people would abandon large numbers of useful tools is one of the intriguing mysteries of the Earlier Stone Age (dating from 3.3 million years ago to about 300 000 years ago). Hand-axes are the signature pieces of the Acheulean technocomplex, part of the Earlier Stone Age, and were shaped through careful planning and the strategic removal of thinning flakes from both faces of a large cutting tool (a.k.a. biface). Analyses show that these were multi-purpose tools, used for butchery, wood working, and other activities[7,8]. They frequently occur with other bifacial tools such as picks and cleavers that have not been as carefully shaped. At Knysna, bifaces were often made on locally-obtained quartzite, using both the cobbles commonly found near beaches as well as outcrops of this stone. This material is often banded with multiple colors of stone, and some are strikingly beautiful. It is possible these objects are some of the longest surviving pieces of portable art, although they undoubtedly were an essential tool as well.

The people who made these tools included those we now classify as *Homo ergaster* or *Homo erectus*, and after about 1 million years ago, an archaic form of our genus continued making bifaces. These ancestors or early people are sometimes classified as *Homo rhodesiensis* or *Homo heidelbergensis* and they preceded *Homo sapiens*. Although we have very few preserved fossil bones from these people, we can make some general statements about their anatomy. They were within the height and body size of modern humans, but with somewhat smaller brain size, low foreheads, heavier brows, and larger facial features. The technological advancements of the Earlier Stone Age, including both the relatively

Figure 2.2 View of the Knysna Heads (Western Head on left), with the straits connecting the Indian Ocean (foreground) to the Knysna Lagoon. The modern coastal platform (approximately level with the top of the headlands), is visible along the base of the Outeniqua Mountains.

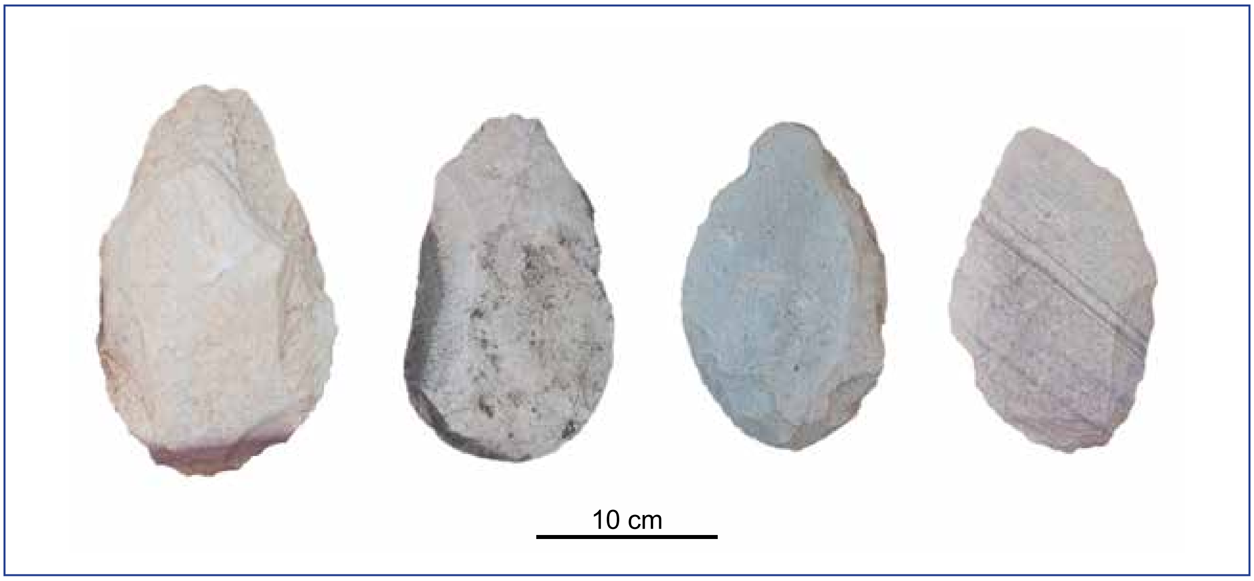

Figure 2.3 Hand-axes recorded during survey of the Western Heads in 2018 (Photograph: © J.K. Murray).

standardized tool forms and the controlled use of fire (after 1 million years ago) suggest that these people had more complex social interactions than earlier groups and may have organized themselves more like humans do today — possibly sharing food and knowledge, and perhaps using a protolanguage around a fire while developing strong social bonds. These people included the ancestors of modern humans.

Open-air Acheulean sites, like the one shown in Figure 2.4, near the ridge top of the Knysna Western Heads, are not unusual along the southern coast. Open-air sites are defined as those that do not occur within the hard shelter of a cave or rock shelter. They are an important but often under-studied part of the Stone Age archaeological record. While caves tend to "trap" and preserve sites, open-air localities are more often ephemeral (briefly used) in nature, poorly preserved (due to exposure), challenging to locate (when obscured by vegetation), and difficult to date (if they are found only at the surface). The identification of a dense concentration of hand-axes in a small area, as at the top of the Western Head, is therefore a potentially useful addition to the Earlier Stone Age record. In 2018, much of the vegetation covering the Western Head was still recovering from the devastating 2017 fires. This exposed an Earlier Stone Age site with a density of more than 100 artifacts per 200 square metres. Comparisons with similar stone tool industries throughout southern Africa and beyond suggest these are at least older than 250 000 years and could be as old as 1.3 million years ago. Future study of the site may tell us more about the landscape and lives of these very early Knysna residents.

A sea level rise of nearly 25 m at 1.1 million and about 11 m at 420 000 years ago[4,6,] would have dramatically changed the Knysna Amphitheatre[9] (the area surrounding the lagoon — see Figure 2.5), and the distribution of archaeological sites. This would have also altered the character of the lagoon with changing salinity, tides, and animal life in ways that are of interest in the context of modern climate change[10]. Without better dates on the Earlier Stone Age sites, we cannot know how these ultra-high sea stands affected local people. However, we can be fairly certain that evidence of the Acheulean (Earlier Stone Age) predating 420 000 years ago in the lower areas of the Amphitheatre and at the coast was either altered or removed through this process of inundation.

Documented Earlier Stone Age sites along the southern coast (all of which are within the Eastern Cape) include Amanzi Springs, Geelhoutboom situated within a paleodune close to the Klasies River Main Site, and sites within the alluvial gravels of the Sundays River, including Penhill Farm, Atmar Farm, and Bernol Farm (see Figure 2.1)[11]. To the west of Knysna, the Earlier Stone Age has been studied at the inland site, Montagu Cave, and at Elandsfontein, on the west coast. The sites at Knysna, if preserved in context, could add much to our understanding of the climate, ecology, environment, and behavior of these early residents of the south coast.

Figure 2.4 A 2018 Archaeological survey of an Earlier Stone Age site at the Featherbed Reserve, Western Heads, near Knysna (elevation ~189 m asl).

Figure 2.5 View to the southeast of the Knysna Lagoon and Amphitheatre, with the Indian Ocean in the background (Photograph: © Domossa).

2.3 The Middle Stone Age and the Emergence of Modern Humans

From about 300 000 to 250 000 years ago people across Africa, and along the southern coast, began to develop new ways of producing stone tools in a shift to what researchers recognize as the Middle Stone Age. For the first time people began to make tools that connected stone to wood handles to produce more effective knives and spears. In the Middle Stone Age, knappers often made stone tools such as flakes, blades, and points through the process of "core preparation". This was a highly strategic approach of knocking flakes from a larger block of stone (the core) with a hammerstone (a harder rounded rock) in a sequence that allowed the knapper to eventually strike off a tool with a specific shape (like the example from Knysna in Figure 2.6). Through this technique, a stone tool knapper could control not only the resulting outline (note the symmetry and length of the tool in Figure 2.6), but also the thickness of the tool across its base (an important factor preventing breakage when used). Edge damage and notches on the sides and tips of these flakes, blades, and points provide clues to hafting arrangements, and the use of these objects as cutting implements and projectile weapons (note the damage to the tip of the stone tool in Figure 2.6). Scrapers used to scrape hides and other materials formed part of the toolkit as well, alluding to the varieties of roles that lithics (stone tools) played in the survival of ancient coast dwellers from this area.

Gradual changes in human anatomy throughout the period leading up to the Middle Stone Age included shifts to less robust skeletons, a more modern looking face and head, and the expansion of average brain size and shape. At some point in this period, all modern humans shared a common ancestor, and paleoanthropologists recognize these people as *Homo sapiens*. Thus, we refer to the people of this time as Early Modern Humans (or EMH). Few fossil EMH representatives of this time exist in Africa and the largest concentrations of these (dating to about 315 000 years ago) are found along the coast of North Africa[12]. There are very few modern human fossils from South Africa (and from sub-Saharan Africa in general) that pre-date the Holocene[13].

The southern coast of South Africa contains some of the most important sites documenting the emergence of EMH technologies and capabilities that we particularly associate with the unique human adaptation. This includes the adoption of

Figure 2.6 A typical Middle Stone Age point from Knysna.

coastal shellfish resources as a regular part of the diet, with the earliest evidence from Pinnacle Point, near Mossel Bay[14], and other notable sites such as Klasies River Main Site, Die Kelders, Klipdrift Shelter, and Blombos Cave (Figure 2.1). On the southern coast, brown mussel (*Perna perna*) and alikreukel (*Turbo sarmaticus*) were among the most popular species eaten, but other types of shellfish such as multiple species of limpets, sand clams (*Donax serra*), and giant chiton (*Dinoplax gigas*) also formed an important part of the coastal diet[15].

Over time, people became increasingly adept at getting to deeper parts of the tide zone. In fact, the earliest adoption of a coastal foraging strategy along the southern coast of South Africa shows that people were able to keep track of complex calendar information[14]. Staying close to the coast for enough time to understand these tidal rhythms suggests these foragers had more limited terrestrial hunting ranges. However, shellfish, in conjunction with the diverse edible plant and animal resources of the estuary (see Appendices 1 and 2), would have provided a stable food base as well as nutrients particularly important to growth and brain development in human infants and children. This would have likely contributed to reproductive success and some population growth. Living the coastal life may have also been key to the early development of complex social strategies in humans — such as the cooperative defense of territorial resources[16]. At Knysna, we find the remains of shellfish feasts left by Middle Stone Age humans.

These early humans also began to explore ways to improve stone tool quality through heat treatment[17], which may have played a role in the earliest production of much smaller stone tools by 71 000 years ago (at Pinnacle Point), for the first time within the range of potential projectile weaponry[18]. The geometric backed tools from the Howiesons Poort technocomplex, about 65 000 years ago, were sometimes used in what is considered the earliest bow and arrow technology[19]. Evidence for some of the earliest personal decoration and production of symbolic and artistic work also appears along this coast — notably early at Blombos Cave near Stillbay[20,21].

2.4 Knysna and environs during the Late Pleistocene

Since the emergence of this new, more modern anatomy and innovative Middle Stone Age technologies, dramatic shifts in global climate changed the Knysna landscape from a coastal lagoon to an inland river valley several times. These drastic changes in the size of hunting territories, the proximity of shellfish resources, and the periodic disappearance of whole ecosystems, may have happened relatively quickly. Fisher and colleagues[22] used global sea level estimates together with local geomorphology and isotopic data to estimate the position of the southern coast and the speed of change through this period. They estimate that when sea level rose, the coastline moved north at an average speed of 2 to 4 km per century. Given the importance of cultural knowledge to success in human subsistence strategies, this change may have caused disruption and stress among near-coastal peoples for millennia.

For long periods, peaking at about 160 000, 71 000, and 21 000 years ago, the coast was far to the south (between 40 and 75 km away south of Knysna)[22]. When the coast was far away, Knysna's residents lived near a river that ran through the rocky headlands and meandered south as a single sinuous channel across a grassland rich in herd animals[2,23]. In character, this waterway would have more closely resembled the wide, slow rivers of West Africa, without the gorges and deep valleys of the modern southern coastal plain[1]. The Knysna Heads and the river channel or straits between them were a constant feature of this landscape throughout this time[24].

At Knysna, evidence for the Middle Stone Age is preserved at multiple cave sites near The Heads. From the high south-facing caves, people would have looked out onto a savannah with diverse large animals, including giant long-horned buffalo (*Syncerus antiquus*), giant Cape zebra (*Equus capensis*), giant hartebeest (*Megalotragus priscus*), elephant, hippopotamus, and even giraffe[23,25]. By living close to The Heads, these people would also have access to an important freshwater source — the river. Some sites face into the Knysna Straits and would have had a more limited view of the Palaeo-Agulhas Plain and the lagoon area. These sites suggest that this short corridor linking these two ecosystems (the modern Knysna Basin and the Palaeo-Agulhas Plain) was possibly itself an important point of interest.

Periodically, sea levels rose, inundating the Palaeo-Agulhas Plain completely and bringing coastal resources back to within the daily foraging range of Knysna's residents. About 125 000 years ago, sea levels rose to about 6 to 8.5 metres above today's level[26], flooding the lagoon and likely washing away many earlier archaeological sites along the southern coast, before retreating slightly. For nearly 50 000 years during this high stand, the shore was not too far from its current position.

Beginning about 74 000 years ago, the coast began a long slow retreat south as the world entered a glacial period. The clear evidence for where people were spending time along the southern coast between 74 000 and 50 000 years ago varies widely. Despite rich records of occupation elsewhere (notably at Pinnacle Point and Klasies River Main Site), it seems that small, highly mobile groups stopped by the Knysna Heads only occasionally and spent little time at high sites overlooking the plain. It is possible we have not yet identified the key Knysna occupation sites for this time period.

At about 34 000 years ago, the Knysna environment and archaeological record changed dramatically. In our excavations at a south-facing site now overlooking the ocean — Knysna Eastern Heads Cave 1 (KEH 1) — we find a change from very little evidence of human presence to intensive occupation dating to about this time (Figure 2.7). Unlike previous people, these new inhabitants had close access to rocky intertidal shellfish, which they frequently brought home for meals (Figure 2.8). Their stone tools, similar to other Middle Stone Age industries, included long triangular points, possibly used as knives and spear points. We find these together with dense accumulations of mussel, turbo (alikreukel), limpet, and giant chiton, among other shellfish. Our findings suggest a rise in sea level that brought the coast within 10 km, perhaps even closer, to the Knysna Heads. This would have meant a loss of large mammal habitat (an important resource for EMH), but these early humans were flexible, and at Knysna we see the continuation of the coastal foraging strategies evident at earlier sites.

This brief rise in sea level at approximately 34 000 years ago, probably lasting less than 5 000 years, is as yet only documented in the KEH 1 archaeological record and may have been so short in duration that it left no other geomorphological evidence along the coast[27]. In fact, there are few other

Figure 2.7 KEH Cave 1 (near Knysna) during excavation.

archaeological sites dating to the period between 40 000 and 21 000 years ago in the Western Cape, and none along the coast, making KEH 1 a unique and significant record. The closest contemporaneous site — at Boomplaas near Oudtshoorn — is about 125 km inland, in a more arid environment, and seems to have had a more intermittent occupation at this time[28]. By contrast, our research at Knysna shows a dense record of human occupation between 34 000 and 20 000 years ago. This supports the hypothesis, suggested by earlier researchers[29], that larger numbers of people lived out on the Palaeo-Agulhas Plain prior to and during the Earth's most recent ice age.

2.5 The Sea Retreats

From 29 000 years ago, global ice sheets began to grow, sea levels slowly dropped, and the grassy Palaeo-Agulhas Plain began to open up to its grazers.

Figure 2.8 A Middle Stone Age tool found in place at KEH Cave 1 (Knysna) next to a cluster of shellfish. The sediment is dark as a result of dense charcoal and decayed organic matter. This feature is found in a layer dating between 34 000 and 29 000 years ago.

During the early part of the glacial (i.e., through about 23 000 years ago), with coastal resources still possibly still less than 40 km away, abundant ungulate herds nearby, and a stable freshwater source (the Knysna River), Knysna may have been the ideal place for human foragers. Although shellfish gathering at KEH 1 diminished, the human presence grew.

At KEH 1 during this time, we find evidence that humans repeatedly visited the site, leaving dense accumulations of stone tools, remains of meals, decorative materials, and constructed hearths. About fifty combustion features (Figure 2.9) were recorded in a relatively small area — 3.5×1.5 m by about 0.5 m deep. Analysis shows many of these features are well-preserved, and several were constructed directly on top of older hearths[30]. These ancient campfires were found in association with the densest accumulation of archaeological materials from the Pleistocene levels of the site. Here, we find abundant evidence of stone tool production, the consumption of a wide variety of game — including large ungulates — and other activities. Ostrich eggs were brought to the site, possibly for cooking or as water flasks (Figure 2.10). Although now associated with the more arid regions north of the

Figure 2.9 Stratigraphic section through combustion features (hearths) at KEH Cave 1. White squares are 2 cm wide. White ash layers overlie dark charcoal layers. These features are found in a layer dating between 26 000 and 22 000 years ago.

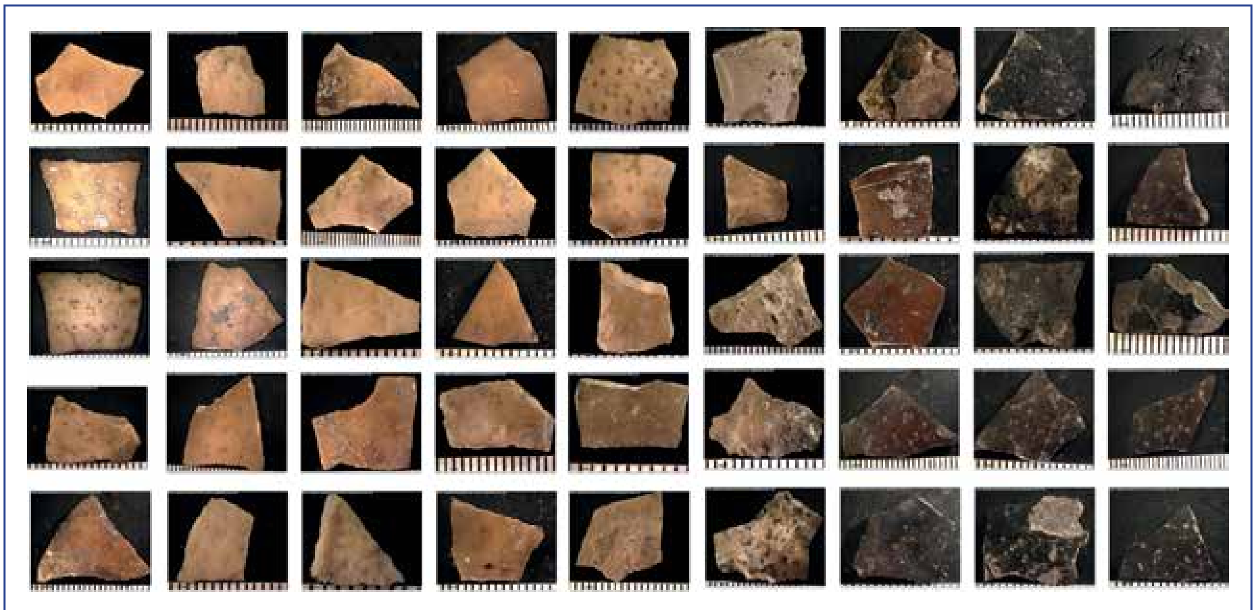

Figure 2.10 Ostrich eggshell fragments from KEH 1 showing color variation related to heating (from Sender et al.[31]).

Outeniqua Mountains, the Palaeo-Agulhas Plain likely supported ostrich to the south of Knysna. We find numerous fragments of these eggshells in campfires[31] and in one case, the deep impression of an egg preserved as a mould in the ashes of a hearth — perhaps set there as it was cooked.

We also find evidence of artistic pursuits. Throughout this period, minerals typically used as pigments — including ochre in a variety of forms — were common. These pigments include iron-rich shale, ferricrete, and hematite, all of which are available in the Knysna area[32], and range from dark red fragments of "crayons" to orange-red and bright yellow powders (Figure 2.11). A slab of stone (~15 cm across) was used to grind red powder. Whether these pigments were used to color objects or people is unclear, although we have yet to identify much of the former at KEH 1. The variety of colors and abundance of materials nevertheless suggest a well-developed interest in the use of color in everyday life.

A preliminary analysis[30] of the stone tools made and used at Knysna from this time shows they are smaller than the earlier forms and increasingly made on different types of raw materials, particularly quartz — a very difficult stone to flake well, but one which is quite durable. These shifts in stone tool technology may be linked to a more widespread move away from the core preparation strategies of the Middle Stone Age, toward the smaller tools of the Later Stone Age. This transition is historically poorly documented across Africa[29,33], but at KEH 1 we find it associated with dense archaeological accumulations before and after the change. This density of material at the Middle to Later Stone Age transition is unique within the Western Cape and KEH 1 is the only site to capture the transition at the coast. The relatively rapid transition from coastal foragers using Middle Stone Age tools to this new technology raises intriguing questions. Was this cultural change within a population adapting to a changing landscape, or did a new group of people move in to claim this optimal location overlooking the plain?

By 18 000 years ago, the world had reached the peak of the last glacial (the Last Glacial Maximum or LGM). Knysna was drier than today and located far inland. At KEH 1, the people who visited the site seem to have come by slightly less often, and for shorter stays than in earlier periods. Their tools were different from those who left the dense accumulations of hearths. Their small, highly standardized bladelets were similar to tools found only 30 km east at Nelson Bay Cave, near Plettenberg Bay. In fact, that tool industry, which archaeologists have named the Robberg, is recognized across southern Africa, suggesting widespread cultural connections.

The people living next to the Knysna River, flowing out between the rocky cliffs we call The Heads, were likely connected to this larger cultural group. Maybe sunnier locations with a view of

Figure 2.11 Red ochre powder on a slab of stone and a mass of yellow mineral powder. Both were found in hearth features dating between 26 000 and 22 000 years ago at KEH 1.

the river within the Knysna Amphitheatre were more attractive than KEH 1 at this time, although large game hunters still came by the site from time to time, and left evidence of their kills—including zebra and giant buffalo. Occasionally, small carnivores, including genets, took up residence at the site[34], further supporting the transient nature of the human presence during the LGM. Humans came to the site less and less frequently and finally not at all.

2.6 The last 10 000 years

Humans were likely in the Knysna area but did not return to the ocean-facing cave KEH 1 until the Holocene (after 11 700 years ago). Once the coast was again near its modern position, residents could harvest shellfish and other marine resources. Several sites around The Heads have thick shell midden accumulations dating to the Holocene. At KEH 1, the shell midden (a deposit made up almost entirely of the harvested shellfish remains) is almost 2 metres thick. This is not unusual - thick shell middens are common along the coast, and sometimes quite horizontally extensive as well. In addition to shellfish, the midden at KEH 1 includes the remains of some fish and mammals, as well as campfires and stone tools.

The loss of the Palaeo-Agulhas Plain not only decreased the amount of territory available to hunters and gatherers, but also meant the loss of the large gregarious herds supported by the nutrient-rich grasses that grew on the plain[2]. This unique ecosystem of the Late Pleistocene became extinct. The land to the north of The Heads—the modern coastal plateau—could not then and does not now support the same density of grazers that were available on the Palaeo-Agulhas Plain. A recent simulation of the impact of the loss of this plain on coastal foragers shows that the people who left the giant shell middens at KEH 1 and many other sites were probably under some amount of resource stress[35]. It is also possible that local Holocene populations were larger than in the Pleistocene and growing. They were almost certainly less mobile as they focused intensively on shellfish and coastal resource extraction, and this may have further facilitated population growth. Based on isotopic evidence from human burials at one of the largest such middens at Matjes River near Plettenberg Bay, Sealy[36] has argued that the later Holocene (the last 3 000 years) may have been a time when groups were increasingly territorial with respect to food resources. We cannot yet determine how the Knysna landscape might have been divided among such groups (if it was), but the straits may have been a logical boundary dividing the eastern from the western headlands (Figure 2.2). There are large shell midden deposits on both sides. In the future, we may be able to directly compare these sites to build a more comprehensive picture of landscape use and the interaction of groups across the Knysna Basin.

The Holocene hunter-gatherers of Knysna undoubtedly combined coastal resources with a rich variety of estuarine animals (including fish, birds, and invertebrates) and edible plants such as sedges (see Appendix 1 for potential species). A recent experimental plant foraging study showed that sand fynbos vegetation, like that still preserved on the Western Head, provides exceptionally good caloric returns[37]. Like the shellfish beds of the coast, the estuary presented foragers with stable, geographically concentrated resources. As others have noted, the presence of rich and defensible resources tends to lower residential mobility (the frequency with which people relocate their home), support population growth (in part because mobility is lower), and foster territoriality among groups[16]. Thus, we can imagine Holocene Knysna as a moderately crowded place (relative to much of the coastal plain), in which people kept a wary eye on the campfires across the lagoon.

2.7 Conclusion

The Knysna Basin and coast have been a magnet for humans throughout the Pleistocene and Holocene. Although there are numerous cave sites along the coast, some having archaeological sites within, our previous survey of the coast near Knysna found these sites were densest close to The Heads. This suggests The Heads are a special and highly attractive feature of the southern coast. As the gateway between the lagoon (sometimes a river valley) and the sea (sometimes a coastal plain), The Heads likely provided a corridor for both humans and animals to move between these complementary ecosystems. Sites facing into the straits may have been used to control or exploit this corridor. Sites like KEH 1, with an elevated perspective over the Palaeo-Agulhas Plain, would have given ancient Knysnans an excellent view of distant foraging resources throughout much of the Pleistocene, and close access to shellfish beds during the Holocene. The Knysna Lagoon is an acknowledged biodiversity hotspot. It is also an archaeological hotspot, with an invaluable and rich long-term record of human adaptation and environmental change.

Figure 2.12 Sea view to the west of The Heads, across the Knysna Straits (Photograph: © Naomi Cleghorn).

Acknowledgements

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Chapter 3 : Tracks Cast in Stone

Charles Helm, Hayley Cawthra, Jan De Vynck, Mark Dixon,
Willo Stear, Guy Thesen & Fred van Berkel

3.1 Introduction

West of the Knysna Estuary, between Wilderness and Brenton-on-Sea, there are numerous outcrops of rocks that provide a proverbial 'window' into a period of geological time known as the Pleistocene Epoch, and the creatures that lived there then and left their tracks and traces for us to recognize and interpret today. A similar phenomenon occurs to the east of Knysna at Robberg.

These distinctive rock deposits are the remnants of ancient dunes, beaches and lagoons. They can be dated, using a technique called Optically Stimulated Luminescence (OSL). In this region their age is mostly between 140 000 years and 70 000 years[1], while some at Robberg are as young as 35 000 years[2]. The 'Late Pleistocene' extends from ~126 000 years ago to 11 700 years ago, hence most of the deposits fall within this category, while the older ones occur in the terminal stage of the 'Middle Pleistocene'.

Exposed surfaces (palaeosurfaces) within these rocks have the capacity to record, sometimes in exquisite detail, events that transpired on them when they were still composed of unconsolidated sand. Analysis of the resulting fossil tracks and traces forms part of the discipline of ichnology, and this stretch of coastline provides one of the most productive areas in the world to pursue such studies. Fortuitously, Pleistocene palaeo-climatic conditions allowed for the rapid cementation, and therefore

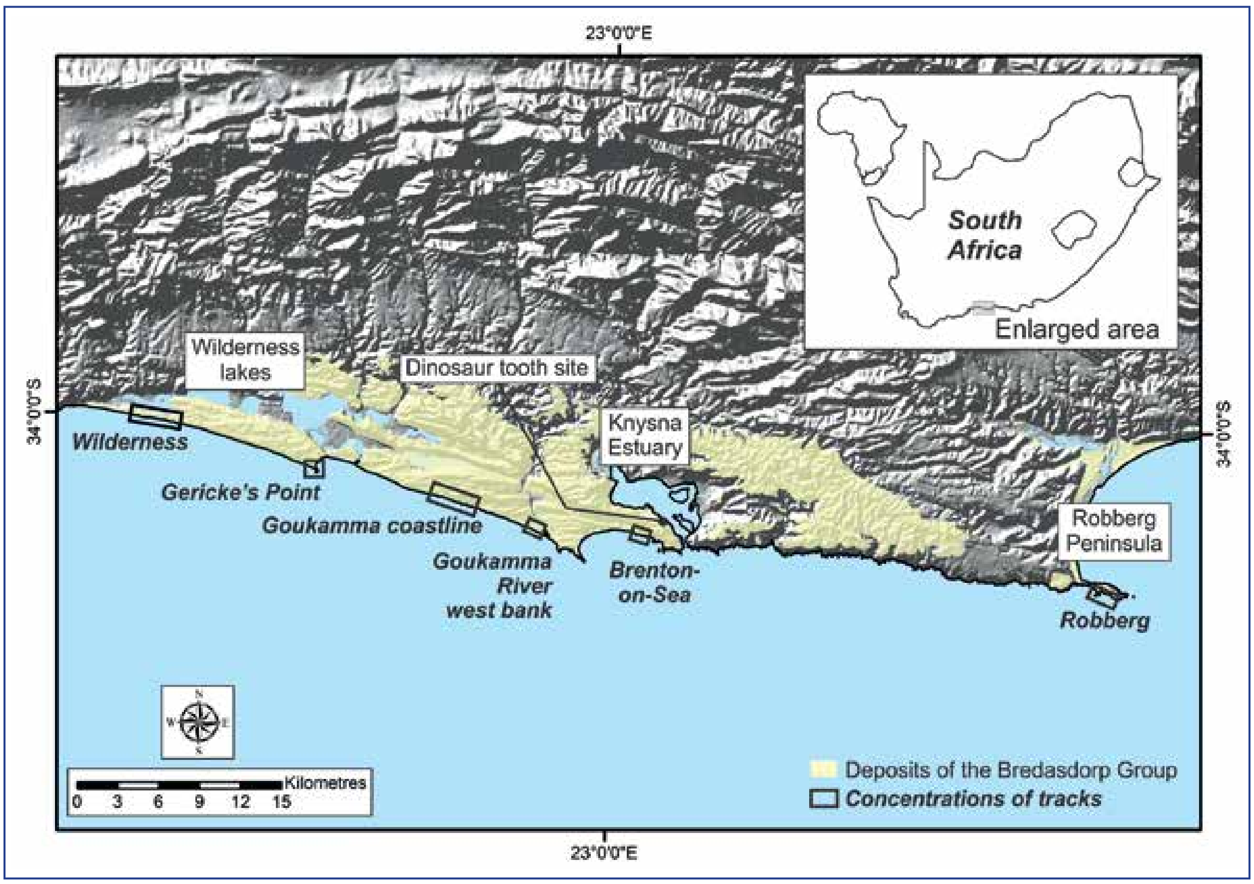

Figure 3.1 Map of the coastline between Wilderness in the west and the Robberg Peninsula in the east, showing Bredasdorp Group deposits and areas with concentrations of fossil tracks.

preservation, of these features and surfaces.

Over the past 15 years, we have studied aeolianite outcrops (cemented dunes) and the trace fossils they contain as part of the Cape South Coast Ichnology Project, based out of the African Centre for Coastal Palaeoscience at Nelson Mandela University. Thus far, 132 vertebrate (reptile, bird and mammal) tracksites have been identified along the 45 kilometres of coastline between Wilderness and Brenton-on-Sea, and a further twelve sites have been identified at Robberg (Figure 3.1).

Much of this section of coastline is protected in the coastal portion of the Garden Route National Park, the Goukamma Nature Reserve and Robberg Nature Reserve. Outside of a few popular access points to the beach, most of it is pristine. Frequently, when exploring for fossil tracksites in these remarkably spectacular coastal settings, other people are seldom encountered. This might be taken for granted by local residents, but is immediately apparent to visitors from afar.

The Pleistocene was a time of profound climatic instability. It was characterised by long, cold glacial phases punctuated by short, warm interglacials (Figure 3.2). The resulting sea level oscillations, often cyclical, had profound effects on what is now the southern Cape coast and continental shelf, and resulted in the repeated exposure and inundation of the huge Palaeo-Agulhas Plain[3–6]. This currently submerged landmass, reaching its greatest extent southwest of Knysna, was mostly flat and contained extensive dunefields, floodplains, wetlands, and meandering rivers. During maximum lowering of sea levels (marine regressions) as much as 85 000 km^2 of land was exposed offshore of the Cape Floristic Region.

The tracksites do more than just provide a census of which animals were moving across dunes and beaches in those times. Indeed, the inferences that can be drawn contribute to the understanding of the broader Pleistocene palaeo-environment, palaeo-ecology and ecosystem as a whole. Moreover, the trace fossil record does not just independently confirm the information that can be gleaned from the body fossil record, but it complements this record through unanticipated evidence. This occurs not only through the reptile, avian and mammal trace fossil sites that have been identified, but through the ichnological evidence left behind by our distant *Homo sapiens* ancestors during a time of pivotal importance in human evolution. In this chapter we report on some of these discoveries and consider their implications.

3.2 Regional geology

The Pleistocene rocks on the Cape south coast were formally studied and described by Jean Malan in the late 1980s and early 1990s. Aeolianites (named after Aeolus, the Greek god of the winds) are geologically assigned to the Waenhuiskrans Formation[7]. In contrast, cemented foreshore (beach) deposits, along with shallow marine, lagoonal and estuarine deposits, comprise the Klein Brak Formation[8]. These two formations form part of the Bredasdorp

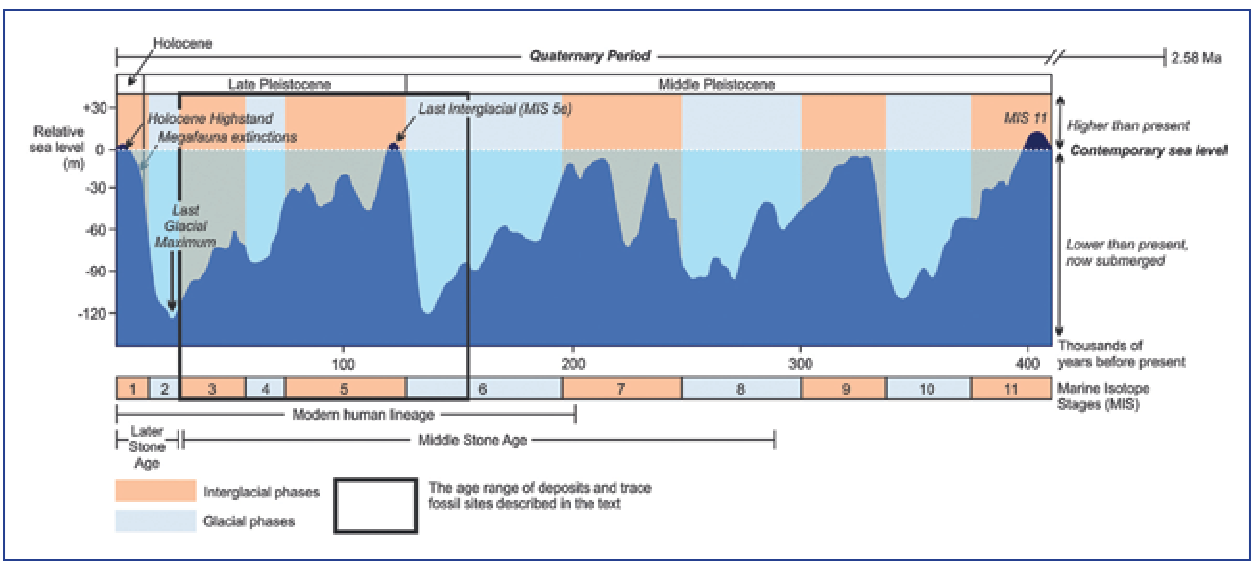

Figure 3.2 Quaternary sea-level fluctuations in response to climate changes over the past 400 000 years as reflected in Marine Isotope Stages (MIS) 1-11, modified from Spratt & Lisiecki (2016). The black box indicates the age range of deposits described in the text (160 000 years – 35 000 years).

Group of sedimentary rocks, and Pleistocene outcrops at Robberg form the eastern extremity of this Group.

While many of these coastal outcropping rocks have been broken by erosion into loose blocks and slabs that have tumbled down to lie on the beach near the high-water mark and are therefore ex situ, the cliffs above, from which they originated, comprise the in situ deposits. Because tectonic activity was minimal along this coastline during the Pleistocene[9], the in situ sedimentary layers lie at or close to the original angles of deposition. In the case of aeolianites this is often the angle of repose of wind-blown sands, being the steepest inclination at which the deposited material was piled up by wind without slumping. Aeolianites exhibit characteristic high-angle cross bedding of sedimentary layers when viewed in vertical profile.

In the case of cemented foreshore deposits, the orientations of bedding plane layers are typically horizontal or at low angles, and beds are commonly thicker than in the cemented dunes. Beaches usually contain coarser-grained, higher-energy material than dunes, and lagoon environments may contain much finer-grained deposits that reflect depositional quiescence. It is clear from a walk along the coast today that there are transition zones between beaches and dunes. In cases where it is not immediately macroscopically evident whether an exposed Pleistocene palaeosurface represents an ancient dune, beach or lagoon deposit, examination of thin sections of the rock by microscope (petrography) can be extremely helpful.

The Gericke's Point area contains the tallest aeolianite cliffs in the Knysna-Sedgefield area, displaying spectacular examples of aeolian (wind-formed) cross-bedding, and extensive undercutting by high sea levels that expose fresh surfaces. The low-relief cliffs just east of the Swartvlei Estuary mouth at Sedgefield contain classic examples of the Klein Brak Formation, where the basal layers of the stratigraphic sequence of rocks comprise relatively flat-lying foreshore deposits, overlain by cross-bedded aeolianites of the Waenhuiskrans Formation. The contact zone between them forms a sea level index point for the Last Inter-glacial sea-level high stand, ~126 000 years ago[10]. Together, these two easily accessible sites provide a representative portrayal of the Late Pleistocene geology of the region (Figure 3.3).

In addition to these Pleistocene outcrops, the coast contains Palaeozoic quartzite exposures of the Cape Supergroup (e.g. at the Knysna Heads) and exposures of the Cape Granite Suite, and Precambrian Kaaimans Group metasediments. The geology at Robberg includes sandstones and conglomerates of the Jurassic Robberg Formation, and Jurassic Cretaceous rocks of the Enon and Buffelskloof formations. Cretaceous deposits of the Brenton Formation also occur at Knysna, as described further below. In many cases the coastal rocks are draped by extensive unconsolidated dunes that were established during the Holocene and still remain active.

Between Wilderness and Brenton-on-Sea the Cenozoic stratigraphy falls within the Wilderness Embayment[1]. The large, approximately shore-parallel ridges of this embayment are referred to as cordon dunes, and are separated by back-barrier lakes. The oldest lithified dune cordon, furthest inland, may be ~400 000 years old, but is yet to be dated. The large middle cordon has been dated to between 241 000 years and 221 000 years at its base, and is capped by Marine Isotope Stage 5e (Last Interglacial, ~126 000 years old) aeolianites. The rocks of the seaward cordon, such as the coastal aeolianites exposed at Gericke's Point, are typically in the 140 000 – 70 000 year age range.

The dramatic sea-level oscillations of the Pleistocene had profound effects on the location, and the rates of change of migration, of the shoreline and the extent to which the Palaeo-Agulhas Plain was exposed at different times[3–6]. The variability of the width of the shelf affects the coastline distances at specific locations. For example, around 137 000 years ago, at the peak of a major glacial phase (Marine Isotope Stage 6), sea levels were 129 metres lower than they are at present, and at Mossel Bay the shoreline would have been just under 100 km seaward of its location today[11].

At the other extreme, during a sea high-stand around 400 000 years ago, levels were 8.5 – 11 metres higher than current levels[12,13]. During another high-stand 126 000 years ago, around the time when many of the tracks were registered (Marine Isotope Stage 5e), the sea level was between six and eight metres higher than at present[10]. Sea levels are slow to fall as ice sheets accumulate, and quick to rise following glacial terminations (i.e, melting of ice sheets).

3.3 Ichnological principles

Whether a track or trace is well preserved or poorly preserved depends on a number of factors. These include the consistency of the substrate and the moisture content. For example, if sand is either too firm or too soft, or too wet or too dry, a high preservation quality is most unlikely. In between these extremes there lies a 'sweet spot', or an ideal zone, in which optimal preservation is possible.

Grain size of the substrate is another important variable. As a general rule, the finer-grained the

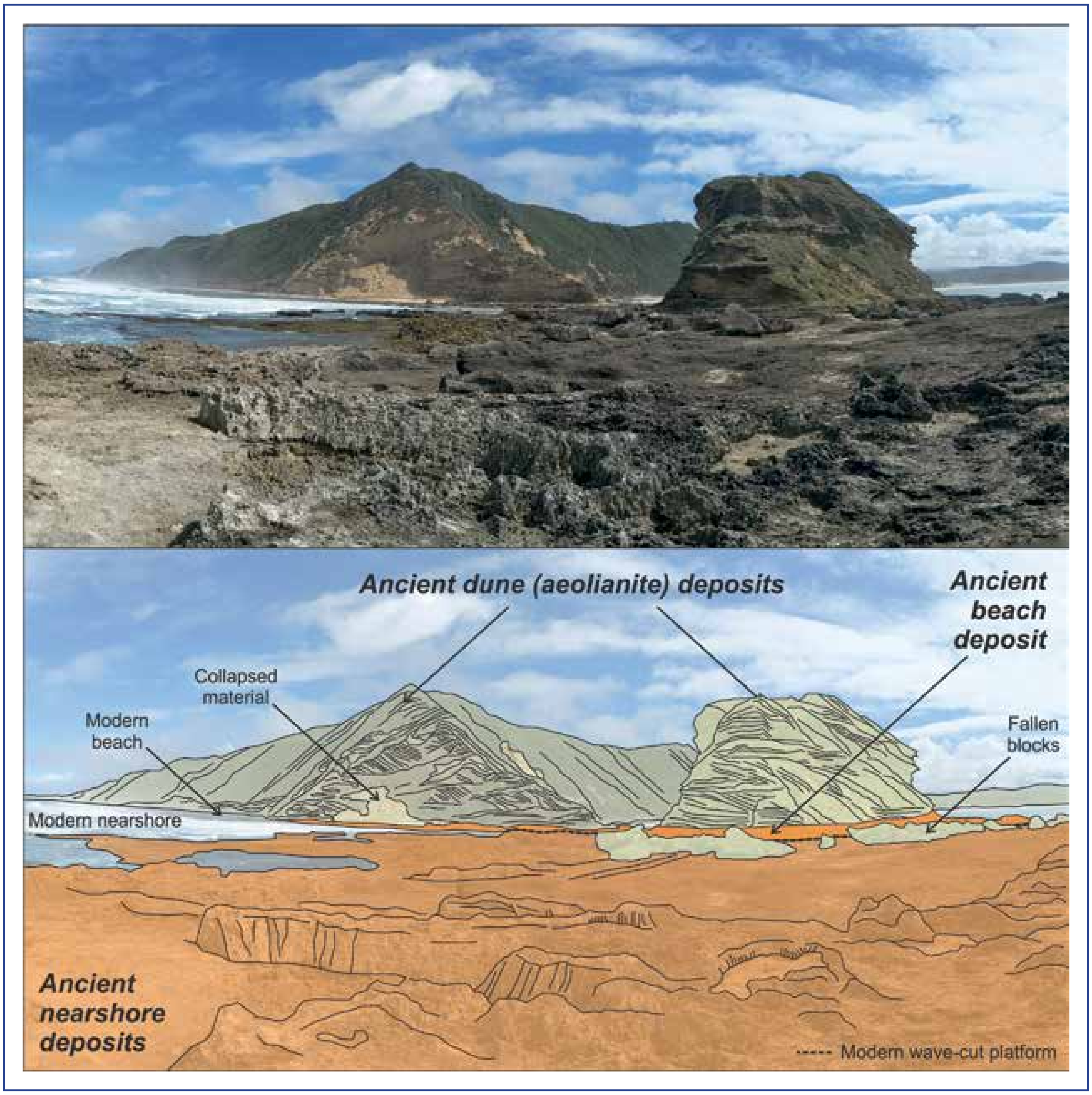

Figure 3.3 A panoramic view of the Gericke's Point area, showing the main geological features.

sediment, the greater the likelihood of fine detail being preserved on its surface. On the Cape south coast, silty environments therefore offer the best conditions for outstanding trace fossil preservation, something that cannot be said for the coarser-grained beach sediments. Regrettably, the Cape south coast track-bearing palaeo-surfaces do not exhibit the quality of preservation that can occur in substrates with the finest grain size, such as snow, muddy cave floor deposits or volcanic ash deposits[14], as this is a high-energy open coast shoreline, and has been throughout the Pleistocene[15]. While the lack of ideal preservation conditions is acknowledged, this is balanced with the knowledge that invertebrate traces (e.g. made by molluscs, crustaceans and insects) are commonly encountered in these rocks, and that trackways of smaller creatures such as spiders and gerbils have been recorded and interpreted without difficulty.

Another variable involves sand distribution, which often occurs in a seasonal pattern. Some sites may be buried under metres of sand, and may only transiently be exposed and available for interpretation for a few days after an interval of years. If such sites are situated close to the low tide mark, then if they are exposed for a length of time they tend to become encrusted with barnacles and covered with algae, which makes the tracks unrecognizable or uninterpretable. Awareness of substantial changes in sand distribution therefore can lead to a timely search for newly exposed sites when they can be appreciated fully.

The profusion of tracksites on the Cape south coast can be attributed to a combination of the cohesiveness of moist sand (which provides an effective moulding agent), high sedimentation rates (which promote swift track burial), rapid lithification via partial solution and re-precipitation of bioclasts (shell fragments), followed by shoreline erosion, which exposes the fossil-bearing surfaces again[16]. The same forces of wind and water which contribute to shoreline erosion act on the newly exposed track-bearing surfaces. Therefore, the sooner newly-exposed tracks can be identified, the better. The time window during which the surfaces are amenable to interpretation before losing their quality and detail due to weathering by natural elements can sometimes be as short as months or weeks. The ephemeral nature of the tracksites adds to their mystique and requires constant vigilance and re-examination of known terrain, especially after events which are likely to expose new surfaces, such as storm surges.

This raises the issue of the optimal way to try to preserve or replicate the trace fossils and reduce the risk of vandalism. If nothing is done, the surfaces will certainly deteriorate, and their value will be lost. Recovery of specimens and having them reposited in regional museums presents one option. For larger surfaces for which this is not feasible, replication options can be considered. Traditional means of replication such as manual casting with latex or silicone run the risk of inadvertently damaging the tracks, and are unfeasible for sites that lie below the high tide mark or are extremely moist. 3D imaging through photogrammetry provides a non-invasive option, from which highly accurate replicas can be created[17]. In most cases this forms the most logical approach. We do not apply substances like Paraloid® to a track-bearing surface in the hope of prolonging its 'half-life', as this can create unsightly visual effects.

Modern-day trackers use numerous clues, including use of all the senses, awareness of the time of day and environmental conditions, and often being able to follow a trackmaker for a considerable distance. In contrast, fossil tracking simply involves pattern recognition on rock surfaces. The exposed surfaces on the Cape south coast are typically fairly small, and long trackways are a rarity. However, fossil trackers learn to read the rocks and develop skill sets of their own, aided by phenomena that may come as a surprise to modern-day trackers. For example, tracks may not only be preserved on the surfaces on which they were made (as natural moulds, or in 'epirelief'). They may also be preserved on the surfaces that filled in the tracks (as natural casts, or in 'hyporelief'). In fact, on the Cape south coast the natural casts of tracks often provide a better quality of preservation and are often more amenable to interpretation.

Furthermore, fossilised tracks can be examined in cross section or profile where they occur in cliff settings, where they deform underlying sedimentary layers in a predictable pattern, depending on the weight of the trackmaker. This allows for inclusion of the dimension of time into interpretation, as repeated use of an area over time can be assumed if similar tracks are apparent in multiple sedimentary layers. And whereas a coprolite (fossilised dung) will only be apparent on the surface on which it was deposited, tracks made by heavier creatures will often be transmitted to underlying layers, and may be evident as 'undertracks' or 'transmitted tracks'. Timing and weather conditions are also important so that angled sunlight can illuminate track-bearing surfaces from an optimal angle and reveal unexpected detail, and in this regard clear summer days are ideal.

Finally, although the study of fossil tracks and traces on the Cape south coast examines a direct record of the creatures that traversed the sandy dunes and beaches, this record tends to be biased towards larger, heavier animals that created larger, deeper tracks that are more easily recognized today. However, the body fossil record also has inherent biases, as it is dependent in large part on remains found in predator and scavenger dens, which are not fully representative of the fauna. The trace fossil record and the body fossil record therefore have the potential to productively complement each other.

3.4 The trace fossil sites

Highlights of our findings are presented here, beginning with trace fossils of reptiles, then of birds, then of mammals. Humans are of course mammals, but the implications of the hominin sites are profound enough that they are addressed in a separate section. Although invertebrate trace fossil sites are abundant, they are not included here as we are at an early stage in studying them.

Reptile tracks and traces: large crocodiles and baby turtles

In November 2018 an email message was received, along with attached photos, from Andre and Emily Brink: "Please let us know if you agree they may be tracks and if you haven't seen them yet." The tracksite was in the Garden Route National Park, and we were indeed not aware of it. The photos suggested a large trackmaker with powerful claws, and in the ensuing phone call the word 'crocodile' was mentioned for the first time. A few days later we were examining the tracks (Figure 3.4a) with the Brinks, a pair of dedicated citizen scientists, and over the course of the following few weeks 14 track-bearing slabs were identified within 330 metres of coastline.

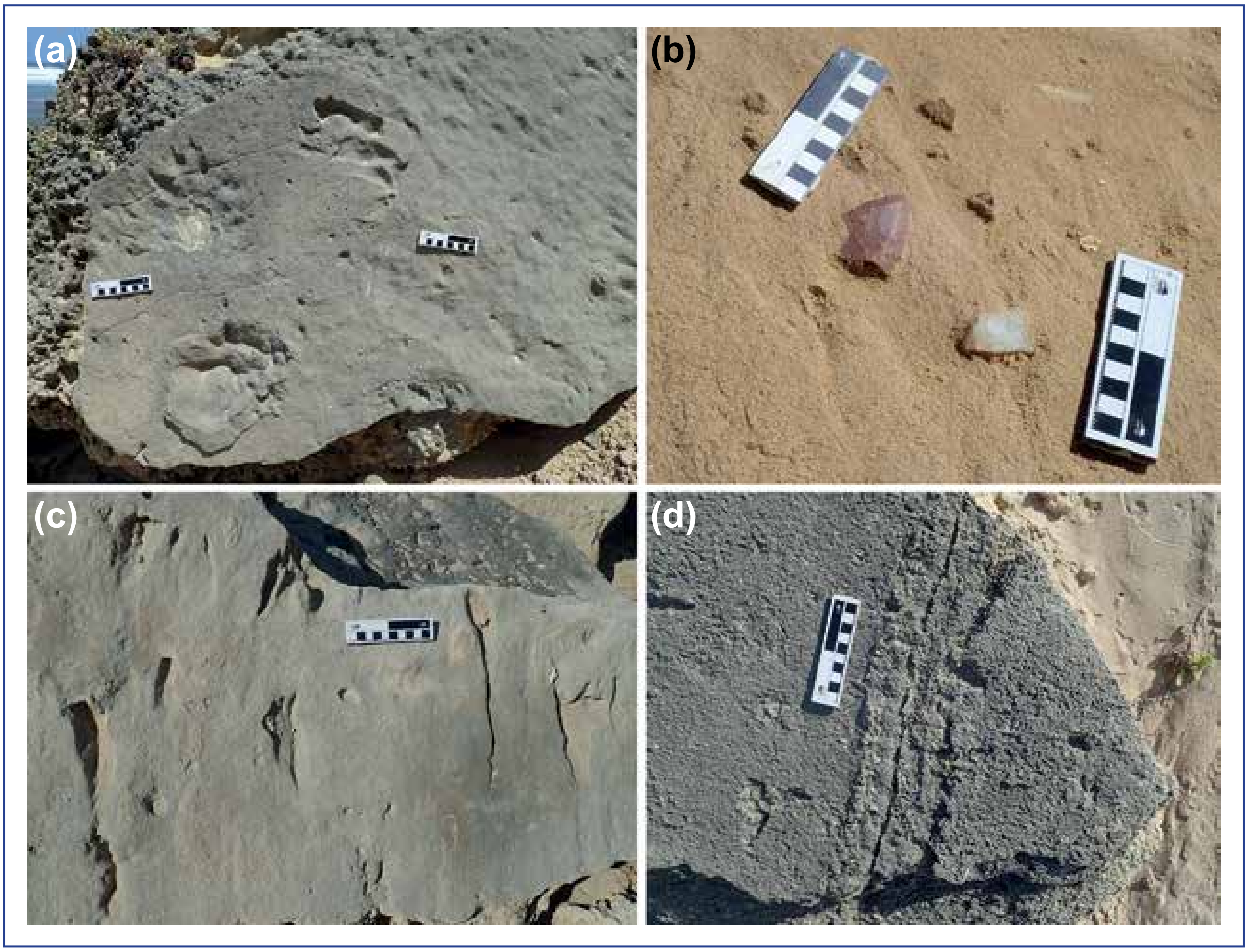

Figure 3.4 (a) A crocodile trackway. (b) Middle Stone Age tools on a surface that also contains crocodile tracks. (c) Crocodile swim traces. (d) The paratype for *Australochelichnus agulhasii*, a baby turtle trackway. All photos from the Garden Route National Park; all scale bars = 10 cm.

What was different about all of these sites, compared to other tracksites we had encountered, was that the surface layer comprised a veneer of silt and fine sand, above and in contact with a heavily bioturbated layer containing many fossilised roots and root casts. The tracks appeared to have been made on soft, damp substrates or underwater (e.g., a lagoon or interdune lake). The claw impressions, the size and morphology of the tracks (as much as 22 cm long), and the gait pattern with a wide straddle all pointed in one direction: crocodiles (*Crocodylus niloticus*). We also noted tantalizing evidence not only of crocodile tracks, but of crocodile swim traces, whereby swimming crocodiles scrape the bottom with their claws and leave distinctive sub-parallel scratch marks (we were familiar with the appearance of swim traces from other global localities, and could therefore recognize them, but they had never before been described from Africa).

The body fossil and archaeological evidence for the presence of crocodiles in the southern Cape during the Pleistocene was minimal and of uncertain provenance[18], and the palaeo-environmental implications of these tracks would be profound, with inferences of warmer temperatures than at present, presumably during an interglacial phase. We asked regional historian Hugo Leggatt whether 'Kaaimans River' had anything to do with crocodiles or 'caymans', and concluded that it did not[19]. Moreover, survivors of Portuguese shipwrecks between Plettenberg Bay and Mpondoland in the 16th and 17th centuries reported lots of wildlife, but no crocodiles.

We found ourselves asking what else could have created such tracks, as usually a process of elimination is necessary with such sites, and debated the possibility of large water monitors (*Varanus niloticus*). In order to be as diligent as possible, we collaborated with the Tracker Academy, bringing Master Trackers to the sites, and invoking the help of expert crocodile researchers. The conclusion was that there was evidence of both larger crocodile tracks and smaller monitor lizard tracks[20]. Based on track length, we could calculate that the crocodile trackmaker was more than 2.5 metres in length. These expert trackers were not able to provide a conclusive opinion on the swim traces. For understandable reasons there is little interest in entering often muddy crocodile-infested bodies of water to see what traces might have been registered on their lower surfaces by reptilian claws.

There was one further, unexpected bonus: embedded in one of the large surfaces containing both crocodile and monitor tracks we found two Middle Stone Age stone artefacts (Figure 3.4b). While no tracks on this surface were of hominin origin, we could at least conclude that there had been a spatial and temporal association in this environment between humans and large reptiles.

Fortuitously, another slab became detached from the cliffs above in 2019, tumbled down to the high tide mark, and landed the right way up. This time the evidence for crocodile swim traces was unequivocal (Figure 3.4c), supporting our initial conclusions[21]. It was the tracks of reptiles that provided some of the most profound palaeo-environmental indicators, due to their ectothermic biology and temperature requirements for successful breeding. Along these lines, a completely unexpected discovery was made east of Still Bay in 2016, with seven sub-parallel trackways providing the first global record of hatchling turtles scampering for the sea. As a result, the genus and species name *Australochelichnus agulhasii* was created for tracks consistent with those of baby loggerhead turtles (*Caretta caretta*). These trackways preserve an incredibly brief moment in time, and they tell us of how turtle breeding ranges have changed over the millennia[22]. Today the closest example of where these turtles are found nesting lies more than 1 000 km to the northeast of Knysna.

While the site east of Still Bay represents the holotype for *Australochelichnus agulhasii*, the paratype lies just east of Kleinkrantz in the Garden Route National Park (Figure 3.4d). Here, two loose slabs lie in close proximity to each other, on a dune slope above the high water mark, and each contains a segment of trackway, truncated by the edges of the slabs. Correlation to regional deposits suggests that these slabs form the cemented remains of an ancient beach. A short avian trackway on one of these slabs establishes the orientation of the rock without any doubt, and enables the identification of this as a second hatchling turtle tracksite. To find the next evidence of fossilised sea turtle tracks we need to go all the way back to the Jurassic Period in western Europe, more than 140 million years ago.

Bird tracks: larger than expected

We have identified 14 fossil avian tracksites on the coast between Wilderness and Robberg. Globally, avian tracks tend to be less common and less obvious than mammal and reptile tracks. This is partly because birds fly and perch, with the result that their tracks are relatively uncommon. Most fossil bird tracks are found on surfaces that were once the margins of lakes and lagoons. Many of our findings of bird tracks are on what were once beaches and dunes, and this is therefore unusual at a global level, but consistent with modern avian behaviour on this coast.

There is nothing in the body fossil record to suggest Pleistocene avian extinctions, or birds that may have been larger than their extant descendants. Yet that is what our ichnological findings seem to indicate. Two special sites within the Garden Route National Park illustrate these concepts[23]. One site was reported to us on the sloping ceiling of a small cave. Although the surface was friable, it was still intact when we were able to visit it and document it (Figure 3.5a). The trackways showed the distinctive features of a flamingo trackmaker, except that the tracks, which had a mean length of 13.1 cm and a mean width of 14.2 cm, were larger than those of the extant Greater Flamingo (*Phoenicopterus roseus*). It is known that some Pleistocene bird species were larger than their modern counterparts and that they subsequently became smaller over time. This might account for our findings at this remarkably well preserved site, where we also documented flamingo feeding traces for the first time. Watching flamingos feeding today reveals that they often indulge in what has been termed rapid "rhythmic stomping" or "marking time": through this action they stir up their food supply while moving slowly backwards. The result is a series of "tramline traces", and remarkably we were able to detect evidence of these on the cave ceiling.

We were able to follow the track-bearing layers a few metres to the east, to where they were exposed in cliff layers. Here we found evidence of similar tracks, but in cross section. They possibly represent the first description of any fossil avian tracks in cross section.

A nearby site presented accessibility challenges, being situated in high, brittle cliffs on the under-surface of the ceiling of a tiny overhang (Figure 3.5b). Initially, only two tracks were visible (Figure 3.5c). However, following some excavation in this precarious position we were able to identify five large tracks in a trackway, and had cleared just enough space to take photos for photogrammetric studies. These enabled us to create a 3D digital model of the trackway which otherwise could not be adequately visualized or studied (Figure 3.5d). Track length was more than 17 cm, with a relatively large pace length of about 38 cm. A slight intoeing gait and a narrow straddle were evident, and the outer digit impressions displayed slight inward curvature (a proxy for the presence of webbing). In fact, low-relief evidence of infill of web impressions may have been present in one track. When we combined and analysed all this evidence, we could not confidently link the tracks to any member of southern Africa's existing avifauna.

This raises the possibility of previously unsuspected Pleistocene avian extinctions. For example, we could hypothesise that a large, web-footed bird species may have been driven to extinction by a change in climate that flooded the wetland habitat of the Palaeo-Agulhas Plain. Why, then, are there no findings in the body fossil or archaeological records to support such a contention? The most logical answer is that we are looking at different time periods. The former extends back to about 80 000 years ago, whereas most of the avian tracksites we have documented appear to be from the 130 000 to 90 000 year range. Pleistocene avian extinctions may therefore have predated any evidence that may be available through the skeletal record.

At the other end of the size spectrum is a trackway comprising three tracks near Gericke's Point. Track length is just 2.5 cm, track width is 3.5 cm, and pace length is 13 cm. The outer digits clearly display an inward curvature, which, as mentioned above, can be regarded as a proxy for webbing. The only extant wader to show this is the Pied Avocet (*Recurvirostra avosetta*), which creates substantially larger tracks. Likewise, no extant members of the duck and goose family (Anatidae) or gulls (family Laridae, sub-family Larinae) are capable of making tracks this small. The trackmaker therefore appears to have been a tern: small and medium-sized tern species typically make tracks about 2.5 – 3.5 cm long and 2.2 – 3.5 cm wide, with incurving outer digit impressions.

There is no better example to illustrate the ephemeral nature of tracksites on the Cape south coast than the splendid flamingo site. Tracks are made on a surface of sand, covered by another layer of sand, and then buried for 100 000 years or more. Yet once exposed through the forces of erosion and cliff collapse, they are destined to disappear within a very short period of time, at the hands of those same forces of erosion. As we had feared, the flamingo tracksite was obliterated by a powerful storm surge in the winter of 2020. Fortunately, we had obtained a photogrammetric record, with the capacity to produce an exact replica of the surface.

Elephant tracks and trunk-drag traces

Everyone loves elephants, it seems, and for many the words 'Knysna' and 'elephant' are synonymous. No fewer than 22 fossil elephant tracksites have been identified between Wilderness and Robberg, including the first reported example in the global fossil record of an elephant trunk-drag impression[24]. This site is situated just 18 km from the forest inhabited by the lone remaining "Knysna elephant". The profusion of Pleistocene elephant tracksites supports Holocene and historic evidence that elephants once made widespread use of open

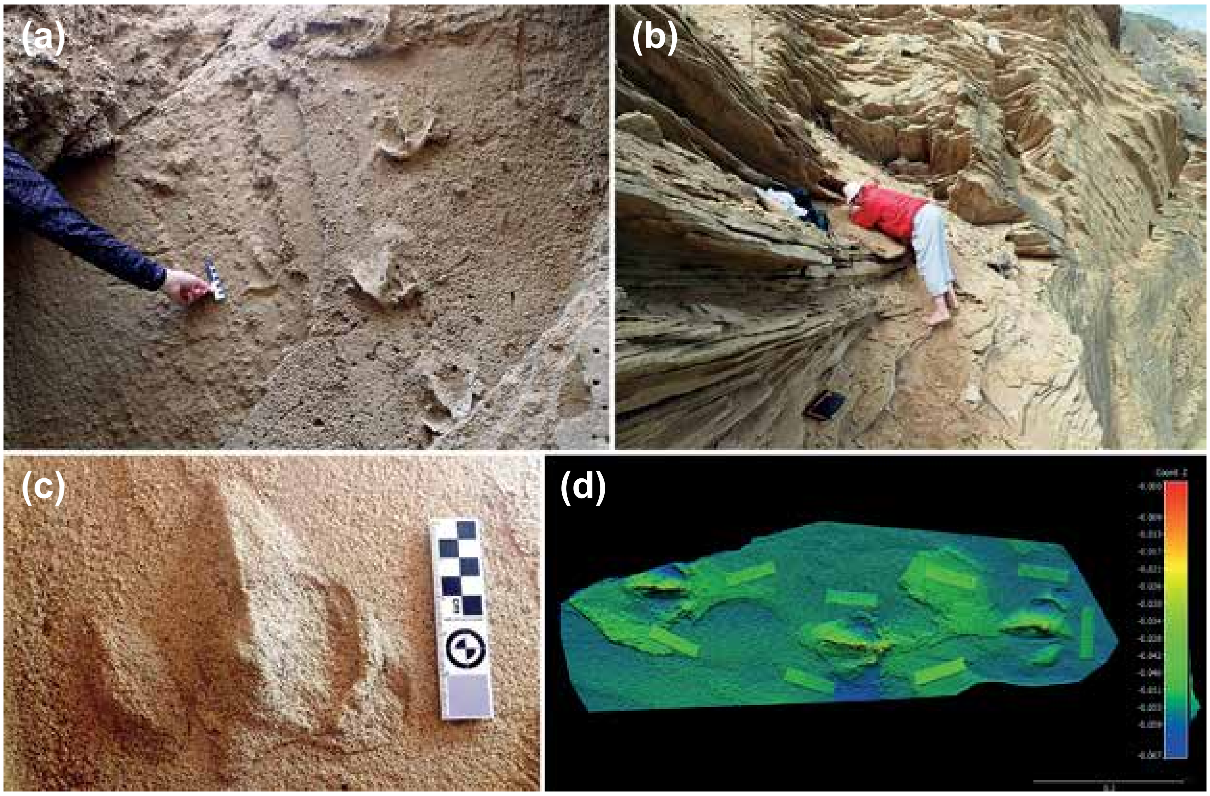

Figure 3.5 (a) Large flamingo tracks, with feeding traces; scale bar = 10 cm. (b) One avian tracksite is situated among high, brittle cliffs. (c) A well-outlined large avian track on the ceiling of a small overhang at (b); scale bar = 10 cm. (d) 3D photogrammetry of trackway at (b); horizontal and vertical scales are in metres. All photos from the Garden Route National Park.

areas in the region, and that the remaining elephants retreated into dense afrotemperate forest for protection in recent centuries, where hunters had difficulty finding them.

The trunk-drag site lies within the Goukamma Nature Reserve. It is only exposed at low tide, and is sometimes subjected to intense wave action. More often, though, it is covered by thick layers of sand. After rare periods of longer exposure it becomes covered with algae and barnacles, rendering it almost invisible.

Here, beside an elephant trackway comprising 13 tracks, we encountered a serpentine sequence of two long, slightly curved groove features, one on each side of the trackway (Figure 3.6a). African elephant (*Loxodonta africana*) bulls often indulge in trunk-dragging during musth, a cyclical period involving a heightened level of testosterone production; this represents the likeliest scenario for the features that are present.

Fossil elephant tracks can take a number of forms, from familiar depressions, to natural casts representing the layer of sand or silt that filled in the tracks, to profile views that indicate how underlying layers were deformed in a predictable fashion by as much as 30 cm (Figure 3.6b). In some cases, elephant tracks on beaches were precursors for the much later formation of potholes (Figure 3.6c) on their cemented remnants[25]. In some places, they have been eroded into weirdly beautiful shapes, which hikers on the coast admire and pass by without realising their intriguing origins (Figure 3.6d).

Analogies can be drawn between Pleistocene elephant tracks and Mesozoic dinosaur tracks: in both scenarios they were the largest tracks of their time, made by the heaviest creatures. It appears that the fossilised elephant tracks we identified at Robberg, measuring as much as 70 cm in diameter, are among the largest tracks ever identified since the "Age of Dinosaurs" (Figure 3.6e). Nearby rock pools contain the only examples we have found thus far of underwater tracks, in this case made by elephants (Figure 3.6f). At another site elephant tracks are evident in profile in multiple successive layers over a vertical distance of 26 metres, implying repeated use of an area over time[26].

Figure 3.6 (a) Elephant trunk drag impression beside an elephant trackway in the Goukamma Nature Reserve.
(b) Elephant tracks in profile in the Goukamma Nature Reserve, indicating how underlying layers were deformed.
(c) Elephant tracks were the precursors of these potholes in the Garden Route National Park.
(d) Arrows indicate elephant tracks that have been eroded into unusual shapes in the Goukamma Nature Reserve.
(e) These transmitted elephant tracks in the Robberg Nature Reserve are among the largest tracks ever identified since the Mesozoic.
(f) Measuring underwater elephant tracks at Robberg.

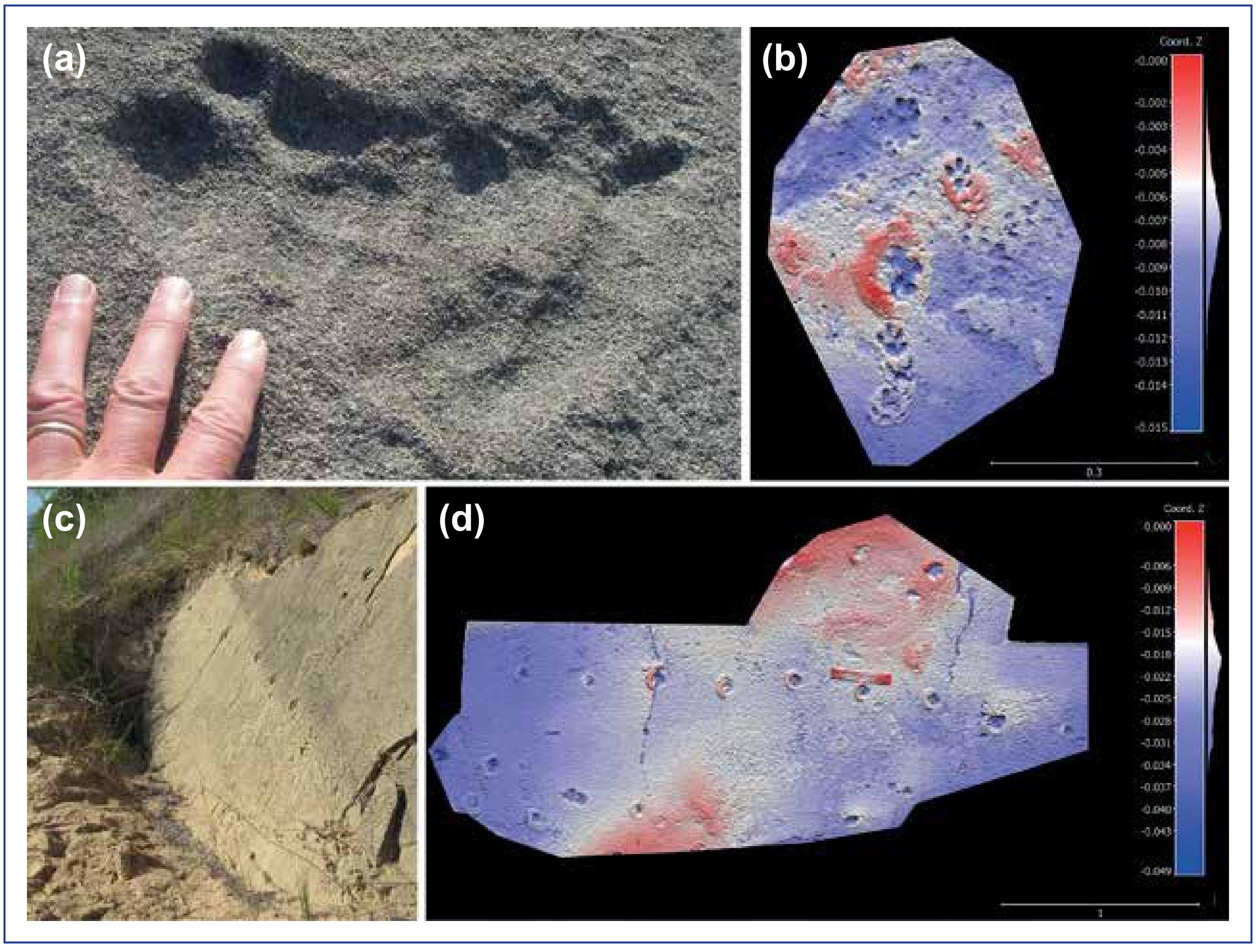

Figure 3.7 (a) Large lion tracks (possibly of the Cape lion) in the Goukamma Nature Reserve.
(b) 3D photogrammetry of a trackway of a small-to-medium-sized canid or a larger herpestid beside the Goukamma River; horizontal and vertical scales are in metres.
(c) Four parallel, straight, medium-sized carnivoran trackways above the Goukamma River.
(d) 3D photogrammetry of the tracks shown in (c); horizontal and vertical scales are in metres.

Elephant bones are not commonly encountered in the regional Pleistocene body fossil record. It is the frequency of tracksites that therefore indicates their substantial presence on the landscape, from which palaeo-environmental inferences can be made. Elephants are ecosystem engineers, and they may well have helped to develop and maintain the mosaic of woodland and grassland habitats that characterised the Palaeo-Agulhas Plain during the Pleistocene[6].

Carnivoran tracks

There are challenges associated with the identification of fossil carnivoran tracks on the Cape south coast, and they are related to the degree of morphological detail that is evident on the relatively coarse-grained surfaces. We have noted how subtle features such as claw marks may be apparent in carnivoran tracks soon after they are exposed, but how, as wind and water erosion take their inevitable toll, such claw marks become less evident over a period of as little as a couple of years. The problem is that the presence of claw marks is an important feature in distinguishing canid or herpestid (mongoose) tracks from felid tracks. Often we have to be satisfied with simply identifying "medium-sized carnivoran tracks" and not trying to indulge in over-interpretation.

Nonetheless, there are welcome exceptions, and the Goukamma Nature Reserve coastline provides a classic example. Two parallel trackways contain large lion tracks with clear evidence of a main pad impression and four digit pad impressions without claw impressions[26] (Figure 3.7a). The absence of large displacement rims associated with the tracks suggests that the lions were travelling on a level inter-dune area rather than on a dune face. There is no Pleistocene trackmaker in the region other than the African lion (*Panthera leo*) that could make tracks of this size and shape, as the extinction date of the sabre-toothed cats greatly predates the age of the trackway.

Intriguingly, the track dimensions are slightly larger than those recorded of this species nowadays, and there are two possible explanations for this. The first is that the tracks were made by the extinct (and slightly larger) Cape lion subspecies (*Panthera leo melanochaitus*). The second relates to the observation that carnivoran body size may vary with climate changes in the Pleistocene, with glacial phases being characterized by larger sizes. At a global level, the record of fossil lion tracks is indeed sparse, and the Goukamma tracks join a select group containing Pliocene tracks from Laetoli in Tanzania, Pleistocene tracks from Germany and a couple of Holocene tracksites from North America.

The only fossil tracks that are not close to the beach are found on the slopes above the Goukamma River within the Goukamma Nature Reserve. At river level we encountered a loose slab with a trackway comprising fourteen tracks with well-defined main pads, digital pads and claw impressions (Figure 3.7b). These must have been made either by a small-to-medium-sized canid or a larger herpestid (mongoose). In what we considered a neat touch, we found modern tracks in mud made by a water mongoose (*Atilax paludinosus*) right beside the slab of rock containing the fossil tracks[26].

On the sandy slopes above this site we came across a larger, very fragile loose slab with four parallel, straight, medium-sized carnivoran trackways, the longest of which contained 11 tracks (Figure 3.7c, d). While it can be inferred that the trackmakers were travelling up a dune slope, they cannot be identified to family level.

Before leaving the subject of carnivorans, there is the issue of pinnipeds to consider, the clade that includes the true seals, fur seals, sea lions and walruses. Despite an extensive, globally distributed body fossil record that extends back to the Oligocene (~30 million years ago), there appears, to the best of our knowledge, to be no trace fossil record of seals, a group that includes the largest extant carnivorans. This may be because these mammals spend much of their time in the ocean, and, when they do emerge onto land, often prefer rocky habitats which would not readily preserve tracks and traces. If our interpretations are correct, then the two sites that we have identified on the Goukamma coastline, just 500 metres apart from each other, represent the first seal trace fossils ever identified. They suggest a Cape fur seal (*Arctocephalus pusillus pusillus*) presence during the Pleistocene on Cape south coast beaches[27].

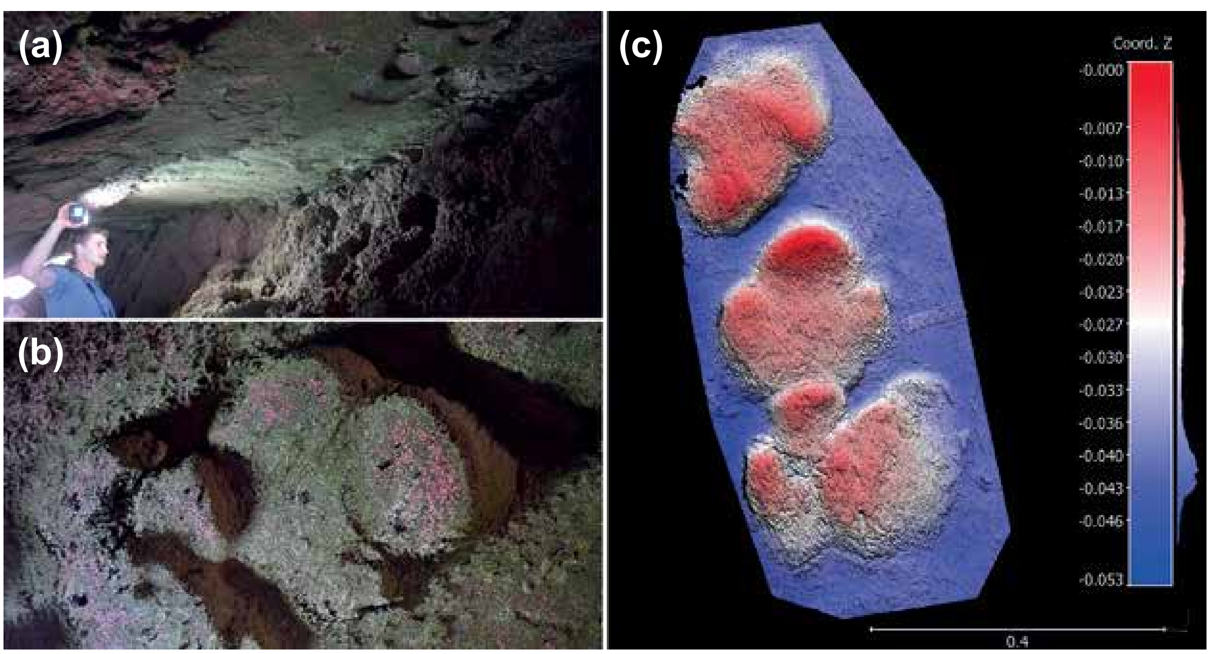

Figure 3.8 (a) Daniel Helm illuminating the tunnel ceiling containing rhinoceros tracks in the Robberg Nature Reserve. (b) Black rhinoceros track in the Robberg Nature Reserve. (c) 3D photogrammetry of black rhinoceros trackway, Robberg Nature Reserve; horizontal and vertical scales are in metres.

Rhinoceros tracks

Well preserved rhinoceros tracks should be easily identifiable through a combination of track size and the presence of three substantial digit impressions with distinctive morphology. However, in soft, sandy substrates the two middle toes of a hippopotamus track may appear to fuse, in which case the resulting track may resemble a tridactyl rhinoceros track[28]. Juvenile elephant tracks could potentially be confused with very poorly preserved rhinoceros tracks. A site east of Wilderness qualifies as a possible rhinoceros tracksite, whereas a splendid if hazardous site at Robberg provides indisputable evidence of a rhinoceros trackmaker[29].

The Wilderness example contains two in situ trackways, with a total of 10 tracks. The site, near the high tide mark, is often covered by sand. The Robberg site lays claim to the finest example of rhinoceros tracks thus far identified. The tracks occur as natural casts on the ceiling of a 16 metre tunnel, with maximum height of 2 m and width of 2.5 m (Figure 3.8a). Most of the time the tunnel is subjected to intense wave action, and the fact that the tracks on the ceiling survive this twice-daily onslaught is remarkable in itself. Extreme low spring tides are therefore a prerequisite for a site visit. Two rhinoceros trackways are present, with a total of 6 tracks that exhibit a characteristic 'clover leaf' pattern (Figure 3.8b, 3.8c). Track detail is well enough preserved to permit identification of the black rhinoceros (*Diceros bicornis*) as the trackmaker. The black rhinoceros was historically more common than the white rhinoceros (*Ceratotherium simum*) in the south-western Cape, and has been recorded more often in the body fossil record.

Bovids and the extinct long-horned buffalo

A dictum in ichnology is that "hooves follow horns": animals with long, laterally-extending horns tend to be associated with wider hooves, and hence with wider tracks[30]. We were able to put this to the test when we noted a distinctive type of large bovid track that was wider than it was long. Such a track is not made by the hindfoot or forefoot of any extant (i.e. currently living) bovid in southern Africa. The extinct long-horned buffalo (*Syncerus antiquus*), with a prodigious horn span, was the likely suspect, and we found corroboration of this concept by comparing the track dimensions of short-horned cattle from the southern Cape (a variety of *Bos taurus taurus*) with long-horned Ankole cattle (a variety of *Bos taurus indicus*) in Tanzania. The Ankole cattle tracks were consistently wider than they were long, whereas shorthorned cattle tracks exhibited a width that was equal to or less than their length.

While we were working with a colleague in Tanzania to obtain this data, Nikki Smit, a local cattle farmer, beach runner and amateur tracker, joined us for a tracking hike on the Goukamma coastline. In the course of our conversation she related how she farmed with both Afrikaner cattle (short-horned) and Nguni cattle (with horns of medium length), and how she was easily able to distinguish one group's tracks from the other's by paying attention to the relative dimensions of track length and width (the width-to-length ratio being greater in the Nguni trackmaker group). Sometimes one just needs to chat to the local experts to learn about tracks!

The most compelling example of this track type lies in the Goukamma Nature Reserve, and forms the trackway most often noticed and reported by beach hikers, as it is obvious and can be spotted from a distance (Figure 3.9a). Here a fallen block contains a 5-metre-long trackway exhibiting 17 consecutive tracks: mean length is 11.8 cm and mean width is 12.8 cm[26] (Figure 3.9b, c). The tracks within this slightly sinuous trackway are highly variable along its length. The first three tracks are partially covered by a thin layer of infill. The final three tracks are poorly preserved transmitted tracks on an underlying layer. Tracks 4 to 8 were made on a firm substrate, are relatively shallow, and provide the best-preserved morphology. Tracks 9 to 14 were made on a softer substrate, and are large and deep. It seems that the tracks were made in a relatively horizontal, interdune area.

Elsewhere on the Goukamma coast a large, deep track (15 cm wide and 14 cm long) contains not only digit impressions but also well-preserved dewclaw impressions. And a single large bovid track, 11 cm wide and 10 cm long, was found on a loose slab near Gericke's Point. It was cached above the high-tide mark for future retrieval, pending permission. If this specimen is retrieved it would be the first track with this morphology and of this extinct species to be collected, with the potential for exhibition in future.

Tracks of the Cape buffalo (*Syncerus caffer*) are also encountered. The most spectacular examples are at Brenton-on-Sea, where they occur in situ. However, they are almost always covered by sand, and are only exposed under exceptional circumstances, and usually just for a few days.

The situation is different at Robberg on a cave ceiling. Here, low tide is the only safe time to crawl in, hoping there are no rogue waves, and by gazing upward, an exceptional example of track morphology can be seen[29]. Natural casts of track pairs, the

Figure 3.9 (a) Martin Lockley working on the long-horned buffalo trackway in the Goukamma Nature Reserve. (b) The long-horned buffalo trackway viewed from below. (c) A portion of the long-horned buffalo trackway viewed from above. (d) Infilled large bovid tracks hang down from a ceiling in the Robberg Nature Reserve; gemsbok, roan antelope, giant hartebeest and blue antelope are among the plausible makers of these long, narrow tracks.

infill of a series of large bovid digit impressions that hang down from the ceiling, are exquisitely preserved (Figure 3.9d). One can be forgiven for thinking one has entered a limestone cave adorned with stalactites. The 7 cm depth of these features provides their aesthetic appeal. The length of 12 – 13 cm excludes all but the largest bovid trackmakers of the Pleistocene. However, it is the width that is intriguing: 8 – 9 cm. This excludes the long-horned buffalo, and while the Cape buffalo and eland are possible candidates, the relatively narrow width would be unusual. Gemsbok and roan antelope are plausible, but there are also two further extinct members of the Pleistocene megafauna on the Cape south coast, and their tracks have never been recorded: the giant hartebeest (*Megalotragus priscus*) and the blue antelope (*Hippotragus leucophaeus*). While a larger sample size would be needed in order to draw firm conclusions, and we are therefore in the realm of speculation, the mere fact that we may have come across the only known tracks of these species (and in such a spectacular setting) is for us an evocative concept.

Tracks of smaller buck species are commonplace, but they are very challenging, if not impossible, to identify to trackmaker species level. One example can be found beside the standard route to the top of Gericke's Point. Here three consecutive layers contain fossil buck tracks.

Equids and the extinct giant Cape horse

Another extinct member of the Pleistocene megafauna is the giant Cape horse (*Equus capensis*), a species which appears to have preferred drier environments. Its tracks were almost double the size (Figure 3.10a) of the other equid tracks we find on the coast, which were most likely made by the quagga (Figure 3.10b), the southern subspecies of the plains zebra (*Equus quagga*) that became extinct in the 19th century[29]. The giant Cape horse tracks

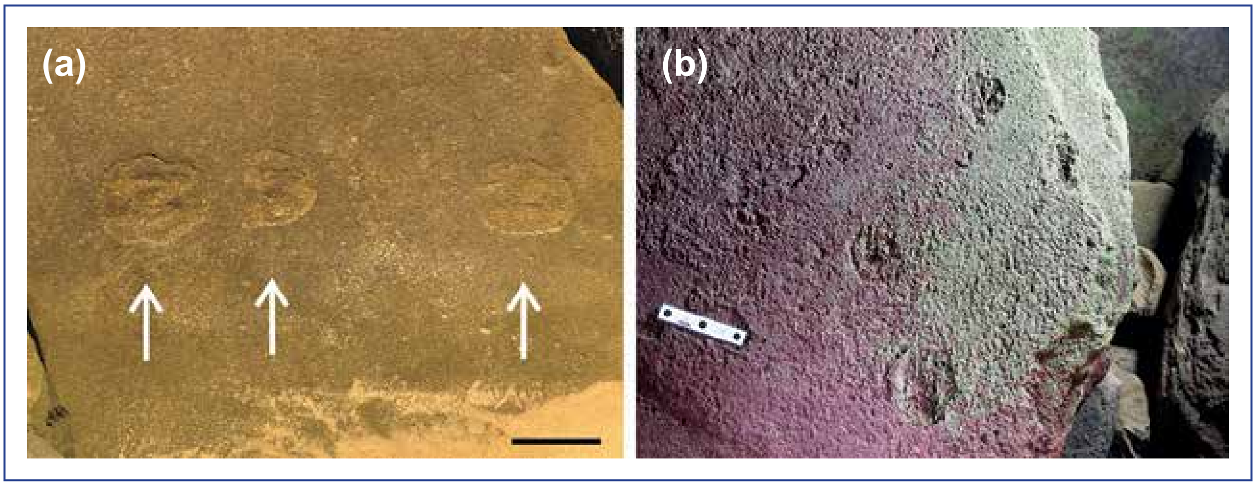

Figure 3.10 (a) Giant Cape horse tracks in the Goukamma Nature Reserve; scale bar = 15 cm. (b) Probable quagga tracks in a cave in the Robberg Nature Reserve; distance between outer black circles in scale bar = 10 cm.

are best seen at a site east of Wilderness, which can be regarded as an outdoor ichnology classroom. Here tracks are seen in the form of depressions on an in situ surface, which can be followed round to the cliffs above to an overhang, where they are visible on the ceiling as natural casts. Follow the layer further along the cliffs, and tracks can be seen in profile, where they deform underlying layers in a typical pattern. Ichnology in a nutshell!

Hippopotamus tracks

The common hippopotamus (*Hippopotamus amphibius*) was likely well suited to the floodplain grasslands of the Palaeo-Agulhas Plain, although it is not commonly encountered in the body fossil assemblage. Its presence is borne out by two probable hippopotamus tracksites, one east of Wilderness and the other at Brenton-on-Sea. Well preserved hippopotamus tracks should be easily identifiable through a combination of track size and the presence of four substantial digit impressions, but to date the 'perfect' hippopotamus track has yet to be encountered. A natural cast trackway containing four tracks (partially obscuring other tracks) was identified on two adjacent fallen slabs east of Wilderness. Although the tracks appeared eroded, with resulting loss of detail, the dimensions (track length 19 – 20 cm, track width 19 – 21 cm, depth 5 cm, pace length 59 – 63 cm) and digit morphology were consistent with those of a juvenile hippopotamus[31].

A trackway can just be distinguished on the ceiling of a small cave overhang in the cliffs at Brenton-on-Sea. The three large, very shallow tracks are preserved in hyporelief. Although they are inaccessible, and have therefore not been measured, at least one track appears to contain the infill of four toe impressions, making this a probable hippopotamus trackway.

These would be the third and fourth records of fossilised hippopotamus tracks in the world. The first two published reports were from Kenya, and included a transition from bottom-walking tracks to swim traces. The Cape south coast sites appear to provide the first descriptions of dryland tracks of this family.

Golden moles

Some of the finest golden mole burrow traces that we have identified are to be found at Robberg[32]. Here branching burrows, measuring as much as three metres in length, occur right beside the boardwalk that has been built to keep hikers from trampling sensitive vegetation on The Island (Figure 3.11a). They were probably made by a species like *Amblysomus hottentoticus*, and are in the 42 000 to 35 000 year age range.

Closer to the tip of the Robberg Peninsula we identified further branching fossilised golden mole burrows (Figure 3.11b). Fortuitously, at the south-western edge of the surface of this loose block one of these burrows was evident in both cross-section in longitudinal section, and it ended in a chamber 10 cm in diameter. In this case the burrows were made somewhere between 67 000 and 56 000 years ago.

Perhaps even more impressive is a metre-long trackway of a sand-swimming golden mole found near Gericke's Point in the Garden Route National

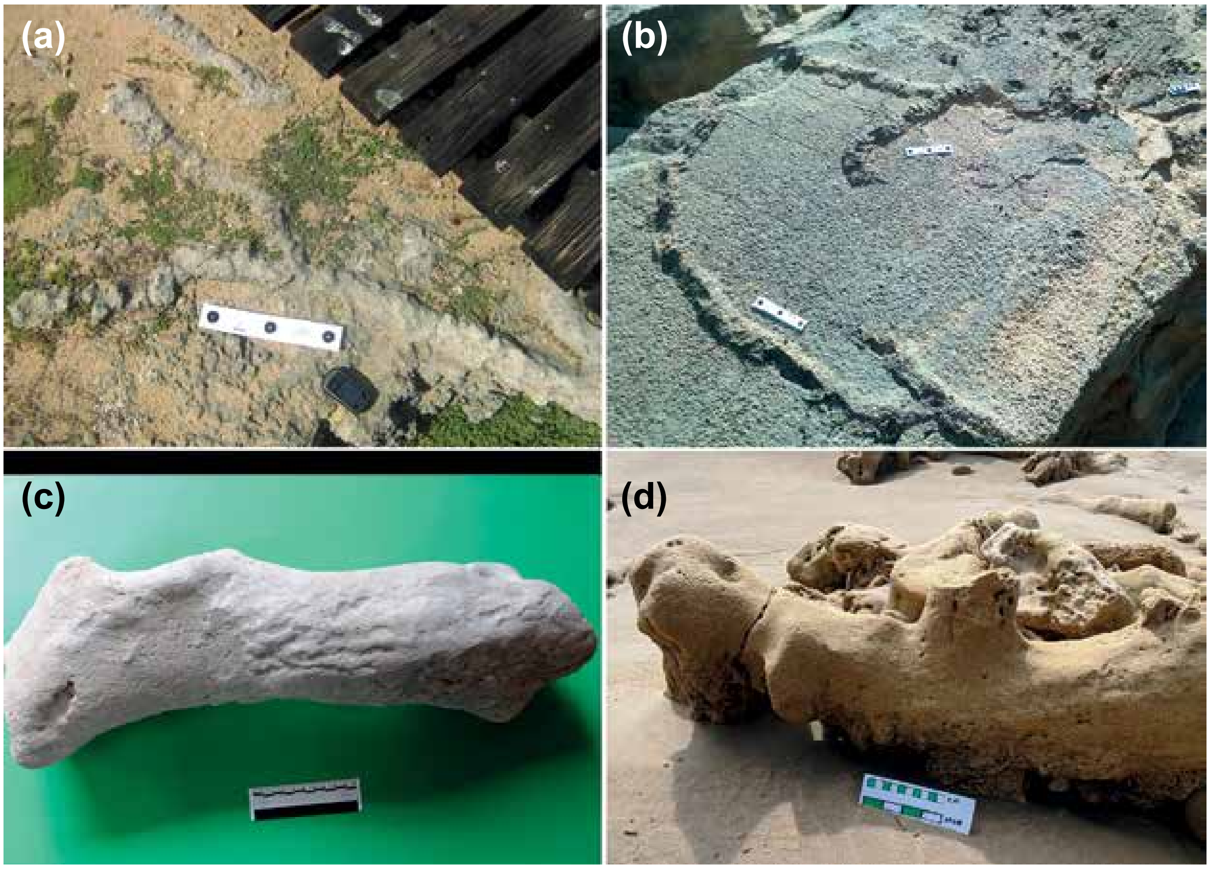

Figure 3.11 (a) Branching fossilised golden mole burrows beside a boardwalk on The Island in Robberg Nature Reserve. (b) Fossilised golden mole burrows near the tip of the Robberg peninsula. (c) Internal cast of a molerat burrow found east of Wilderness; the longitudinal parallel striations represent the 'track' of the molerat. (d) A probable 3D molerat burrow complex east of Buffelsbaai.

Park (Figure 1.20 in the Introduction). Here a fragile loose slab lies above the high-tide mark. It has landed upside-down, so the traces are preserved in hyporelief. The only living creatures capable of making such a trail are two species within the genus *Eremitalpa*. These unusual golden moles occur in the dunes of the Namib desert and the northwest coast of South Africa, and have a unique mode of locomotion, 'swimming' just below the surface of the sand and creating distinctive traces. Palaeo-environmental inferences can be drawn of the presence of substantial dune fields on the Cape south coast during the Pleistocene[32].

Molerats

Anyone who has hiked the 5 km Cape dune molerat trail near Rondevlei knows all about molerats and their ubiquitous burrow mounds, and may inadvertently have fallen into a burrow or two. However, it is difficult to gain an appreciation of what a three-dimensional burrow, or burrow complex, might look like. On the coast east of Wilderness we found infilled burrows, consistent with the dimensions of molerats, and one of these contains a 'clincher'. When examined under optimal angled lighting, an unexpected and remarkable feature becomes evident: longitudinal parallel striations that represent the 'track' of a molerat (Figure 3.11c).

Further east, unique features have been encountered at three seldom-exposed sites east of Buffelsbaai. Collaborating with global molerat experts, we suspect these are extensive complexes of infilled burrows (Figure 3.11d). The Cape dune molerat (*Bathyergus suillus*) has been reported frequently from archaeological sites on the Cape south coast, and our ongoing research into these sites will hopefully help to buttress the body fossil record.

Coprolites

The study of coprolites (fossilised dung) is an important sub-discipline in ichnology, and the results can be of great benefit in palaeo-environmental reconstruction through, for example, pollen studies, isotope studies on ingested bone, and phytolith analysis on ingested plant matter. In addition, coprolites can provide clues as to trackmaker identity. We were not actively searching for coprolites, knowing that globally there was a paucity of any such 'open-air' records in aeolianite deposits, and certainly none that had been reported from southern Africa. Furthermore, the Pleistocene herbivore coprolite record is extremely sparse. In contrast, a number of carnivoran dens and scavenger dens in caves and shelters on the Cape south coast have yielded coprolites of the brown hyaena (*Hyaena brunnea*), and genet latrines were reported from Klasies River to the east.

While we suspected that coprolite preservation on Pleistocene sandy surfaces might be unlikely, we also knew the capacity of these palaeosurfaces to provide a faithful record of events that transpired on them. The discovery of four coprolite sites between Wilderness and Brenton-on-Sea, two of which were compelling and two more speculative, thus came as a pleasant if not totally unanticipated surprise. Our research into these is ongoing, but it is safe to say that they hold the potential for novel palaeo-environmental interpretation.

One site contains coprolites of a medium-sized bovid such as a bontebok (*Damaliscus pygargus pygargus*), with a trackway passing right through them. Another was consistent with the latrine site of a small carnivoran, with multiple layers indicating use over an extended period of time. In this case too, tracks around the coprolites substantiated this interpretation. Elephant and large equid tracks that traversed the site conjured up an intriguing vision of possible interactions between these denizens of the Pleistocene. A third site contains a possible crocodile coprolite (white in colour) alongside crocodilian swim traces which implied a subaqueous environment. If substantiated, this would be the first reported specimen of a coprolite of a Nile crocodile.

3.5 Hominin tracks and traces

The discovery of a number of hominin tracksites, in what is perhaps the greatest concentration of such sites in the world, is of considerable significance. We knew from the outset that early members of our species, *Homo sapiens*, had in all likelihood trodden and traversed some of these Pleistocene dune and beach surfaces, particularly given the abundance of Middle Stone Age archaeological sites on the Cape south coast. Searching for evidence of their presence thus became a 'holy grail' quest, and in 2016 we were rewarded with the discovery of the first tracksite, at Brenton-on-Sea. In subsequent years further sites have been identified, in addition to patterns in the sand that our ancestors probably created, and possible evidence for the use of footwear. In attributing these sites to *H. sapiens*, it is acknowledged that species such as *H. naledi* and *H. helmei* cannot be absolutely excluded, although they are less likely.

Hominin tracksites

Prior to the identification of the Brenton-on-Sea tracks, two other southern African hominin tracksites were known about, at Nahoon to the east (near East London) and at Langebaan on the west coast[33]. The Nahoon tracksite, containing three tracks, was identified in 1964 and was subsequently dated to ~124 000 years. The Langebaan tracksite, also containing three tracks, was identified in 1995 and was dated to ~117 000 years.

The Brenton-on-Sea tracks, totalling around 40, were found on the ceiling and side walls of a small wave-cut cave in aeolianite cliffs[34] (Figure 3.12a, b). In all probability they would have been discernible for years, perhaps decades or more, prior to their discovery. Why, then, had they not been identified earlier? Firstly, not everyone chooses to crawl into tight caves. Secondly, the notion that natural casts of tracks occur on cave ceilings and under rock overhangs is initially counter-intuitive. Thirdly, one needs to 'get one's eye in', as one seldom finds what one is not looking for. The tracks, then, had probably been 'hiding in plain sight' for some time.

A large-carnivoran trackway was found on the floor of the cave, and elephant tracks and bovid and equid tracks of various sizes were found close by. While the four carnivoran tracks do not show much morphological detail, based on size alone the likelihood is that they were made by a lion. Just 500 metres east of the tracksite, Middle Stone Age tools are embedded in an aeolianite surface in association with bone and shell fragments. A short distance further east there is an unexcavated cave (containing stone tools) in Cape Supergroup rocks that may have been available for hominin use at the time the tracks were made.

Stratigraphic correlation to nearby sites that had been dated through OSL, combined with the amount of carbonate cementation that had taken place in the host layer, allowed for a date estimate of about 90 000 years to be made for the tracks. At

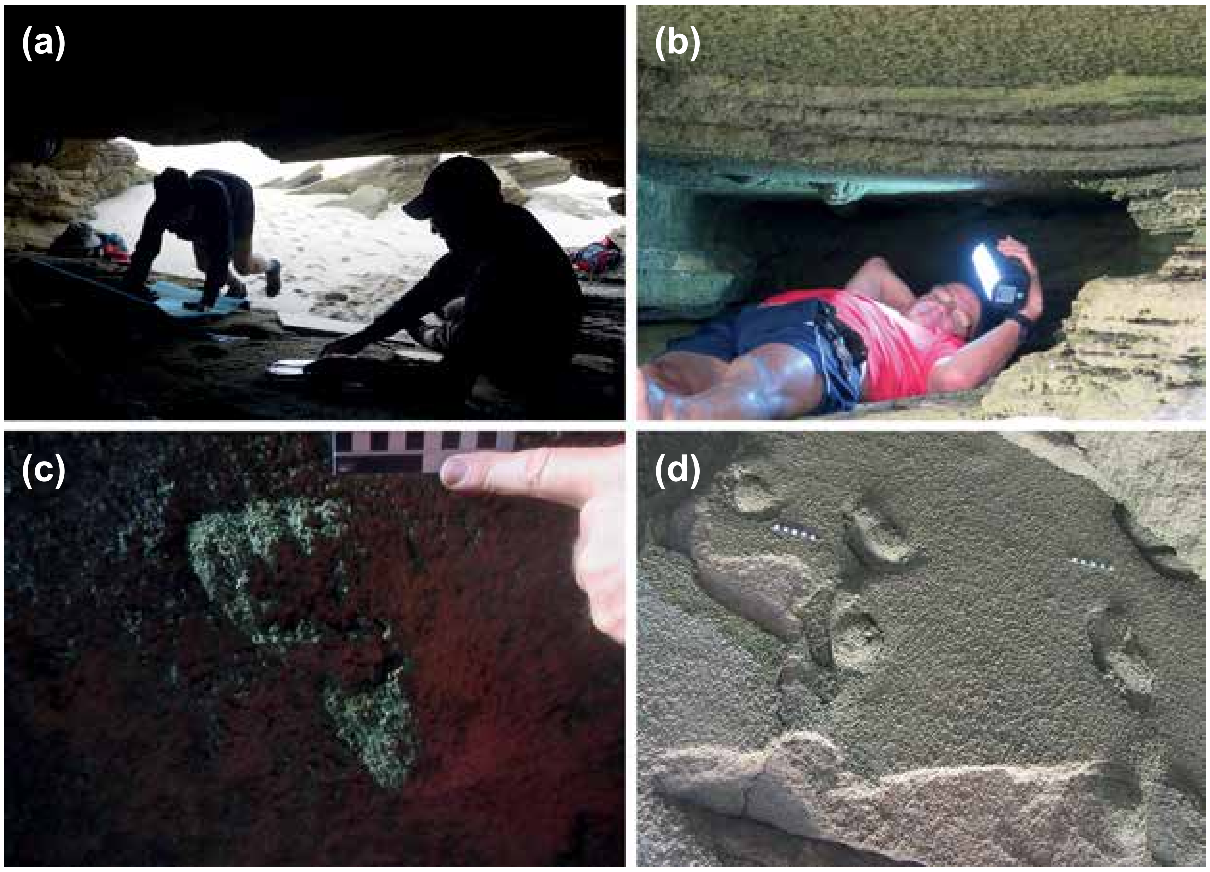

Figure 3.12 (a) Linda and Charles Helm logging data in the Brenton-on-Sea cave containing hominin tracks. (b) The hominin tracks occur on the cave ceiling, and the floor and ceiling are not very far apart. (c) One of the better preserved hominin tracks, with clear evidence of toe casts. (d) The tracks on the ceiling towards the mouth of the cave were made in soft, non-cohesive sand.

that time the shoreline would have been a couple of kilometres to the south. It was evident that a variety of track sizes was present, suggesting a group of people of various ages. It was estimated that the largest tracks were made by an individual who was ~1.53 metres tall. Almost all the tracks were heading in the same direction, down a gentle dune slope. The pace length and stride length indicated a high trackmaker velocity, suggesting jogging or running. If so, this would be the oldest known evidence of running humans, and as a result a productive collaboration ensued with Prof. Tim Noakes of the University of Cape Town[35].

The site illustrated the importance of substrate consistency. The tracks in the deepest part of the cave had been made in firm sand, and clear evidence of toe outlines was present in at least nine of these (Figure 3.12c). In contrast, the tracks that were preserved on the ceiling towards the mouth of the cave had been made in soft, non-cohesive sand. While a general hominin footprint outline was present, details such as toe outlines were absent (Figure 3.12d). The track-bearing surface was clearly not manually recoverable, and traditional methods of replication such as casting with latex or silicone would be challenging, given the twice-daily high tides that enter the cave (on one occasion a rogue wave washed into the cave as we were working, soaking everything and taking our backpacks with it as it receded). Furthermore, there would be a risk of damaging the fragile tracks. Instead, photogrammetry technology was employed, and thousands of photographs were taken. This presented its own challenges, due to the cramped surroundings and the small distance of about 50 cm between floor and ceiling, and camping pads proved essential to reduce the strain on the photographer's elbows and knees. Strategically placed LED lanterns illuminated the deeper recesses of the cave, improving the photo quality. The resulting 3D images were just what we wished for: without risking the integrity of a single track, we had created a digital version of the surface, with the potential to produce an exact replica in future.

Undoubtedly, the moment of discovery of this site was a high point in our ichnological work. The close confines in the cave make for a quintessential 'in-your-face' experience, with the tracks hanging down from the ceiling a few centimetres from one's nose. Consequently one has to squint slightly in order to focus and appreciate them properly. We have subsequently shown the site to a variety of colleagues, students and dignitaries. It clearly inspires a sense of reverence. It would be hard to imagine a track site in more spectacular surroundings, with pristine beach, cliff and ocean views close by that help to create feelings of awe and wonder. Perhaps being in a cave environment creates a further atavistic spur. However, probably the most powerful factor involves a simple thought experiment: either that little band of humans travelling down a dune slope was somehow obliterated before they had time to procreate, or else they were our direct ancestors about 3 600 generations ago.

The site remains both the largest and best preserved archive of Late Pleistocene hominin tracks discovered so far. The subsequent collapse of a portion of the cave roof, resulting in the loss of a number of tracks, serves as a reminder that our work is not without hazards, and that tracks are ephemeral. However, while they are vulnerable to erosive forces, the tracks extend to all edges and corners of the cave ceiling, and those same forces have the potential to expose a larger portion of the surface.

Through our work at this site we gained an appreciation of the appearance of hominin tracks in profile. This allowed us to identify a second site, 300 metres to the east, where seven tracks seen in profile in the aeolianite cliffs were suggestive of a hominin track-maker[36]. A formal excavation of this site would be required to confirm this.

In 2019 Dr Martin Lockley, internationally acclaimed ichnologist from the University of Colorado, joined our research team on the Cape south coast. Together we analysed tracksites in detail, and were able to identify two further hominin tracksites, one in the Goukamma Nature Reserve and one in the Garden Route National Park[36].

The Goukamma Nature Reserve site is perhaps globally unique among hominin tracksites, in that the surface in which the tracks were made can be seen on a fallen slab that lies on the beach below a cliff, and the corresponding infill layer of natural casts is evident in situ under an overhang in the cliffs above (Figure 3.13a,b). Thirty-two tracks were present, with a variety of trackways and track sizes—all were made on a sloping dune.

The Garden Route National Park site (Figure 3.14a) contains 18 tracks. Some of these are amorphous, but six could be identified as hominin tracks, occurring as natural casts on a cave ceiling at the foot of aeolianite cliffs. Tracks of various sizes were present, and the largest track (Figure 3.14b), with a length of ~24 cm, yielded a height estimate for the trackmaker of ~1.60 metres. Storm surges and spring high tides pound the interior of the cave, and

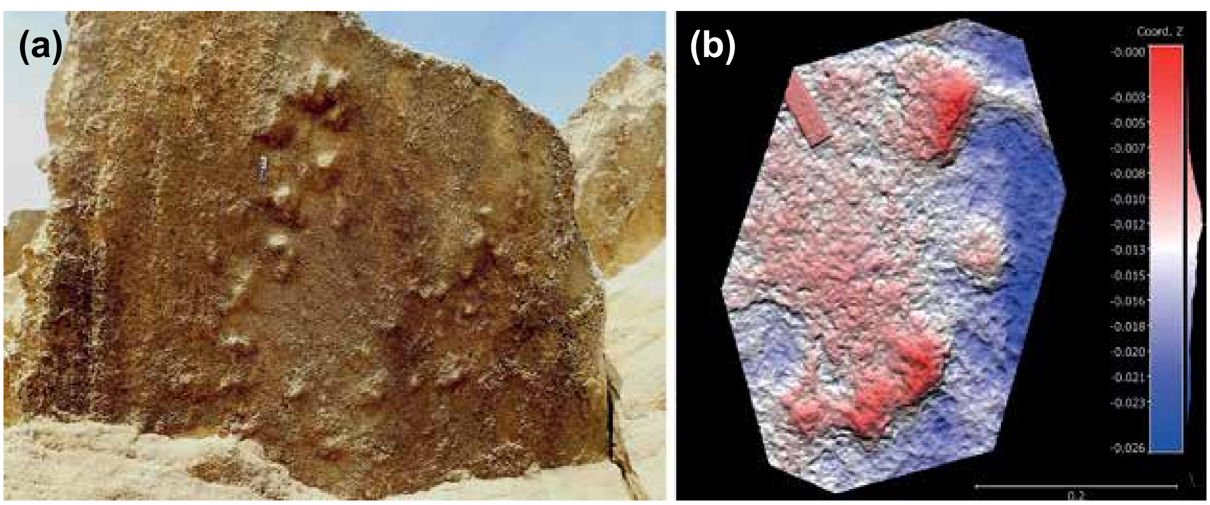

Figure 3.13 (a) Sunlight catches the infill layer of natural casts of hominin tracks in the Goukamma Nature Reserve. (b) 3D photogrammetry of two of the hominin tracks at the Goukamma Nature Reserve tracksite; horizontal and vertical scales are in metres.

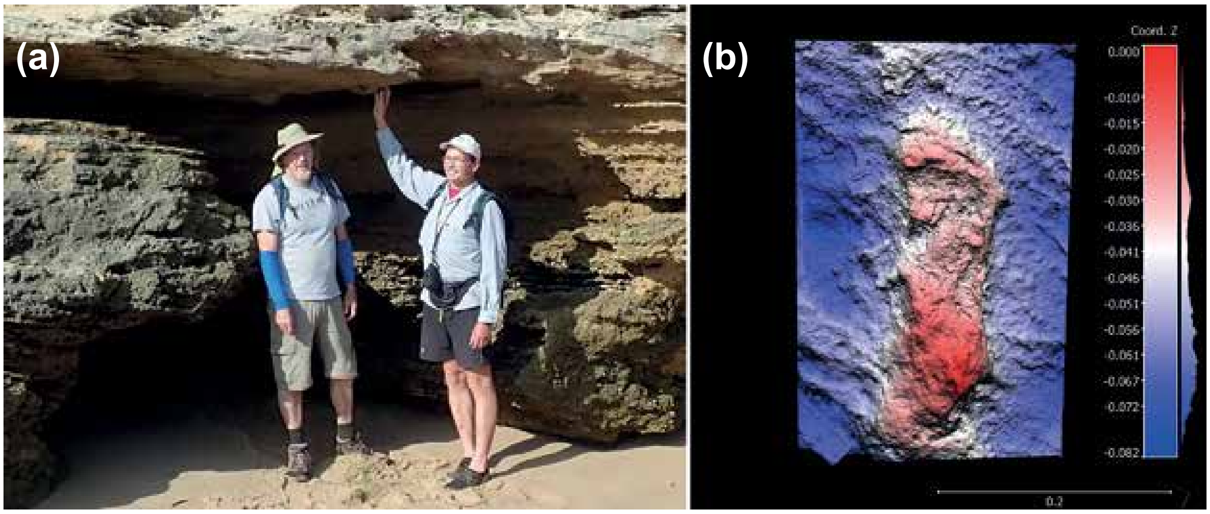

Figure 3.14 (a) Martin Lockley and Charles Helm at the Garden Route National Park hominin tracksite. (b) 3D photogrammetry of the largest track on the ceiling of a cave at the Garden Route National Park hominin tracksite; horizontal and vertical scales are in metres.

unfortunately track degradation has been noted over time.

The final unequivocal hominin tracksite provides a bridge between tracks and ammoglyphs (defined and described in section 3.5.3), and is therefore discussed below. Where does this combination of southern African tracksites fit into the global hominin track record? Firstly, such sites are more common than was previously supposed, and further discoveries can be anticipated. Secondly, these are the oldest sites in the world that have been attributed to *Homo sapiens*, along with one site on the Arabian Peninsula[37]. Internationally, there are only six or seven older hominin tracksites[38]. The importance of the Cape south coast in understanding modern human origins adds to the significance of the sites.

From a global perspective, the occurrence of the southern African tracksites on fossilised dune surfaces in aeolianites is rare. Commoner substrates are solidified volcanic ash and undisturbed cave floor deposits. The prevalence of track preservation as natural casts on ceilings and overhangs, representing the infill layer, is also a globally rare phenomenon.

The possibility of shod hominins

Before moving on to the topic of ammoglyphs, the possibility that Middle Stone Age hominins on the Cape south coast sometimes made use of footwear needs to be addressed. If they did, the chances of such perishable materials surviving and being identifiable must be vanishingly small. Searching for trackway evidence of footwear use may therefore be the most promising way in which to investigate this possibility. In addition, there are interesting proxies: the Cape south coast contains some of the earliest records of bone awls and blades[39], which may have been used to fashion complex clothing, and possibly footwear[40]. Plausible motives could include the need to prevent lacerations from intertidal foraging on sharp rocks (a laceration may have been a death sentence), or protection against extremes of heat and cold.

The global track record of shod hominins is indeed sparse. In fact, the only three Middle Stone Age examples are from Europe. Two sites have been reported from France[41,42] and one has been reported from Greece[43]. More recent examples dated to around 5 000 years from North America, or from the Roman era in beach rock on one of the Greek islands, are hardly surprising. The problem is that identification of shod-hominin tracks may depend on an absence of features (such as toe impressions or a medial longitudinal arch), and may thus resemble tracks made by unshod hominins in soft or otherwise suboptimal substrates. The resulting understandable caution among researchers may then lead to a bias in which shod-hominin tracks are under-identified and under-reported. Convincing evidence for shod-hominin tracks thus needs to be sought on surfaces that preserve ideal or near-ideal substrate conditions, in which track outlines are suitably crisp, but such a level of preservation is not often seen in aeolianites or cemented foreshore deposits. Despite these challenges, the Cape south coast remains a choice region in which to search for hominin tracks, be they shod or unshod.

The candidate sites for shod-hominin tracks that have thus far been identified exhibit relatively small surfaces, without long trackways. The most promising site lies east of Kleinkrantz in the Garden Route National Park, but only two tracks are present (Figure 3.15a, 3.15b). They are crisply outlined with appropriate dimensions and shapes, and are unlike anything else we have encountered in 14 years of examining aeolianite and cemented foreshore surfaces. However, an impeccable standard of evidence would be required to make a plausible claim of Pleistocene shod-hominin tracks, and in this case a larger surface with a longer trackway would have been immensely useful.

Further searches are warranted, but our current approach also involves neo-ichnological experimental studies, which entail recording the details of shod human tracks being made in modern, unconsolidated beach and dune sand of similar composition to the ancient examples we have described. These would permit the development of criteria for the identification of shod-hominin tracks, as a baseline for further work.

Ammoglyphs

We coined the term 'ammoglyph' ('ammos' being Greek for 'sand') to describe a pattern made by ancient humans in sand, which is now evident in rock, in order to distinguish it from other forms such as petroglyph, dendroglyph, geoglyph and pictograph[44]. Appreciating the potential of ammoglyphs involves asking a question: did Middle Stone Age humans just leave their footprints on these surfaces of sand or did they leave other evidence of their activities, which might include signs of foraging, pattern creation, or messaging?

The capacity of the palaeosurfaces to record what happened on them is obvious, so the question is not whether or not such activities might have been preserved and are amenable to interpretation today, nor whether ancestral humans in this time and place had the capacity to achieve this. After all, the world famous discoveries of hashtag (chevron) patterns at Blombos Cave (west of Still Bay) and Pinnacle Point (west of Mossel Bay) attest to their ability to create palaeoart as engravings in ochre or as a drawing on a rock surface[45–47]. Instead, the question becomes whether the patterns that we have found in aeolianites provide an acceptable standard of evidence, and whether they demonstrate the existence of ammoglyphs to the satisfaction of others. In other words, have we adequately shown that a hominin 'signature' has been identified within the plethora of patterns that are apparent on these rock surfaces (including those made by wind, water, plants, invertebrates, reptiles, birds, mammals, and modern graffiti)?

We speculated on how much easier it might have been in the Middle Stone Age to use a finger or a stick to create a pattern in the sand, rather than to have to transport ochre many kilometres to a cave, and then laboriously create an engraving in it or a drawing with it. We knew that such evidence,

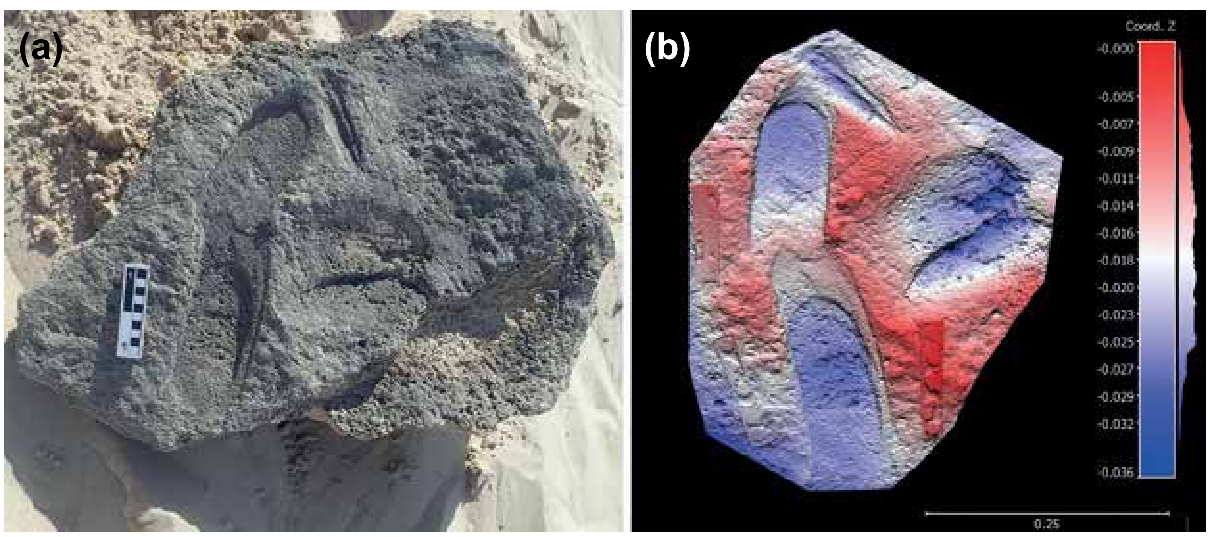

Figure 3.15 (a) Possible shod-hominin tracks east of Kleinkrantz; scale bar = 10 cm.
(b) 3D photogrammetry of possible shod-hominin tracks; horizontal and vertical scales are in metres.

if we succeeded in identifying it, would provide a previously undocumented form of Middle Stone Age human expression and activity, and we began to think of sand as a potential large-scale ancient canvas.

Works of art made on trees do not persist for as long as those made on surfaces of bone or shell, which in turn do not persist as long as those made on stone, and pictographs fade relatively rapidly when considered in the context of geological time. There is a bias in early art (protoart) that favours materials that endure over time, and in all likelihood such art (in the wider sense) was commoner in early human history than is apparent through the evidence that has been reported thus far[48]. While thoughtful observers have speculated that sand was probably the original medium for the creation of palaeoart, sand had not been considered capable of preserving such patterns—until now. Therefore, the potential addition of another medium through which the behaviour and creations of our distant ancestors could be interpreted cannot be overstated.

There are three main areas in which we have identified probable ammoglyphs: east of Still Bay, an area of concentration in the Garden Route National Park, and an area of concentration in the Goukamma Nature Reserve[44,49]. Some of the findings from the latter two areas are further described here. Firstly, there is a possible 'smoking gun': an association between tracks and patterns that were made in the sand, which we found in the Goukamma Nature Reserve. Clustered around what appears to be an impression of a left human forefoot, with a big toe and three further digits, are small circular depressions and eight linear sub-parallel groove features, some of which are surrounded by rims (Figure 3.16a,b). They are orientated in an approximate upslope-downslope direction, on a 25° inclined in situ aeolianite surface. The length of the longest groove is 39 cm. Two further partial tracks are present on different layers, along with further groove features, indicating a repeating pattern over time. It seems plausible that these features were created by a hominin using a stick or a finger, suggesting the possibility of foraging or messaging[36,44].

One of the most compelling examples was part of a cluster of four possible ammoglyphs within less than 40 metres of the Garden Route National Park coastline. Andre and Emily Brink, with their keen sense of shape and pattern, noticed it first: on the surface of a half-buried loose rock slab there was a deep groove feature forming an arc. As we exposed more of the rock it became evident that the arc formed part of a near-perfect, almost-complete circular feature, 30 cm in diameter, with a small depression in its centre that hinted at its origin (Figure 3.17a).

Just outside the circle were two oval, slightly depressed areas and between them there was a very slight break in the continuity of the circle. In one portion, the circular groove formed the edge of the rock surface and here we could measure that it was as much as 3 cm deep. Slight rims were evident beside sections of the circular groove and around the central depression.

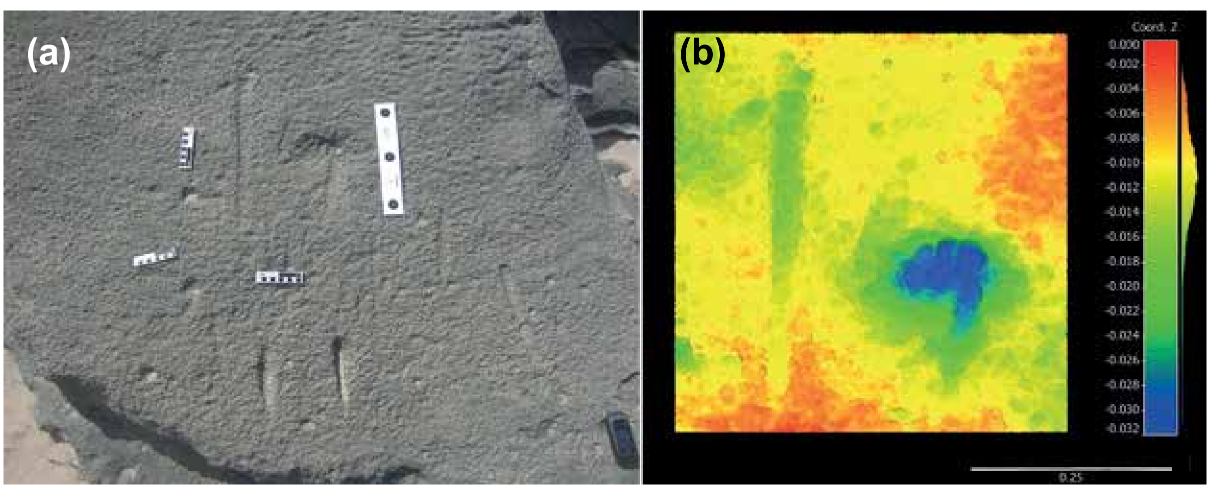

Figure 3.16 (a) A possible 'smoking gun': circular depressions and sub-parallel groove features clustered around a probable left hominin forefoot impression; scale bars = 10 cm and 30 cm. (b) 3D photogrammetry of the probable hominin forefoot impression, surrounded by groove features; horizontal and vertical scales are in metres.

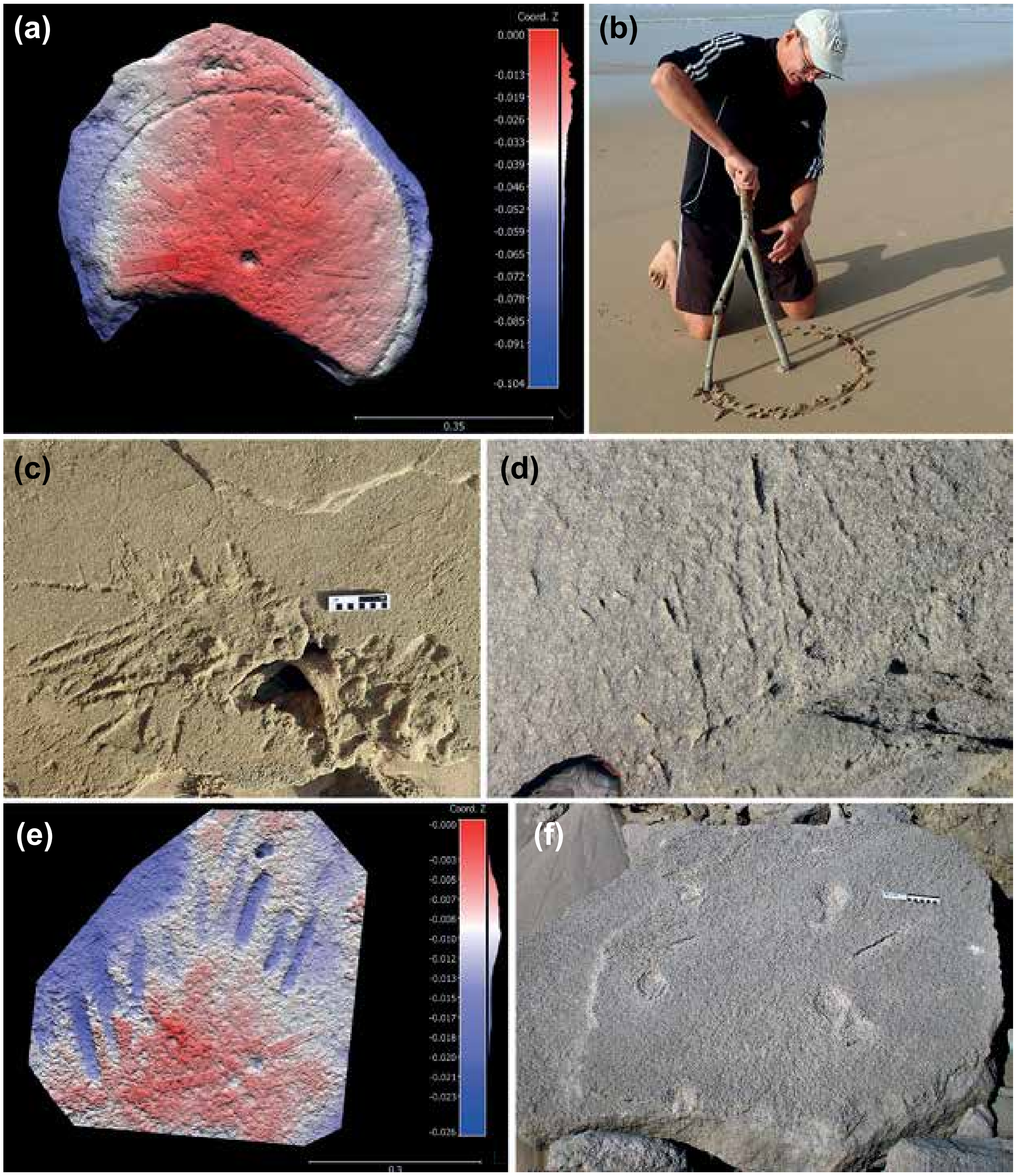

Figure 3.17 (a) 3D photogrammetry of the 'circle ammoglyph' in the Garden Route National Park; horizontal and vertical scales are in metres.
(b) Charles Helm demonstrates how the 'circle ammoglyph' may have been created.
(c) A possible ammoglyph in the Garden Route National Park: a complex arrangement of grooves, some of which are surrounded by rims, surround a central cavity and are flanked by possible tracks; scale bar = 10 cm.
(d) A cross-hatched pattern of narrow grooves, ~25 cm long, in the Goukamma Nature Reserve.
(e) 3D photogrammetry of a fan-shaped pattern of grooves in clusters in the Goukamma Nature Reserve; horizontal and vertical scales are in metres.
(f) The distinctive features beside these two possible hominin trackways in the Garden Route are two diagonally orientated grooves; scale bar = 10 cm + 6 cm.

Our interpretation was that a kneeling human probably created the features, using something like a forked stick, in the same way that a circle is created nowadays in geometry classes using a compass (Figure 3.17b). The slight discontinuity in the outline, between what we interpreted as probable knee impressions, may represent the area where the circle was started and finished (similar to what occurs frustratingly often when using a compass). The presence of rims established that the feature was created when the surface was composed of unconsolidated sand, and excluded a more recent origin. Other possibilities had to be considered, and a common cause of a circular groove in the sand is a frond, anchored to a central plant stem or root, repeatedly scraping the sand during windy conditions. This possibility did not seem consistent with our observations of such a deep groove and the absence of a central rhizolith.

Two other loose aeolianite slabs were lying just one metre and seven metres from the slab displaying the circular feature. Each of these had a circular depression on one side and a corresponding protrusion on the other. Both suggested possible hominin foraging activity. A further thirty metres away was another loose slab containing at least thirteen grooves in a complex arrangement (sometimes in a parallel pattern, sometimes in a radial pattern), with some flanked by substantial rims. These surrounded a central cavity, and occurred beside possible tracks (Figure 3.17c).

All of these rocks were being buffeted by high tides and were at risk of being buried by beach sand. Three of them were portable and were successfully recovered with the assistance of SANParks personnel. The Blombos Museum of Archaeology in Still Bay has them on exhibit.

Two sites, situated close to each other in the Goukamma Nature Reserve, suggest further possible ammoglyphs. The first, on a loose slab which is no longer identifiable, contained a cross-hatched pattern of narrow grooves that were ~25 cm long (Figure 3.17d). Beneath the cross-hatched area was a 15 cm long horizontal groove. This pattern resembled the hashtag (chevron) motifs described from Blombos Cave and Pinnacle Point surface[44–47].

The second site contained three surfaces on a large fallen block. Each surface contained a pattern of grooves in clusters, indicating repeated use of an area. The grooves in these clusters exhibited a fan-shaped pattern, with the middle groove typically being the longest (Figure 3.17e). Vertebrate claw-drag or scratch marks were postulated as an alternative explanation, and a definite conclusion as to their origin could not be reached.

Further suggestive evidence was found in the Garden Route National Park, sometime after a rockfall event created a large debris fan above the high water mark. One of the loose blocks which had slumped down a sandy slope contained two short, parallel trackways, with track dimensions and pace lengths consistent with a hominin trackmaker. However, the level of preservation was sub-optimal, and had the surface been identified immediately after the rockfall, more diagnostic detail would likely have been present. Nonetheless, two deep grooves could clearly be identified, orientated diagonally to the axis of the trackways, and parallel to each other. In each case the groove lay ahead of and to the right of the second track in a strikingly similar pattern (Figure 3.17f). A plausible interpretation would be of two humans using sticks while walking, creating deep linear depressions in the sand. Had the rock slab been larger and the trackways been longer, and had the relationship between tracks and grooves been repeated, the case for ammoglyphs would have been much stronger. Consequently, we had to accept that the evidence was tantalizing, but not incontrovertible. Since its discovery in 2018, this surface weathered steadily, with further loss of detail, before slumping into the sea. The surest way to demonstrate the prevalence of ammoglyphs is to find more of them. However, the human population in the region would have been relatively small at the time, and only a tiny fraction of Pleistocene dune surfaces that they may have left markings on are exposed. Perseverance is therefore required in order to identify further examples that might become exposed after storm surges, cliff collapse or landslide events. 'Citizen science' has an important role in such exploration and identification.

It is fortuitous and coincidental that the same region in which *Homo sapiens* developed numerous innovations in the Middle Stone Age happens to possess some of the finest aeolianites in the world. The remarkable result is that a Pleistocene canvas of sand as a medium of cognitive expression is amenable to our recognition and interpretation today. Humans on beaches and dunes today love creating patterns in the sand, and such activity has clearly been enjoyed for a long time. Until now there has been no reported evidence to indicate how far long ago in human history this may have occurred. The notion of ammoglyphs suggests something evocative: this activity may stretch all the way back to the Middle Stone Age on the Cape south coast. When we draw patterns on firm beach sand at low tide, knowing that the incoming tide will probably remove our creations, we may be indulging in something that is profoundly atavistic.

3.6 Graffiti

A threat is posed to these palaeosurfaces by the increasing presence of graffiti, which may deface or destroy fossil tracksites[50]. The relatively soft, friable nature of aeolianite surfaces makes them popular canvases for modern graffiti artists. A hammer and chisel can easily deface or destroy in a matter of seconds the trace fossil features that have been preserved and concealed for many thousands of years, and only recently been re-exposed. Regrettably, the prevalence of graffiti appears to be increasing. One of the most egregious examples in the Knysna area is near Brenton-on-Sea, where the sloping floor of a small cave is adorned with multiple examples of graffiti, to the point where the underlying trackways are deformed beyond recognition (Figure 3.18a). Sadly, the indications are that these may have been hominin tracks. At another site, etched graffiti occurs within a few metres of hominin tracks (Figure 3.18b).

In fact, it seems that the presence of fossil tracks and traces may even encourage the creative urge in the graffiti artist. One surface at Brenton-on-Sea that contains spectacular invertebrate burrow traces also contains deeply etched graffiti (Figure 3.18c). Another surface on a fallen slab in the Garden Route National Park not only contains etched graffiti, but has been daubed with an erosion-resistant black substance, and is therefore visible from a considerable distance (Figure 3.18d). Unfortunately the graffiti transects the only example we have observed thus far of a fossilised hare trackway.

Figure 3.18 (a) The sloping floor of a small cave at Brenton-on-Sea is full of etched graffiti, deforming the underlying possible hominin trackways beyond recognition. (b) Etched graffiti within a few metres of hominin tracks in the Goukamma Nature Reserve. (c) Spectacular invertebrate burrow traces at Brenton-on-Sea are marred by deeply etched graffiti. (d) Etched graffiti and an erosion-resistant black substance transect a hare trackway in the Garden Route National Park; scale bar = 10 cm.

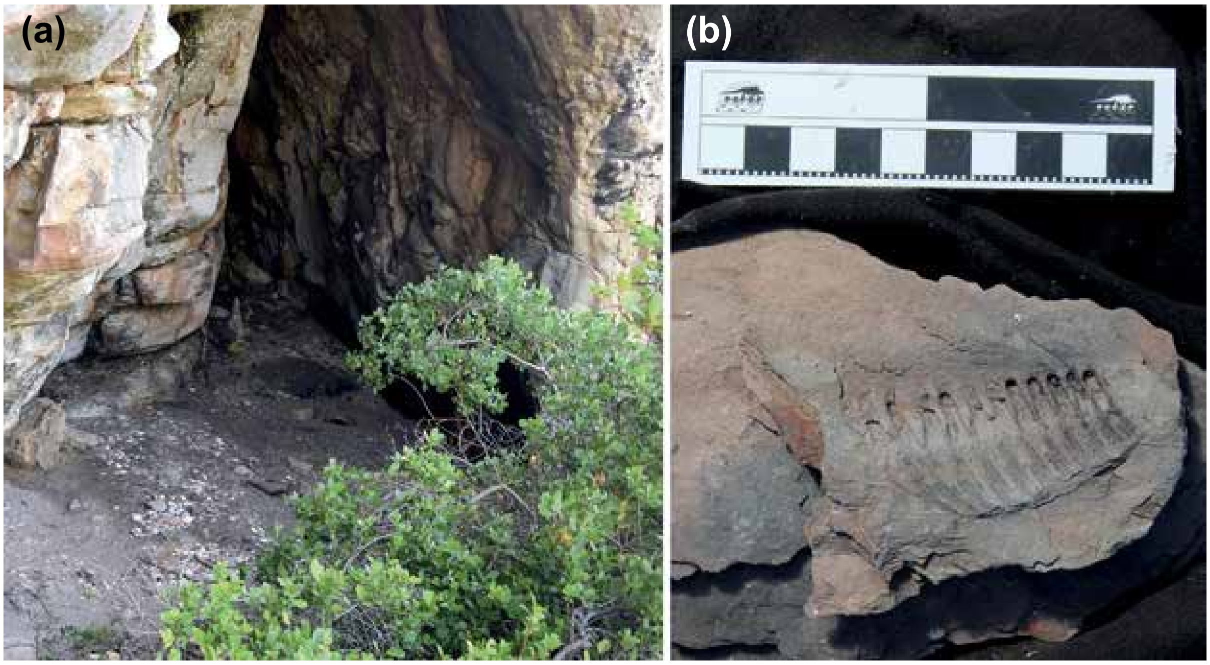

Figure 3.19 (a) "Cave 17" in the Robberg Nature Reserve. (b) The "Robberg" trilobite.

3.7 Back to the Palaeozoic and the Mesozoic

Everything discussed thus far has been of Pleistocene age. However, there are two evocative stories that deal with much older rocks, and they both involve interaction between humans and fossils. One involves a trilobite fossil found on Robberg, and the other involves a dinosaur tooth found beside the Knysna Estuary.

The Robberg trilobite

In 2013 Guy Thesen, a resident of Belvidere, was walking the main hiking trail at Robberg, and his perceptive eyes focused on something that others had missed. Spilling down the sandy, bushy slope onto the trail were what seemed to be the contents of a shell midden. Intrigued, Guy explored upslope, and came to a small shelter which had been labelled "Cave 17" during archaeological work in the early 1970s (Figure 3.19a). Cave 17 is situated about 35 metres above sea level, and commands an expansive view of Plettenberg Bay, the Tsitsikamma coastline, and the Tsitsikamma Mountains on the horizon. And on the floor of the shelter he noticed a trilobite fossil (Figure 3.19b).

The Robberg area mainly comprises rocks from three distinct time periods: Palaeozoic rocks of the Cape Supergroup, Mesozoic rocks of the Robberg Formation and the Pleistocene aeolianites that form the focus of our ichnological work. Cave 17 lies within Mesozoic deposits, but trilobites had already disappeared from the fossil record at the end of the Palaeozoic following the massive end-Permian mass extinction 252 million years ago. Furthermore, trilobites are not found in the Cape Supergroup rocks that occur on Robberg. To find the nearest exposures of the trilobite-containing Gydo Formation (early Devonian) in the Bokkeveld Group, one has to travel east to Keurboomstrand, a linear distance of 10 km or a walking distance along the current beach of 18 km. A subsequent surface survey of artefacts on the floor of Cave 17 suggested recurrent Middle Stone Age and Later Stone Age occupation, dating from a few hundred years to more than 40 000 years. The fragile trilobite was reposited with CapeNature—it measures 5 cm × 3 cm, making it easily portable. It is an external mould of a partially complete trilobite thorax belonging to the *Bainella* genus. The conclusion is inescapable: an ancestral human must have picked up the trilobite and transported it to what is now known as Cave 17 on Robberg. It is thus an example of a manuport, which is defined as an unmodified object collected, transported and deposited by hominins in a setting where it could not possibly occur naturally.

Such manuports typically possess something that aroused sufficient curiosity for them to be picked up and carried for some distance. They imply a kind of aesthetic geological awareness.

The Robberg trilobite manuport can be compared with two similar examples from the Cederberg. At Klipfonteinrand in the eastern Cederberg a complete *Burmeisteria* trilobite was excavated from Middle Stone Age deposits and would have been transported at least 400 metres. And at Vleiplaas a *Burmeisteria herscheli* trilobite was found in Later Stone Age deposits, and would have been transported at least 10 km[51].

The Knysna dinosaur tooth

In 2015 Brenton-on-Lake resident Ben Ingel, aged 13 years, went looking for kingfisher nests in the crumbly, yellow cliffs that fringe the western shore of the Knysna estuary near his home. He looked down and saw a block of rock that had fallen from the cliffs above. Sticking out of it was what he recognized to be a large dinosaur tooth (Figure 3.20a, b). Like many kids, Ben was familiar with dinosaurs, and even wondered if it might be the tooth of an *Allosaurus*.

It appears that Ben overcame some initial healthy scepticism from family members, and his grandfather put him in touch with Dr Rob Muir, a local geologist, who was immediately able to confirm that Ben had indeed found a dinosaur tooth. Ben and his grandfather, Vernon Rice, travelled with the tooth to the Albany Museum in Makhanda, where they were met by renowned palaeontologists Dr Rob Gess and Dr Billy De Klerk. Dr Gess was able to confirm that it was a tooth of a large carnivorous theropod dinosaur.

The tooth was donated to the Albany Museum by Ben and his grandfather. It measures 4.5 cm in length, and has the typical serrated edge of a theropod tooth (just like a steak-knife, hence good for tearing into flesh). It was the first dinosaur fossil to be found in the Knysna area, but was not a complete surprise to the palaeontologists, as a small coastal basin formed in the area in Jurassic-Cretaceous times, and filled with sediment. Those sedimentary deposits are known as the Brenton Formation, and are clearly of the right age for finding dinosaur fossils. The Algoa Basin, northeast of Gqeberha, has similar geology and has yielded a number of such fossils.

Ben's find was a clarion call to others to search for further dinosaur fossils in the area. A couple of years later a piece of fossil bone was picked up on the beach at Brenton-on-Sea following a storm. It was identified by Prof. Jonah Choiniere at the Evolutionary Studies Institute at University of the Witwatersrand as part of a tibia of an ornithischian dinosaur. It is likely that as cliffs are eroded, dedicated searching will find more dinosaur fossils in the Knysna area.

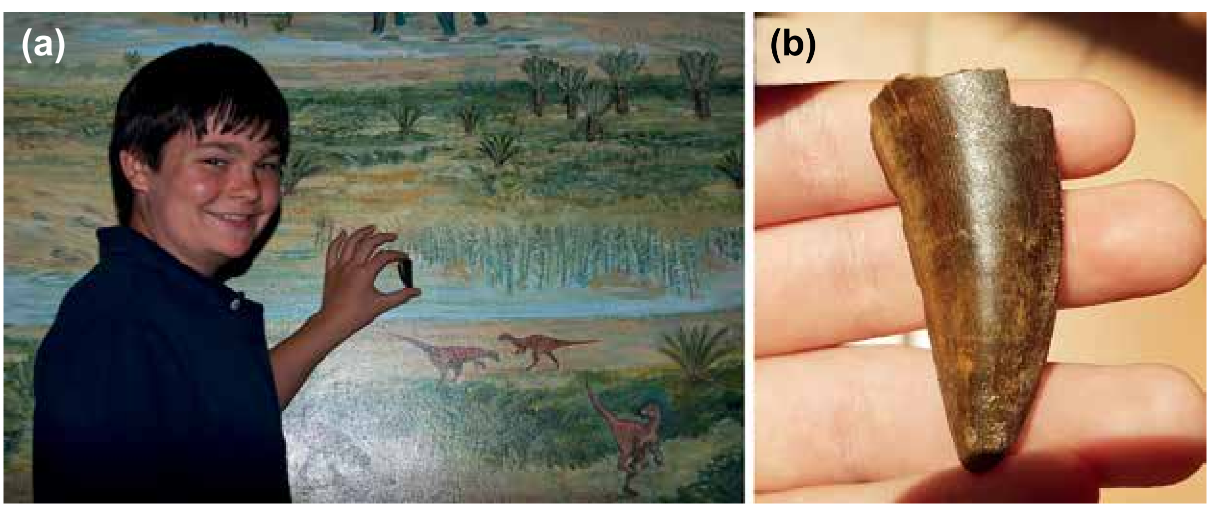

Figure 3.20 (a) Ben Ingel holding the theropod tooth that he discovered at Knysna. (b) Close-up of the theropod tooth.

3.8 Conclusions

Ichnology involves a mix of pattern recognition with an understanding of regional geology, palaeontology, archaeology and, perhaps most importantly, curiosity. In learning to read the rocks as accurately as possible, there is no substitute for experience, in what is an ongoing learning exercise. It helps to have a global ichnological perspective and understanding, e.g. the first crocodilian swim traces in Africa could be identified as a result of awareness of this trace fossil form from a different continent and hemisphere.

Our team is comprised of people with different specialisations (including anatomy, art, geology, archaeology, sedimentology, and conservation) and we collaborate and cooperate effectively. Sometimes, what appears insignificant to one, proves critical to another, and so we tell our stories, drawing on these diverse perspectives. Being able to look through this window into deep time, and then to contribute to the understanding of this remarkable area and its palaeoanthropology and palaeoenvironment, has been an enormous privilege. We think of each and every trace fossil site as a minor miracle of preservation, one that survived against great odds and then became apparent to us for our appreciative interpretation.

Trackways, in comparison to body fossils, have been likened to movies as opposed to photographs. They immediately convey a sense of motion and behaviour and are evocative for many, easily transporting us back to the time and place of the origins of our species, and forcing us to see our current challenges of climate change and rising sea levels in a broader perspective. It helps also that the sites are mostly incredibly appealing, untouched coastal settings that many of us who have grown up in the region often tend to take for granted. Furthermore, many of the tracks are eroded into aesthetically impressive forms that our research team refers to as 'works of art'. Ichnology has delivered numerous unexpected findings to the study of the Cape south coast. The list of regional, continental or global 'firsts' from this relatively short stretch of coastline is unexpectedly long, and includes hatchling turtles, crocodile swim traces, bigger-than-expected birds, elephant trunk-drag impressions, the largest tracks ever identified since dinosaurs became extinct, the only known probable seal traces, the tracks of extinct species, and insights not only into our ancestors' footprints but also their activities. With regard to ammoglyphs, we realized that the concept was novel and unanticipated enough that there were no rules to follow, yet profound enough that we had to create a set of rules for others to critique and fine-tune. (A giraffe tracksite east of Still Bay provides another example of a substantial Pleistocene range extension identified through our ichnological work, with major palaeo-environmental implications.)

The ephemeral nature of these sites means that our work is never done, and that there is a dynamic equilibrium between established sites slumping into the sea or becoming faded through erosion, and new sites becoming exposed. This creates an ongoing and exciting opportunity. Who knows, for example, when a sufficiently long trackway might be exposed that confirms our hypothesis that our ancestors on this coast were the first to use footwear?

We have become aware of many important sites through the observations and astute perceptions of people who love this coast, who keep their eyes open and report to us the things that they encounter. Tracking and pattern recognition are ancient skills. Refreshing these skills and putting them into practice on the rock surfaces of our magnificent coastline, with the accompanying opportunity to contribute to scientific understanding for the greater good, can be a worthy goal of good citizen science.

Acknowledgements

We are grateful to Alan Whitfield and his team for the invitation to contribute this chapter, and for ongoing support and encouragement.

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Railway line crossing the Knysna Lagoon (Photograph: © Duran De Villiers).

Chapter 4 : Evolution of the Knysna Estuary

Andrew Cooper & Andrew Green

4.1 Introduction

All modern South African estuaries have been shaped by the combined processes of rivers, waves and tides over many millennia. This has been accompanied by various phases of erosion and weathering on the one hand, and deposition of sediment on the other. As a result of differences in the local geology and the dimensions of the inflowing rivers, many different types of estuary exist around the South African coast[1]. Some are separated from the ocean for long periods by sandy barriers that open after storms or river floods, while others, including the Knysna Estuary are permanently open and experience regular tidalexchange with the sea.

In this chapter, we explore the evolution of the Knysna Estuary during the past 120 000 years. Although this is a comparatively short geological interval, it has seen sea level fall and rise again by over 130 metres. As it has done so, the land and subsea surface has been exposed and then reflooded and the shoreline has shifted from its modern position to the edge of the continental shelf, almost 80 km offshore at Knysna[2].

We begin by outlining the geology surrounding the Knysna Estuary and adjacent coastline, as well as that of the Knysna River catchment. We then describe the dramatic sea-level changes of the past 120 000 years that have controlled the position of the coast and estuary over that time period. These two sets of information lead on to an account of the estuary's position and morphology at key time intervals, leading up to and helping understand its contemporary geomorphology.

Figure 4.1 Aerial view of the Knysna Estuary from the east showing the coastal landforms that influence the current boundary for the estuarine system (Photograph: © Domossa).

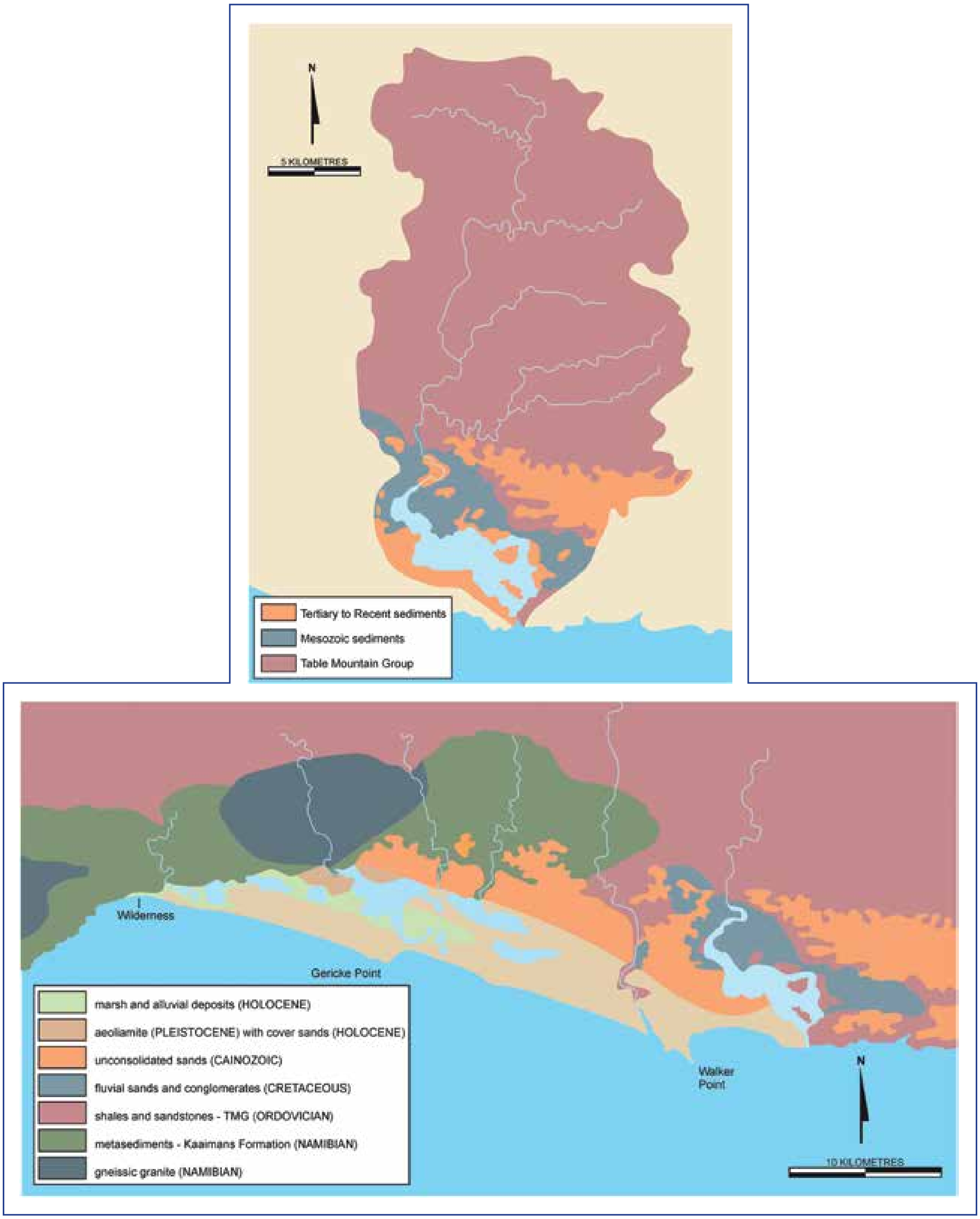

Figure 4.2 Geology of the Knysna catchment area[3] as well as the more immediate coastal zone[4].

Figure 4.3 Pebble and boulder conglomerate of the Enon Formation underlain by sandstone of the Kirkwood Formation on the north-western shore of the Knysna Estuary next to the N2. The conglomerate was probably deposited by the ancient Knysna River during the Cretaceous Period some 145 – 66 million years ago (Photograph: © Alan Whitfield)

Figure 4.4 Partly cemented relict coastal dune deposits together with pebbles and boulders of the Algoa Formation on the southern shore of the Knysna Estuary. This material is a possible source of estuarine sediments by water erosion and subsequent deposition in intertidal areas of the system (Photograph: © Alan Whitfield).

4.2 Geological setting

The solid geology around an estuary sets the context for the processes that formed and shaped the estuary itself (Figure 4.1). A rock's resistance to processes of weathering and erosion influences the shape of an estuary as it is affected by river currents, waves and tides, as well as subaerial weathering processes. Similarly, the geology of the inflowing river catchment influences the composition, texture (mud, sand, gravel) and volume of sediment being derived from landward sources. These factors are also at times exacerbated or ameliorated as the estuary changes shape and size in its response to the processes of sea-level rise and fall.

The coastal and nearshore marine environment is also a potential source of estuarine sediment and its geology and geomorphology too, exert an important influence on the estuary geomorphology. Estuaries formed along bedrock-framed coastlines are restricted to one position, whereas those in sandy type coastal plains may reposition themselves with floods and storms.

More than half of the 415 km² Knysna catchment area is underlain by rocks of the Cape Supergroup of the Cape Fold Belt. These are predominantly metamorphosed sandstones (quartzites) of the Table Mountain Group's Goudini Formation that are resistant to erosion, and yield small volumes of mainly sand-sized sediment. Mud is derived from some minor outcrops of Cedarberg Formation shales which yield a small amount of mud to the system.

On the north side of the modern estuary the geology comprises rocks of the Uitenhage Group (Cretaceous to Tertiary age, Figure 4.2). They include red-stained conglomerate and shales of the Enon Formation (that are exposed along the N2 road cuttings adjacent to the estuary), and sandstones of the Kirkwood Formation (Figure 4.3). Partly cemented relict coastal dune deposits of the Algoa Formation are present on the south bank of the estuary (Figure 4.4) and also inland of the Uitenhage Group outcrops.Those on the south bank of the estuary are viewed as a source of contemporary sediment supply to the estuary through direct erosion by the estuary channels and direct inputs by wind action[3].

Much of the town and parts of Thesen Island are underlain by colluvial (slope) deposits of Tertiary to Quaternary age[5]. Outcrops of lignite, termed the Knysna Formation, underlie unconsolidated cover sands (windblown sands) in the catchment at elevations between 220 m and 320 m above sea level. They have recently been ascribed a probable Miocene Age[6].

The Knysna Heads are composed of a type of Table Moun-tain Group sandstone, known as the Peninsula Formation quartzites. These are particularly well exposed on the Eastern Head (Figure 4.5). Intensely fractured and jointed zones, with a northwest-southeast orientation, intersect the quartzite and have been exploited by river channels over the millennia to form the channel now occupied by the modern day Knysna tidal inlet (Figure 4.5).

Adjacent to the Knysna Heads, the coastline is mainly rocky with few accumulations of sand (Figure 4.5). This is important for understanding the modern estuary geomorphology because it limits the amount of marine-derived sediment entering the estuary and prevents a sandy barrier from developing. The marine sediment that does occur along the coast has a high proportion of broken shells, derived from organisms that inhabit the rocky shoreline.

The seabed geology offshore of Knysna is dominated by the Agulhas Bank, much of which was subaerially exposed during low Quaternary sea levels (see below). The surface geology comprises shales and sandstones of the Table Mountain Group[7], covered by a nearshore wedge of sand that thins seaward and extends to approximately 100 m depth in places. Interspersed among the sandy sediments are palaeo-dunes that have been cemented in place and which mark older shorelines formed when sea level was lower than present. On the outer shelf, the surface geology has been interpreted as limestones of the Wankoe Formation[8].

4.3 Sea level change.

About 2.5 million years ago the earth entered a geological Epoch known as the Quaternary. This Epoch has been characterised by alternations between cold (glacial) periods and warm (interglacial) periods. Over the past 800 000 years these have alternated quite regularly on roughly 100 000 year cycles; glacial conditions last for about 100 000 years and warm interglacial conditions for 10–15 000 years. During glacial periods, much of the Earth's water is stored in large polar ice caps that extend far beyond their current limits. During these periods, the amount of water in the oceans is much reduced so that sea levels drop to more than 100 metres below the present. In the warm interglacial periods (including the one we are presently in) the polar ice caps melt, releasing water into theoceans and causing sea levels to rise. During most interglacial periods, sea level has been close to, or a few metres higher than the present level. This chapter is concerned with sea-level changes (Figure 4.6) since the last interglacial (about 125 000 years ago)

Figure 4.5 View of the Knysna Heads towards the east showing the shale, sandstone and quartzite rocks that encompass the channel (Photograph: © Hongqi Zhang).

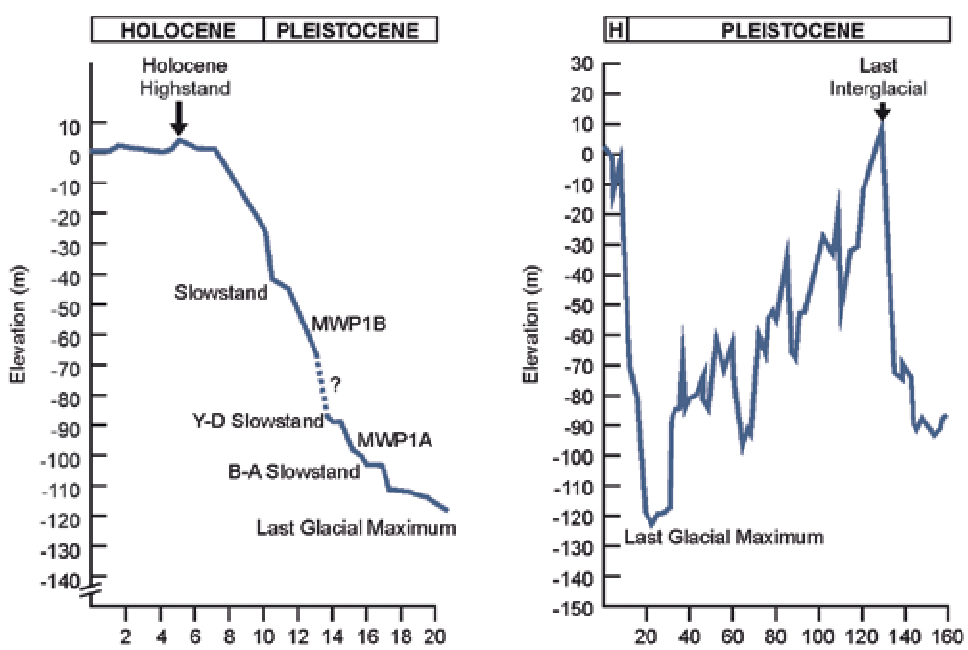

Figure 4.6 Generalized pattern of sea-level change since the Last Interglacial (right) and detailed view of changes since the Last Glacial Maximum (left). Note the periods of slow sea level rise (slowstands), phases of rapid rates of sea level rise during Meltwater Pulses (MWP 1A and 1B), and the Holocene highstand of sea level.

during which the Knysna Estuary achieved its present configuration.

In the last interglacial, sea level was higher than the present for about 20 000 years, during which time it reached a maximum of 8 m above the present around South Africa[9]. Because of this relatively long period of comparative stability in sea level, well-developed shoreline features and deposits were formed. In many locations in South Africa, shoreline and estuarine deposits from this time are preserved close to the modern coast but at higher elevations than present.

After the last Interglacial, the earth entered a 100 000 year-long glacial period during which sea levels were consistently lower than present, reaching a minimum of 130 m lower than present during the peak of the glaciation, known as the Last Glacial Maximum (LGM) just over 20 000 years ago. During this glacial period, sea-level fluctuated up and down, but the long-term trend was downward. It was a period of relatively cool, moist climate[10]. River channels cut into the surrounding rocks, eroding accumulated sediments and forming valleys that extended seawards for tens of kilometres beyond the modern shoreline. These incised bedrock valleys became the focus of ancestral estuarine conditions. For example, under the modern Knysna Estuary, drilling for the railway bridge did not reach bedrock despite almost 80 ft (24 m) being drilled[11] (Figure 4.7). This indicates the presence of a deep river valley in which the modern Knysna Estuary now resides.

The earth began to warm once again after the Last Glacial Maximum and the polar ice caps began to retreat. The melting ice caused ocean water levels to increase gradually before reaching (and for a short time exceeding) the present. The rate of sea-level rise during this period was not continuous and was punctuated by several periods of rapid sea-level rise, known as Meltwater Pulses (MWPs), when large volumes of water were added to the world ocean in comparatively short periods of time. These were separated by periods of slower sea-level rise or slowstands of sea level. Rates of sea-level rise during meltwater pulses were very high. For example, MWP1A involved ~16 m rise (from -100 to -84 m) in sea level between 14 600 and 13 800 years ago (20 mm yr^{-1}) and during MWP1B between 11 500

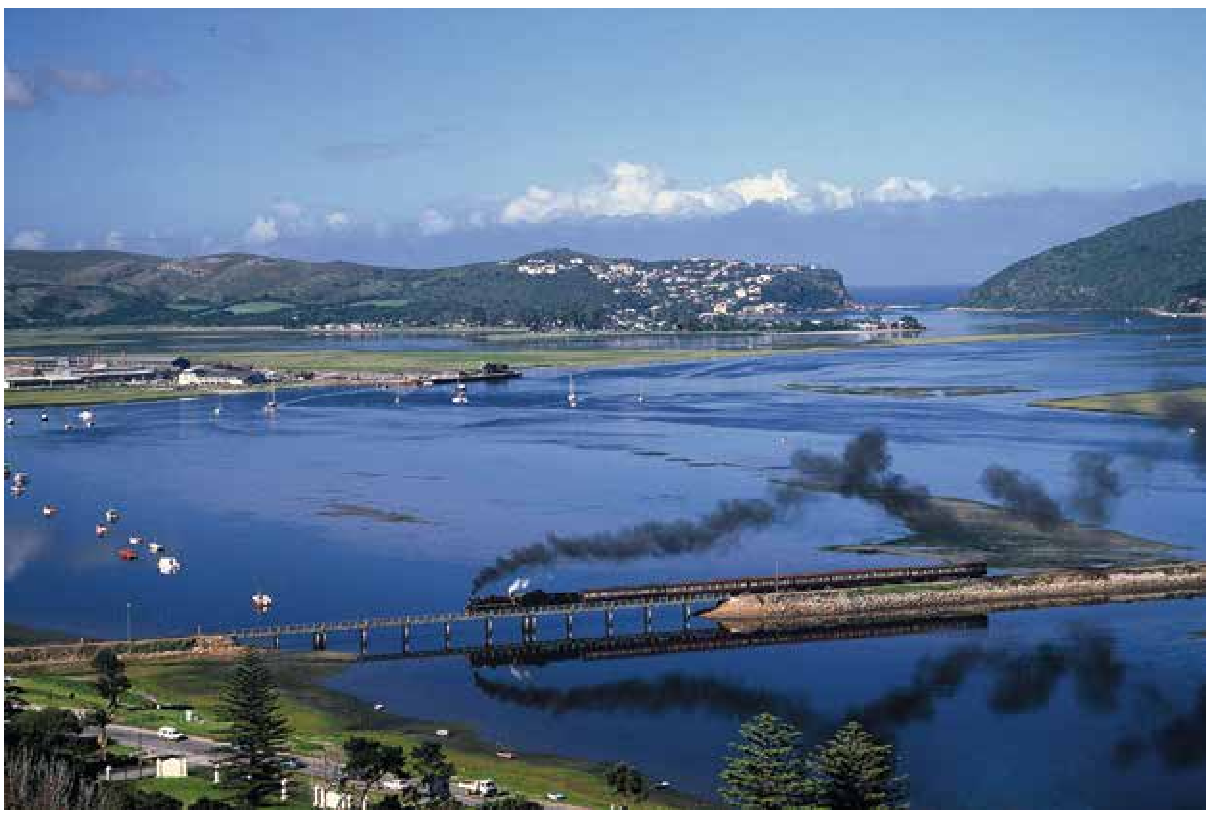

Figure 4.7 Drilling for the railway bridge pylons to 24 m depth failed to reach bedrock of the valley in which the Knysna Estuary is situated (Photograph: © Heinrich Von Horsten).

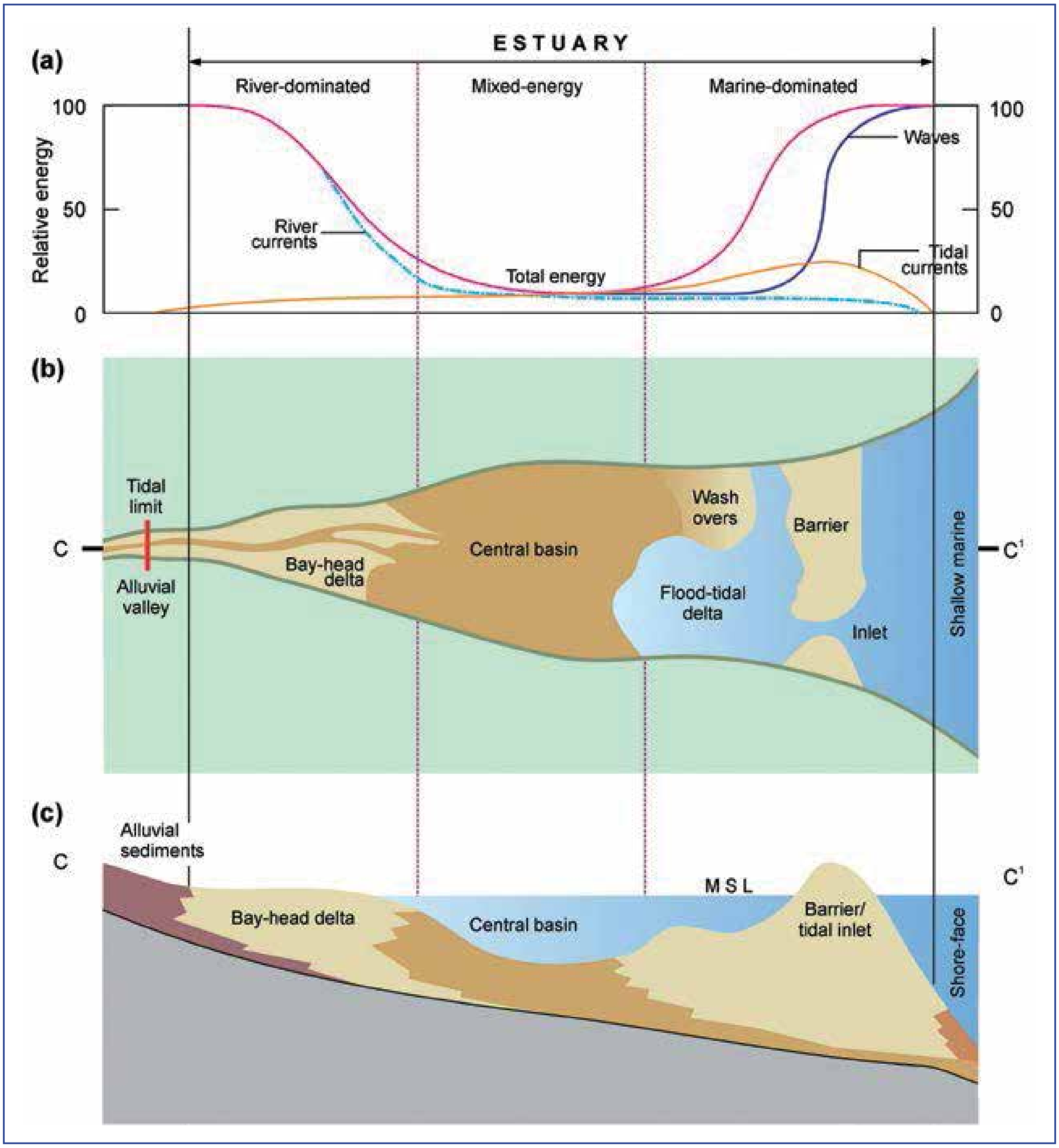

Figure 4.8 Conceptual diagram showing general estuary morphology and primary drivers of sedimentary characteristics[17].

to 11 200 years ago, sea level rose 18 m from -58 to -40 m (60 mm yr^{-1}). These alternations of fast and slow sea-level rise are also broadly reflected in palaeo-temperature records from South Africa[12].

About 11 500 years ago, the most recent geological interval the Holocene) began. It seems to have been preceded by a period of very slowly rising sea levels such as recorded in Maputo Bay[13]. The early parts of the Holocene saw a rapid rise in sea level which, in South Africa, reached the present about 7 500 years ago. Since then, it has fluctuated within a few metres of the present. Periods of higher sea level during the Late Holocene are referred to as the Holocene highstand, which is still poorly defined but seems to have peaked at 3 – 4 m above present about 5 000 years ago, before falling to the present[14]. Between 8 000 and 4 500 years ago evidence from Uitenhage suggest that temperatures were 2 – 3°C warmer than present[15].

Tide gauge measurements indicate that sea level is currently rising around the South African coast at rates of around 3 mm yr^{-1}. Based on new modelling studies, Allison et al.[16] suggest that by 2 100 sea level rise (relative to 1986 – 2005) in South Africa will be around 0.5 m (0.25 – 0.8 m) if greenhouse gas emissions are reduced, or around 0.85 m (0.5 – 1.4 m) under the worst case emissions scenario. These increases are around 10% higher than the global average.

4.4 Knysna Estuary evolution

Introduction

The surrounding geology and sea-level change are the primary influences on evolution of the Knysna Estuary since the last interglacial period. In any estuary, the resistance or susceptibility to erosion and weathering of the various bedrock types determines the shape of the bedrock valley in which the estuary forms. In turn, the geology of the catchment and adjacent coast, influnce the nature and volume of sediment that enters the estuary. During falling sea levels (regressive conditions), shorelines move seawards and river valleys are incised (sediment is eroded and valleys become deeper). During rising sea levels, shorelines migrate landwards, river channels are flooded by seawater and deposition of estuarine sediments takes place.

There are, however, some further subtleties; slower sea-level rise is associated with higher rates of sediment accumulation in estuaries (causing shallowing), while adjacent ocean shorelines are exposed to erosion by waves. High rates of sea-level rise on the other hand, usually promote estuary flooding and deepening, and the stranding of previous shoreline deposits (including old estuaries) on the seabed. Sometimes estuaries are initially deep when they are flooded and then progressively fill in over time (Figure 4.8). If sediment is available in the marine environment a sandy barrier may develop and, next to it, the reversing tidal flows may deposit ebb- and floodtide deltas. At the head of the estuary, the inflowing river deposits sediment as a bayhead delta (Figure 4.8).This creates three major divisions: a shallow sandy inlet area, a deep central basin where muddy sediment accumulates, and a shallow upper estuary of river-derived sediment (often sands and gravels). Over time, the bayhead delta extends downstream and flood tide deltas may extend upstream, filling the estuary with sediment (Figure 4.8). Additional sediment can be delivered to the estuary by wind-blown sand. The Knysna Estuary lacks a sandy barrier but has a flood delta and poorly developed ebb delta. The central basin has been infilled with wind-blown sand that is incorporated into intertidal and subtidal sand bodies (see below).

An over-riding geological influence on the evolution of the Knysna Estuary itself is the strongly contrasting geological setting in which it finds itself between high and low sea levels. During periods of high sea level, such as the present, the coastline is steep and rocky and the river catchment is small but steep. During low sea levels the river channel extends across the Agulhas Bank, enlarging the catchment and elongating the river. The topography on the Agulhas Bank is much gentler and the bedrock significantly more erodible. Consequently, when sea-level is low, the estuary occupies a coastal plain setting, more like the modern coastal plains of northern KwaZulu-Natal and Mozambique than the modern southern Cape coast. These influences are discussed below as we reconstruct the evolution of the estuary.

Last interglacial highstand

During the last interglacial when sea level was up to 8 m higher than present, the Knysna Estuary occupied the same position as it does now. The tidal inlet would have remained in a similar position to that of today, anchored by the bedrock heads. The steep sides of the estuary mean that it did not expand laterally to a great extent (Figure 4.9), although an erosional terrace at 4 – 6 m above modern sea level is developed along parts of the western shores of Knysna Estuary[18]. On parts of this terrace, estuarine deposits are locally preserved and contain a warm water molluscan fauna. Radiocarbon dates of over 40 000 years from these shells are regarded as minimum ages and the deposits most likely correspond

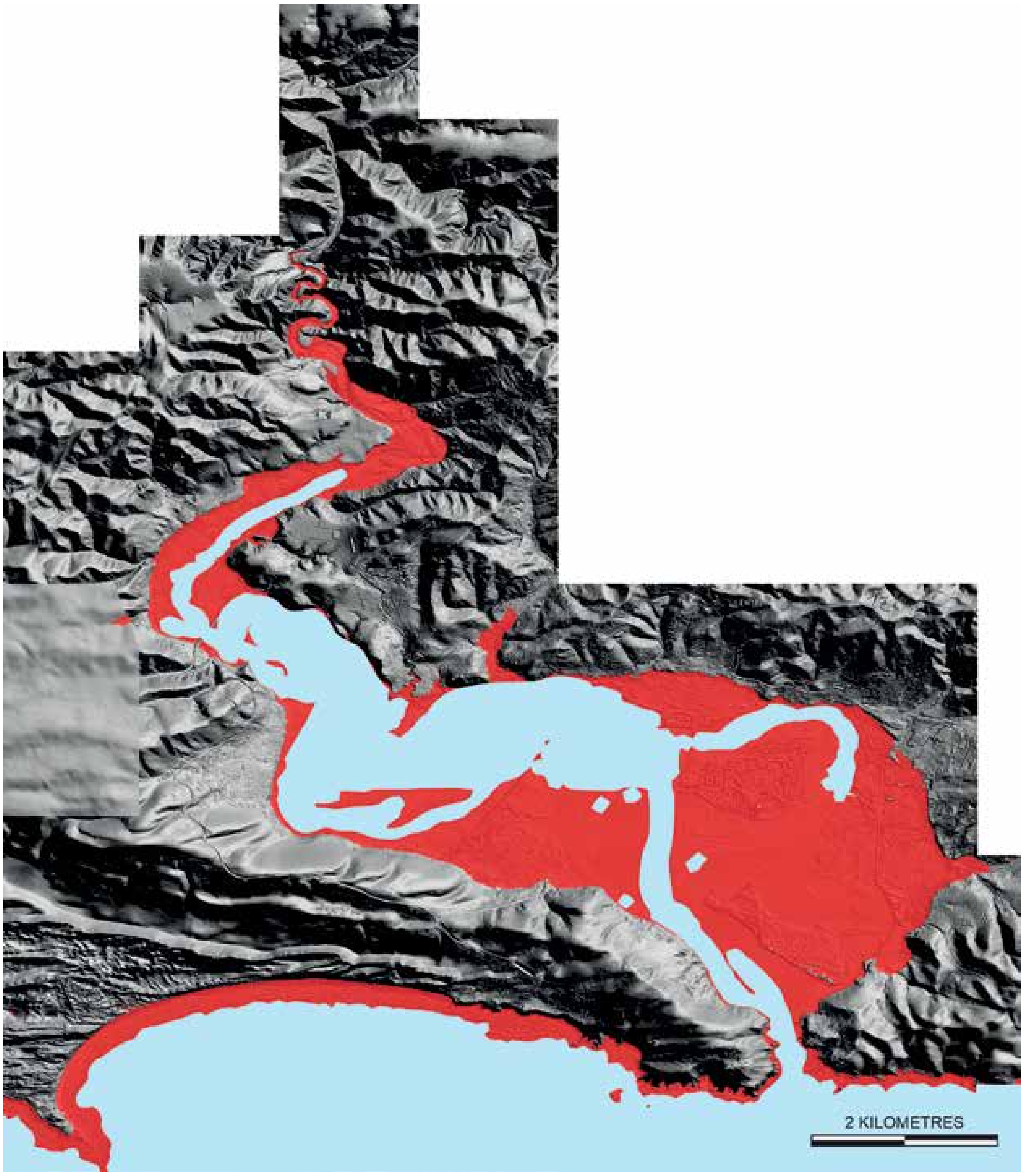

Figure 4.9 Likely extent of the Knysna Estuary (shaded in red) during the last interglacial (120 000 years ago). The outline is based on the 8 m contour from a high-resolution (LiDAR) survey of the estuary (courtesy of the Knysna Municipality). Notice that the outline is not much different from the present high-water margins of the estuary.

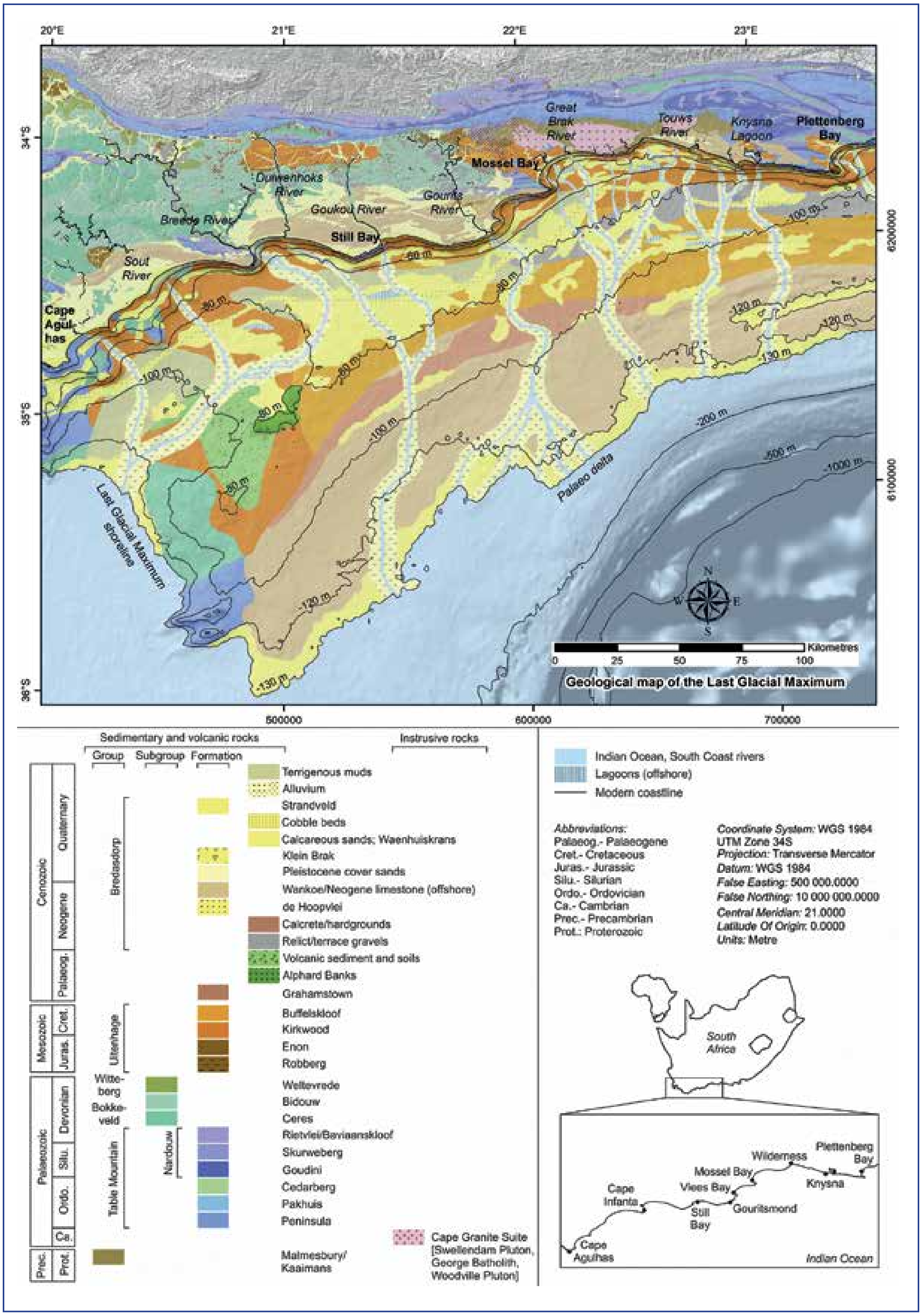

Figure 4.10 Last glacial maximum shoreline and exposed Agulhas Plain, with inferred positions of river courses across that plain[8].

to the high sea levels of the warm Last Interglacial period. The paucity of preserved estuarine sediments from this period preclude a more detailed palaeo-geographical reconstruction other than that provided here. The sediments that accumulated during this time period would have been eroded by subsequent sea level falls as the river scoured its channel downwards and laterally.

Falling sea levels

When sea levels fell after the last interglacial, the area currently occupied by the current Knysna Estuary would have been a narrow and steep sided upland river valley. Sea levels fell and remained below the present after about 100 000 years ago and experienced a series of minor oscillations as sea level fell to its lowest level about 20 000 years ago. For this period, the shoreline fluctuated back and forth across the palaeo-Agulhas Plain, much of which was exposed as dry land. Some former shoreline positions from this (and earlier periods of lower sea level) are preserved as outcrops of cemented dune (aeolianite) on the seabed[4,8].

During falling sea level intervals, the channel of the Knysna River was progressively incised into the underlying bedrock, creating a deep bedrock valley. Short-lived (ephemeral) estuarine conditions developed at the seaward edge of the incised valley during short-lived rises in sea level when the lower reaches were temporarily flooded with seawater. Each subsequent fall in sea level, however, would have likely scoured any estuarine sediments that accumulated during these short-lived estuarine conditions.

Last Glacial Maximum

At the Last Glacial Maximum (LGM) when sea level was about 130 m lower than present, the shoreline was about 80 km seaward of its present position and the whole Agulhas Bank was exposed as a coastal plain[8] (Figure 4.10). Average temperatures in South Africa were 5 to 6° C lower than present[19]. The shoreline at that time was framed by a topographically much lower landscape, characterised by limestone Fynbos[20] on a gentle substrate of Wankoe Formation Limestone. The courses of many rivers combined as they traversed the coastal plain but the limited published seabed investigations hint that the channels of the Knysna River may not have merged with any of the neighbouring rivers[8] (Figure 4.10). This is intriguing, given that the small catchment area of the Knysna River suggests it would be susceptible to convergence with other, larger rivers as a tributary.

The nature of the palaeo-Knysna Estuary at this time can only be speculated upon as it has not been specifically investigated. Its catchment, and any rivers with which it may have coalesced, was much bigger and its overall gradient was lower as the river crossed the wide, gently sloping Palaeo-Agulhas Plain. However, sediment would have been scoured from the bedrock valley and carried over the shelf break and deposited in deep water[21]. Rivers were much longer, and had they coalesced, they may have formed deltas or discharged into lagoons depending on the local topography. The Gourits River to the west appears to have formed a large delta at this time, with several large distributary channels[8] like the modern Zambezi River delta. Given the lack of topographic constraint, the LGM estuary would likely have been a wider and shallower system, forming a feature not unlike the larger St Lucia, Sibaya and Kosi lake systems on the northern KwaZulu-Natal coastline[22].

Rising sea levels

As sea levels rose after the Last Glacial Maximum (Figure 4.6), the shoreline migrated landwards, often at variable rates, and waves progressively eroded the seabed and coast as it was drowned by rising waters, thus preserving very little of the former shorelines. The shoreline position and approximate position of the estuary during these intervals can be assessed by reference to the modern seabed bathymetry (Figure 4.11). The incised river channel would have been partly sheltered from wave erosion and palaeo-estuarine and river sediments were probably preserved in the former incised valleys[23]. Depending on the rates of rising sea level, these old estuaries could be preserved in place on the seabed, linked to the melt-water pulses that occurred during the late Pleistocene and the Holocene[24]. Conversely, very slowly rising sea levels would produce extensive barrier dunes that fronted the estuary and impounded widespread estuarine waters in the back barrier; features not evident in the bedrock-framed Knysna Estuary of today.

Bølling-Allerød and MWP1A

The Bølling-Allerød period occurred from about 14 690 to 12 890 years ago and was marked by warmer and moister conditions compared to the LGM[25]. Sea levels during this period rose very slowly from a stillstand at ~100 m water depth (Figure 4.11). This resulted in the widespread development of prominent shorelines along the coast of southern Africa[24]. The warm, moist conditions likely drove the development of substantial coastal wetlands and large,

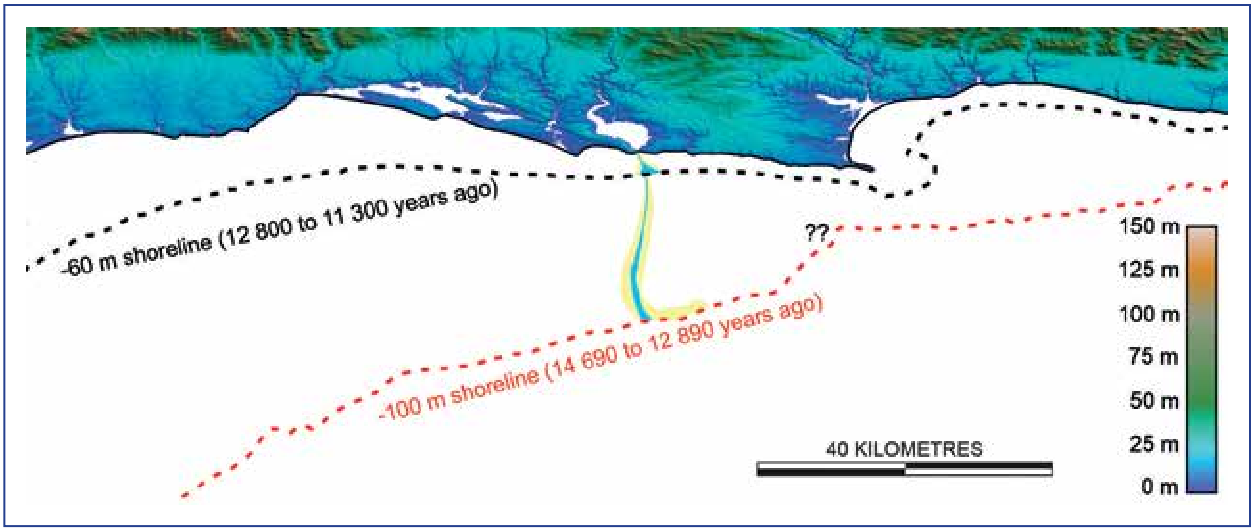

Figure 4.11 Map showing the probable position of palaeo-shorelines and the possible Knysna palaeo-estuary location at key intervals during the rise of sea level after the Last Glacial Maximum.

well-vegetated estuaries, impounded behind the barrier dunes of a sandy coastline[26]. These were promptly drowned in place by the rapid flooding from MWP1A, when sea levels rose by ~20 m over a 300 – year period. This caused such rapid shoreline migration that waves did not erode the shoreline entirely and left it stranded on the seabed. It is likely that any estuarine deposits formed would remain in place on the seabed within the palaeo-incised valley; however, geophysical investigations would be needed to confirm their existence.

Younger Dryas

The Younger Dryas period (~12 800 to 11 300 years ago) was a globally cold period for which there is evidence of cooling in South Africa[19] within the overall warming phase after the Last Glacial Maximum. It was also a period when the rate of sea-level rise slowed and a prominent shoreline developed along the South African coast at a depth of approximately 50 – 60 m below present sea level (Figure 4.11). Like the Bølling-Allerød period, sandy shorelines formed, however the generally cool and dry conditions probably helped foster the development of substantially larger coastal dunes, behind which waters of the palaeo-Knysna Estuary may have been impounded. In this case, lacking the rocky headlands of the modern Knysna Estuary, the system may have resembled the modern Wilderness lakes, where there are various forms of connections to the ocean; these would have fluctuated in time and space[27]. These dunes are preserved as aeolianites on the seabed between depths of 60 to 80 m.

The Younger Dryas shoreline and any estuarine materials were subsequently drowned during a very rapid rise of sea level, known as Meltwater Pulse 1B, where sea levels rose by 13 m in just 300 years.

Holocene sea-level rise

After the Younger Dryas period, the earth entered a new geological epoch, known as the Holocene that persists to the present day. During this time, sea level completed its 40 m rise to the present and the incised valley of the Knysna River would have seen development of estuarine conditions as it was rapidly flooded. Once sea levels stabilised, around 7 500 years ago, the estuary then began to take its current form and was progressively filled by fluvial, wind and marine-derived sediment. The position of the tidal inlet again become fixed by the Knysna Heads as it had been during the last interglacial period.

Superimposed on this general sea-level rise are several smaller peaks in mid-Holocene sea level that again acted to reshape the estuary margins and affect the estuary fill. Evidence of a higher than present sea level is present around the Knysna Estuary and adjacent coast. The most extensive raised beach is at +3 to +4 m. It underlies Lower Old Town, the low areas east of the estuary, Leisure Isle and Thesen Island, and parts of Belvidere[28,29]. Leisure Isle itself is probably an emergent flood-tidal delta (formed by the deposition of ingressing sediment on the floodtide) which was originally deposited when sea level was higher than now. The slight fall of the sea to its present level transformed the intertidal flood delta into an island.

An exposure of a palaeosol or ancient soil, peat and in-situ tree stumps in the intertidal zone on the western shore of the estuary suggests that sea level dropped slightly below the present for a short period. Radiometric dates from the in situ roots and palaeosol material, respectively, place this lower sea level in the 13th to 16th century AD[30].

4.5 Contemporary estuary geomorphology and sediments

The comparative sea-level stability for the past 7 500 years has allowed a mature estuarine morphology to be reached. The modern estuary is developed in a wide basin surrounded by steep hills (Figure 4.12). These consist of Quaternary aeolianite (cemented dunes) on the southern bank and Cretaceous sedimentary rocks on the northern bank[31]. The estuary covers an area of 1 827 hectares at high water spring tide[32]. It is permanently connected to the sea by the 230 m wide tidal inlet[5] bounded by the resistant sandstone rocks that form the Knysna Heads. The unusually wide estuary basin reflects the comparatively soft and more easily erodible sedimentary material (Figure 4.13) in which it forms, as compared to the catchment comprising much harder rocks of the Table Mountain Group.

Twice per day the estuary experiences the entry and exit of up to 19 million m^3 of seawater through this inlet[32]. This exchange of water creates strong tidal currents that flow landward on the rising tide and seaward on the falling tide. The currents are strongest in the tidal inlet (Figure 4.12) and as the jet of water spreads out in the estuary, it slows down, depositing any sand that it has carried as flood tide deltas. These are very well developed in the Knysna Estuary adjacent to Leisure Isle and are composed of medium-grained sand with up to 25% broken shell fragments, indicating a marine origin[3]. The delta surfaces are well exposed at low tide. The ripples on the surface of these tidal deltas take many forms but they tend to be asymmetrical in cross section, i.e. one side is steeper than the other. The steep side indicates the direction in which the ripple is moving when the tidal currents are operating.

The currents during the ebbing tide are deflected by the flood tide deltas, and flow around them in what are known as ebb channels. These tend to be the deepest parts of the estuary that are never entirely dry, even at low tide. The bed of these channels contains ripples that are orientated toward

Figure 4.12 View of a flood tide entering the Knysna Estuary. Note the steep hills surrounding the estuary which give it the characteristic shape that has remained unchanged for thousands of years (Photograph: © Richard van der Spuy).

Figure 4.13 Easily erodible fringing sedimentary material comprising mainly sand and pebbles, constituting the main base of the current Knysna Estuary. See also Figure 4.16 that was taken very close to this picture (Photograph: © Alan Whitfield).

the ocean and the ebb- and flood-directed currents dominate in distinctive zones. As the ebb current flows seaward through the tidal inlet, it too decelerates and deposits any sand that it has carried. In many estuaries this creates an ebb tide delta on the ocean side of the inlet. Reddering & Esterhuysen[3] suggested that a sand shoal found just seaward of the inlet is a poorly developed ebb delta whose extent is limited because of a paucity of sediment and the high wave energy of the open coast.

Landward of the tidal inlet and its tidal deltas, the middle part of the estuary is dominated by extensive intertidal flats, dissected by sinuous subtidal channels. The large intertidal area is unusual for South African estuaries, which are more commonly narrower and deeper in the middle reaches, a factor of the erodibility of the rocks in this area having created a wide and shallow basin for the estuary to now occupy (Figure 4.15). The intertidal areas are mainly composed of fine sand (Figure 4.16), with only local accumulations of mud. The source of the fine sand in the mid-estuary is wind-blown from the Brenton dune and weathered aeolianites that occur at mean sea level[3]. The paucity of mud in this area compared to typical estuarine basins (Figure 4.8) is linked to the lack of mud in the rocks of the estuary catchment.

The intertidal areas are colonised by the seagrass *Zostera*, suggesting low sedimentation rates (otherwise the *Zostera* would be smothered). The high intertidal and low supratidal areas are colonised by salt marsh vegetation which helps trap fine suspended sediment. The surface mud deposits in the estuary are mostly associated with human intervention and are very visible next to the causeway between Knysna and Thesen Island, the embankment of the N2 road bridge and adjacent to the railway bridge embankment.

The inflowing Knysna River has a comparatively small catchment area, dominated by hard, resistant rocks of the Cape Supergroup. In the narrower, upper estuary, bottom sediment is a mix of medium sand and mud (Figure 4.17 and 4.18), derived from the inflowing river and predominantly transported during river floods[3]. A minor component of the estuary sediment here is composed of gravel and small pebbles and old flood deposits of rounded pebbles are exposed in the estuary banks. In the upper estuary the saltmarsh adjacent to the tidal flats is dominated by the reed *Juncus*, reflecting the reduced marine influence.

Based on the relative stability of the Knysna Estuary landforms, Reddering & Esterhuysen[3] regard it as receiving only low amounts of sediment

Figure 4.14 Modern geomorphological features in the Knysna Estuary Lagoon. (a) An oblique aerial view looking seaward toward The Heads. In the foreground, the shallow sand bodies are parts of the flood-tide delta, deposited as incoming tidal currents weaken when they emerge from the constricted inlet.
(b) These elongate sandbars in the middle estuary are affected by a mix of fluvial and tidal currents. They are composed of fine sands, believed to be mainly derived from wind-blown and water-eroded sands of the Brenton dune to the seaward side of the estuary (Photograph: © Duran De Villiers).

Figure 4.15 Aerial view of the Knysna Estuary from the east showing the broad basin in which the estuary is located (Photograph: © Domossa).

Figure 4.16 Aeolianite-derived fine sand and pebbles on the southern shore of the Knysna Estuary (Photograph: © Alan Whitfield).

from the ocean and river sources. Its relatively deep channels were ascribed to this low sedimentation status. Nonetheless, high rainfall events and associated river flooding do deliver additional sediment to the estuary from time to time. Management of the dune and aeolianite areas exposed on the south side of the estuary is, however, regarded as essential to ensure that it does not serve as a source of enhanced sediment supply, causing the estuary to shallow.

Human interventions have, however, caused localised sedimentation in the estuary with recent mud accumulations adjacent to bridge embankments. A plaque at the Old Drift (about 300 meters above the Red Bridge) (Figure 4.20) commemorates a stinkwood slipway built by George Rex in 1826. In 1831 a 140-ton Brig, also made of stinkwood, and named '*The Knysna*', was launched. This vessel would have required a few metres of water but today one can wade across the estuary at this point. This reflects some sediment accumulation at this point.

Human alteration of the estuary's geomorphology is also evident in the dredging of the canal estate on Thesen Island (Figure 4.15), construction of slipways and jetties and in armouring of the shoreline to protect roads and houses (Figure 4.19). Armouring not only changes the composition of the estuary shoreline, but it modifies waves and currents so that their energy is dissipated elsewhere in the estuary. In the longer term, armouring inhibits the estuary's natural ability to adjust its shape in response to changes in sea level.

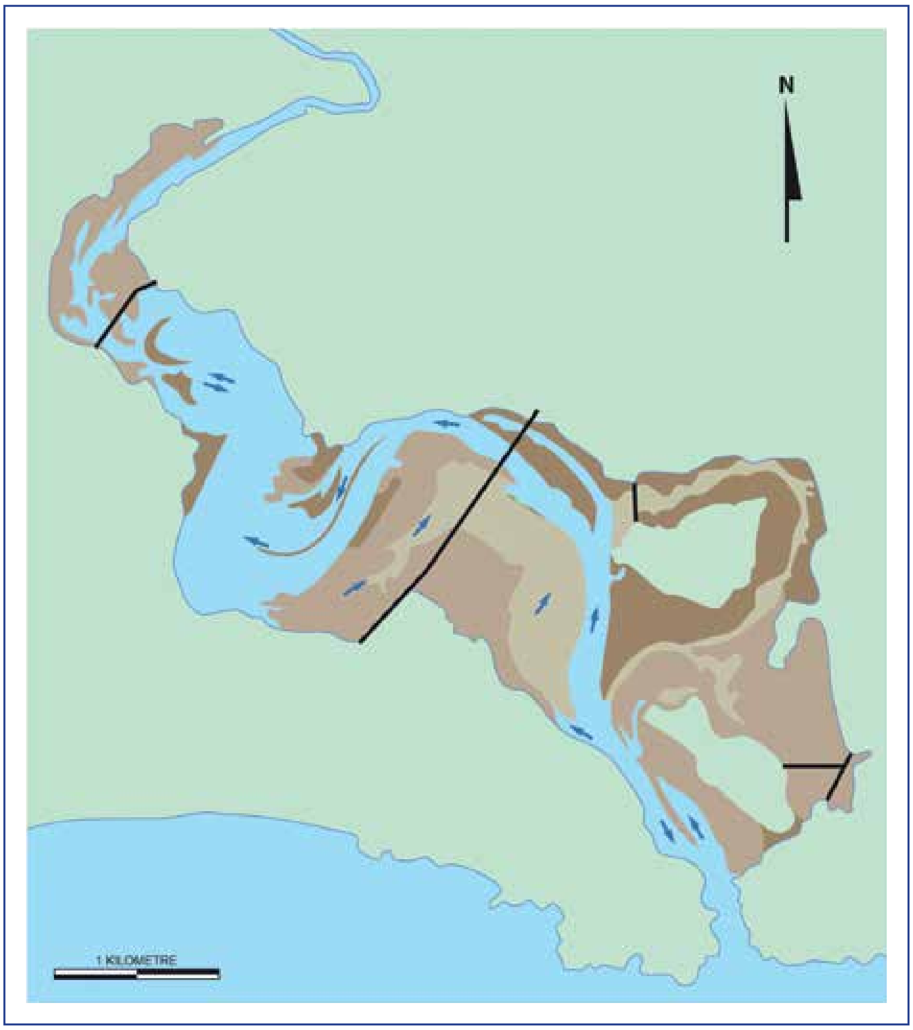

Figure 4.17 Modern sediment transport directions in the Knysna Estuary.

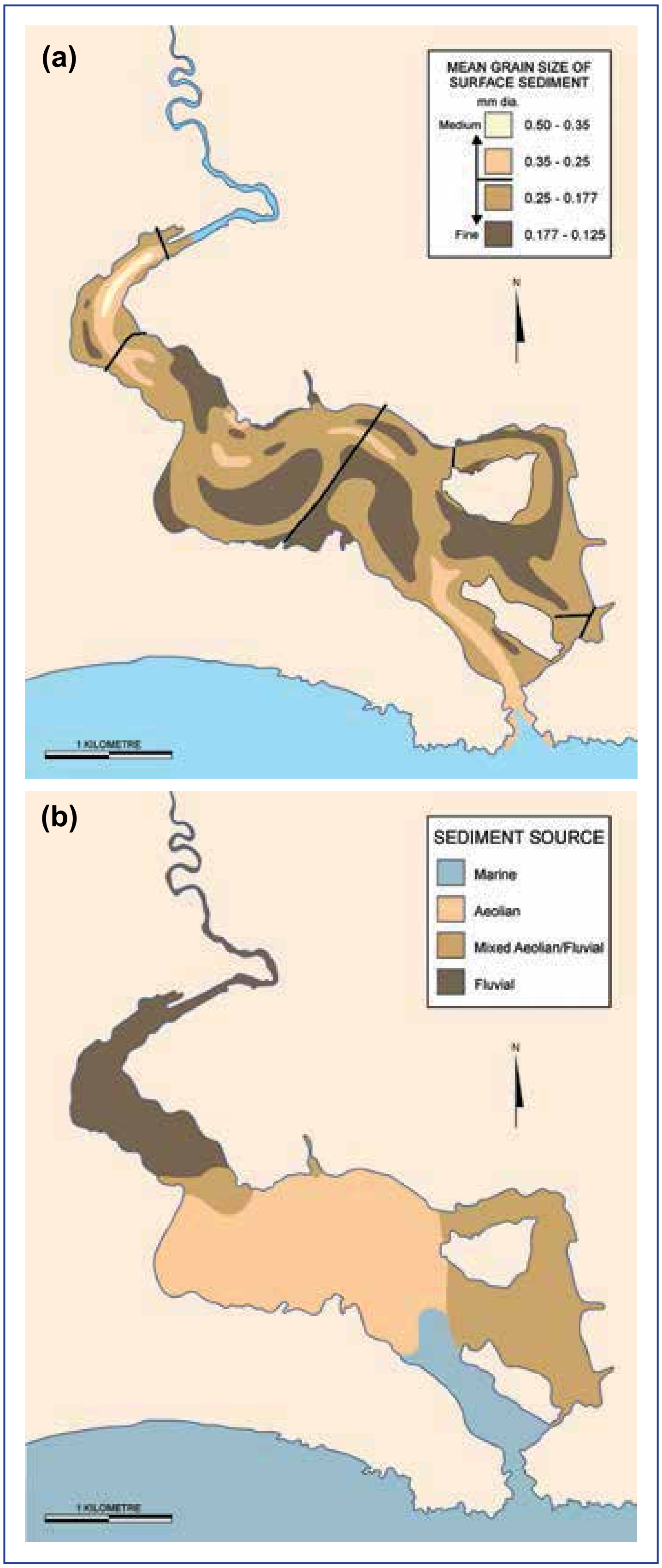

Figure 4.18 Information on sedimentary characteristics of the Knysna Estuary[3] showing (a) mean surface sediment size and (b) sediment source.

4.6 Conclusions

The Knysna Estuary is geomorphologically quite unusual in comparison with other South African systems. This can be ascribed to the specific geology within which it has formed — it is bounded by resistant rock to the south and north and the present large estuarine basin owes its existence to the surrounding erodible substrate. During the past 120 000 years the estuary has seen major changes in morphology and indeed, position. Its location has moved seaward and back again by over 80 km as sea level has fallen and risen again. It has also changed its shape many times in response to changes in the surrounding geology relative to its location. The remnants of the former estuary both onshore and on the continental shelf remain to be further investigated.

The modern estuary occupies much the same location as that of the last interglacial and is bounded by The Heads to seaward and steeply rising topography on all sides. This gives a particular stability in estuary morphology that is reflected in the relative lack of geomorphic change over recent decades, apart from those caused by human interventions. This sets the context for any appraisal of the future evolution of the estuary under future sea-level rise. The steep topography surrounding the estuary means that even when sea level is several metres higher than present (as during the last Interglacial period), the surface area of the estuary changes comparatively little. However, the presence of fringing infrastructure (roads, houses and other property), will render even small changes in water level, something of a challenge for the settled human population that was absent 120 000 years ago. From experience elsewhere, this is likely to lead to increased hardening of the estuary shoreline by hard structures and a concomitant loss of intertidal areas and their associated habitats. Being unable to migrate landwards, they are likely to become narrower and may ultimately be extinguished altogether as sea level rises. In the absence of indicators of increasing sediment supply from the river catchment, rising sea levels may lead to a general increase in water depth throughout the estuary, but this will be accompanied by sandbar migration as the estuary adjusts to the new sea-level conditions and so some areas may shallow as others deepen.

Figure 4.19 Shoreline armouring to protect roads and houses and other property changes the composition of the estuary margins and restricts the estuary's natural ability to change shape. These vertical structures at Brenton on Lake have altered the morphology of the shoreline and will lead to loss of the fronting saltmarsh as sea level rises (Photograph: © Alan Whitfield).

Figure 4.20 Plaque at a boat slipway site constructed by George Rex. The upper estuary at this position is now passable by wading, suggesting substantial sedimentation during the past two centuries in this region (Photograph: © Arland Read).

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Chapter 5 : Knysna Estuary — Meeting Place of River and Sea

John Largier & Lucienne Human

5.1 Introduction

Boundaries like the land-sea interface provide critical ecological habitats as well as increasingly desirable human habitat. This is nowhere more evident than where rivers meet the coast, and where people can access both the benefits of rivers and the sea. Generally known as estuaries, these intersection points host diverse and productive ecosystems at the same time as attracting humans who value the resources and aesthetics of these special places. While larger estuaries like Chesapeake Bay (USA) or Mar del Plata (Argentina) may receive more attention globally, smaller systems like the Knysna Estuary are regionally important, providing significant services and value to local communities — and they may punch well above their weight as small islands of critical habitat that promote regional biodiversity.

Companion chapters in this book outline the history, evolution, and ecology of Knysna — all of which relate to the water motion and water properties in this estuarine basin where the waters from the land meet and mix with the waters from the sea. With the passing of seasons and interannual fluctuations (droughts and floods), the waters in the basin may at times be more like a river and at other times be more like an 'arm' of the ocean — but always a meeting place, where river waters and ocean waters interact. And always there is an incessant rise and fall of the tide that alternately pulls in ocean waters and pushes out estuarine waters — the "breath of the bay"[1], akin to humans breathing in ambient air and breathing out air that has been modified by reactions in our lungs. The essence of the Knysna Estuary is a tidal interplay of freshwater and seawater, which characterizes the water filled Knysna basin that extends from Charlesford Weir to the rocky Heads (see Chapter 1 for photos of these estuary features).

In the Anthropocene, input of material to estuaries has been altered by direct human activity, with river water properties being altered by land use and human activities in the watershed, as well as discharge of wastewater and runoff of stormwater directly from developed areas to the tidal estuary. Human-driven loading combines with natural loading from the watershed and ocean as inputs to the physical mixing and biogeochemical reactions that occur within the estuary. Physical aspects of the estuary can also be altered by development, restricting flows or promoting seawater intrusions through embankments or dredging, respectively. And in the modern era, human-driven global climate change has become an additional modifier of estuary processes, including sea-level rise, ocean acidification and deoxygenation, and changes in precipitation patterns and land runoff (see Chapter 10 for details).

The water motions and water properties in the Knysna Estuary reflect much of what is expected in an estuary, including recent human modifications. But at the same time, it is special and there is no estuary quite like it. There are estuaries that exhibit similar character, however, and we can compare Knysna to global paradigms and other estuaries. For example, for much of the time Knysna can be considered a "low-inflow estuary" relative to its size[2]. As with other basins not carved out by river action alone (Knysna basin lies in a valley between fossil dune fields — see Chapter 4), the inflowing river is small compared with the size of the basin; in Knysna the average river inflow of 3 m^3 per second would take months to fill the basin. Also comparable with mountainous coastal watersheds in the Western Cape or in the Tsitsikamma region to the east of Plettenberg Bay, the unmodified river delivers a low nutrient load and low concentrations of suspended particles.

In contrast to prevailing textbook paradigms, the estuary is primarily fueled by material imported from the ocean shelf[3], which is biogenically rich and accounts for high productivity, biogeochemical cycling, and biodiversity. However, like too many estuaries in the world, pollution is significant and in some parts of Knysna it is severe enough to alter the food web, with phytoplankton/algal blooms, turbid water, and hypoxia replacing clear waters and seagrass habitats[4].

In this Chapter we outline the movement of water in Knysna Estuary and characterize water properties including nutrient, oxygen and phytoplankton levels, in addition to the abiotic properties of salinity and temperature. These physical dynamics

Figure 5.1 Rocky shores at The Heads shelter Knysna Estuary from ocean waves (Photograph: © Fultonsphoto).

provide the stage on which various ecological dramas can play out. While some may still wish to debate whether Knysna is an estuary, there is not much to be gained from that and more is gained from exploring the diverse phenomena that play out in estuaries, whether they are called estuaries, lagoons, rias, bays, vleis, coastal confluences, transitional waters, or whatever. Of these the most common term is estuary, which is increasingly used in an inclusive way to refer to all places where river waters meet the sea, often in a defined basin.

The adjective 'estuarine' introduces some nuance as estuarine circulation may disappear in the dry season when marine salinity prevails and some estuarine species may move into the upper reaches of the system. This intermittency in estuarine features and processes is increasingly recognized as a common phenomenon in many of the world's estuaries. Whether intermittent or not, the two fundamental physical characteristics that shape estuaries are variations in salinity (meeting of river and ocean waters) and the importance of tides (currents, import/export, fluctuations in water level), which are addressed in sections 5.3 and 5.2, respectively. In turn, these water motions advect parcels of water around the estuary and account for mixing between water parcels, in which biogeochemical reactions are happening simultaneously — together accounting for differences in water properties across space and time. Specifically, we address nutrients (section 5.4), phytoplankton (section 5.5), dissolved oxygen and pH (section 5.6), and pollutants (section 5.7). Finally, we address critical changes in parts of the estuary where the food web is changing due to severe anthropogenic nutrient loading (section 5.8)

5.2 Water flows and water levels

Along the coasts of the world, water level rises and falls in response to multiple celestial forces tugging on the great body of water that forms the ocean. This tidal 'heaving' results in water flooding into confined estuary basins as the water level rises in the ocean and some hours later water ebbs out of the basin as the water level drops in the ocean. The rise and fall of water level, the cycle of wetting and drying of intertidal land surfaces, and the strength of tidal currents filling and emptying the estuary are a fundamental characteristic of most estuaries.

While many smaller estuaries on mountainous coasts in South Africa and globally may be shut off

Figure 5.2 Flood tide entering the broad and permanently open Knysna Estuary mouth, with the western Head visible on the far side (Photograph: © Ava Peattie).

from the sea by wave-built sand berms, the mouth of Knysna Estuary remains permanently open despite low river inflow. Not only do rocky headlands at the mouth provide shelter from wave action (Figure 5.1), but they also limit the longshore supply of sand from proximal coasts so that a beach does not form adjacent to the mouth and cannot build across the mouth as for most other estuaries in the region, e.g. Swartvlei Estuary. While there may be some wave-driven sand supply and accretion in or near The Heads, the open-mouth nature of Knysna Estuary is maintained by strong currents due to the large volume of water that moves into and out of the estuary on every tidal cycle.

This large tidal prism is more common in mesotidal or macrotidal regions of the world, but in microtidal areas like South Africa the tidal prism can also be large where there is an extensive tidal area, as in Knysna. Comparable wave-sheltered, open-mouth estuaries in micro/mesotidal California are Bolinas Lagoon and Bodega Harbor with tidal areas of 450 ha and 1 280 ha, respectively, and comparable with the 1 690 ha tidal area in Knysna. Large estuaries with a permanently open mouth and small river inflow are sometimes called embayment estuaries or estuarine bays. Such systems have many characteristics similar to the sea but are calmer and warmer than waters along the adjacent open coast — these are rare in South Africa (e.g. Langebaan Lagoon) but common elsewhere such as in the estuaries of northwest Spain (i.e. the rias in Galicia).

With a relatively deep and broad open mouth, ocean water flows strongly into Knysna on flood tides (Figure 5.2). Tidal currents attain speeds of 1 m per second at The Heads and 0.5 m per second adjacent to Thesen Island[5]. These currents transport sand into the estuary, accounting for flood-tide shoals between The Heads and Leisure Isle (see Chapter 4 for details). Marine sand also contributes to tidal shoals further landward, although the railway embankment has throttled these dynamics and altered tidal morphology.

The tide propagates into Knysna Estuary as a long-period wave that develops non-linear characteristics such as a short flood tide with fast currents and a long ebb tide with slower currents. This tidal asymmetry is most noticeable in shallow waters, where fast flood-tide currents move sediment landward that then settles out during slow ebb-tide

Figure 5.3 Tides are responsible for the daily inundation and exposure of plants and sediments in littoral areas around the Knysna Estuary (Photograph: © Alan Whitfield).

currents, maintaining the very shoals that account for this process. No surprise then that extensive shoals are found either side of the channel. These shoals, in turn, constrict most tidal transport to the channel that acts like an artery connecting the outer, middle and inner estuary.

Near the mouth, water levels can also fluctuate rapidly due to waves or slowly due to wind surge effects. Although waves are sufficiently dissipated at the mouth (Figure 5.1) to preclude beach building, some wave energy propagates through the mouth and plays a role in maintaining beaches in the outer estuary, assisted by short-period waves generated by winds in the estuary (e.g. north-easterly winds that produce waves on the shore between Brenton-on-Lake and The Heads). In addition to swell waves (periods of 5 - 20 seconds), long-period infragravity waves (periods of minutes) can enter from the ocean. These small fluctuations do not last long and are largely unnoticed, but they can be seen to move material quickly over short distances and may be important in exchange between open water and marshes.

In contrast, wind-driven surges in the ocean are noticed in Knysna Estuary because they are larger (they can account for a 0.5 m change in water level, comparable with the neap-tide range) and more persistent (a few days, allowing water to rise slowly even in the furthest recesses of the basin). The wind-driven surge may be due to local winds along the coast, but at times it is a propagating surge, generated by winds further west — these 'coastal trapped waves' propagate eastward along the south coast[6]. The long-period disturbances do not result in significant water velocities and are not expected to be important for changes in morphology nor transport of biogenic material into the estuary. However, they can account for persistently high water levels with significant impact on marshes and adjacent areas, some of which have now been developed by humans. As sea level rises and flooding becomes more of a threat, it is the concurrence of a wind surge and high tide, with high river flow, that is the worst-case scenario for flooding of low-lying developments around the Knysna Estuary.

Tides also account for pelagic-littoral coupling, moving waters on/off seagrass covered shoals and in/out of saltmarsh habitats (Figure 5.3). This lateral exchange of waters between the arterial channel and productive littoral habitats is aided by

Figure 5.4 Aerial photo showing the clarity of estuarine water in the outer estuary (Photograph: © Duran De Villiers).

infragravity waves near the mouth and by local wind-driven water motions that raise water levels locally, pushing water into tidal creeks that drains out when the wind subsides. Inflowing channel waters can be expected to supply marshes and littoral habitats with nutrients, and in turn export organic material during ebb tides (known as 'outwelling').

Water velocities in the upper estuary driven by river inflow are only important during high river flow events. Tidal currents still dominate in mid - and outer estuary where even high river flows account for velocities no more than about 0.1 m per second. However, river flows are important in that they bring low-density freshwater into the basin, resulting in stratification and a mode of circulation in the vertical plane that is critical to water exchange in the inner and mid-estuary (this phenomenon, known as 'estuarine circulation' is outlined in Section 5.3).

While an estuary is a continuum and functions as an integrated system linking river to ocean, there are clear changes in the hydrodynamic character moving longitudinally through the basin. For shallow low-inflow estuaries like the Knysna system, there is a river-dominated inner estuary, an ocean-dominated outer estuary, and a low-energy mid-estuary[7]. Specifically, for Knysna, Largier et al[5] identified and described these zones, identifying hydrographic regimes that migrated tidally. They referred to the inner estuary as the estuary regime, the outer estuary as the bay regime, and the mid-estuary as the lagoon regime. While shifting with the tides, the estuarine regime is generally landward of White Bridge (the main road bridge) and the bay regime is generally seaward of the Railway Bridge.

A primary consideration for water properties addressed in subsequent sections is residence time: how long water remains in an estuary or part of it before being displaced out of the estuary. If the residence time is short, then there is little time for biogeochemical reactions (or surface heating) to alter water properties. However, if residence time is longer than reaction time, then the water properties will be largely determined by these biogeochemical reactions. For example, nutrients imported by tidal inflow or river inflow are typically flushed from Knysna before there is enough time for a phytoplankton bloom to occur, accounting for the clear waters (Figure 5.4). While residence time is a

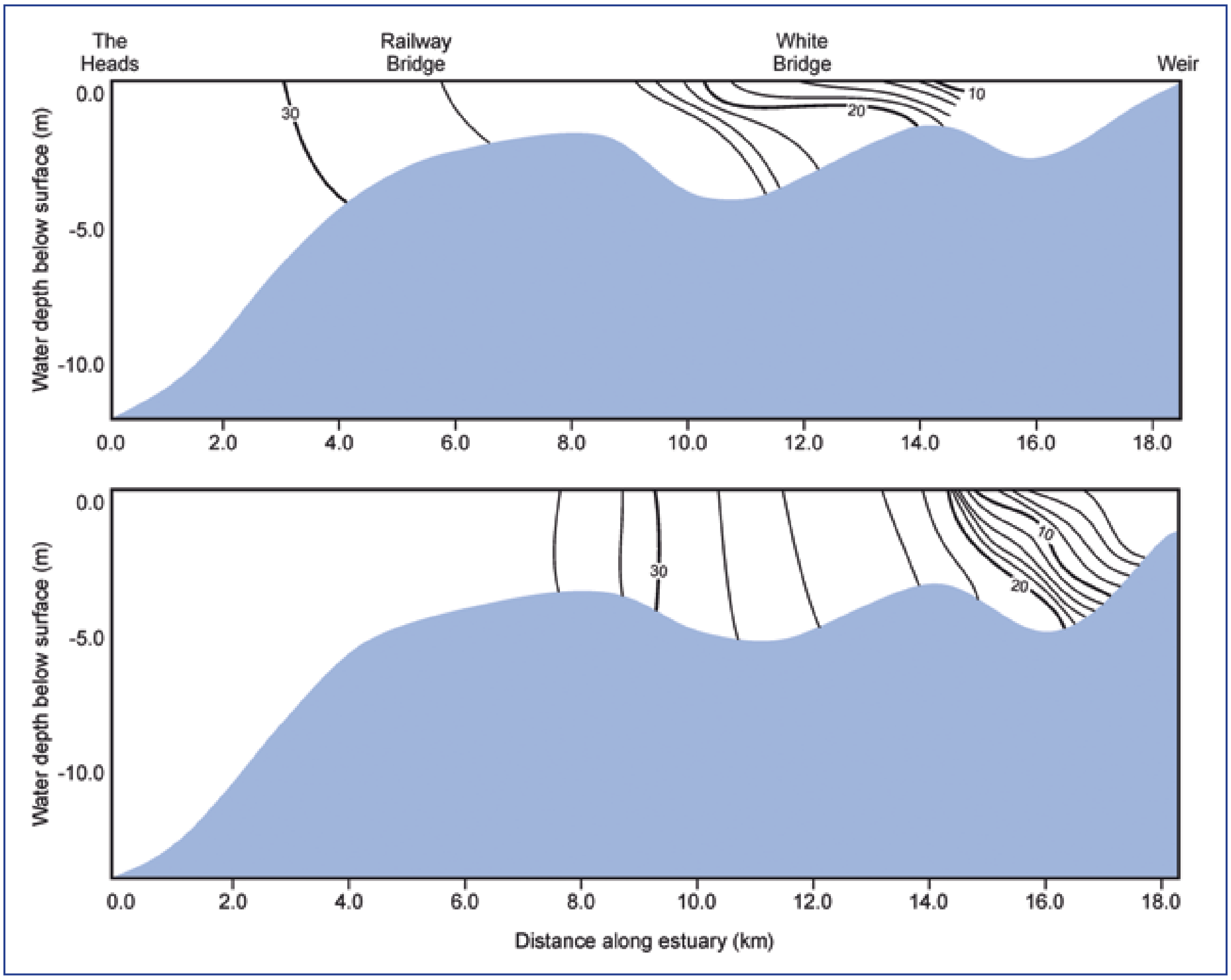

Figure 5.5 Salinity sections at low tide (upper panel) and high tide (lower panel) during average river inflow (2.8 m³ per second on 5th May 1997), showing salinity stratification in the middle estuary at low tide and compression of low salinity water into the upper estuary during high tide[5].

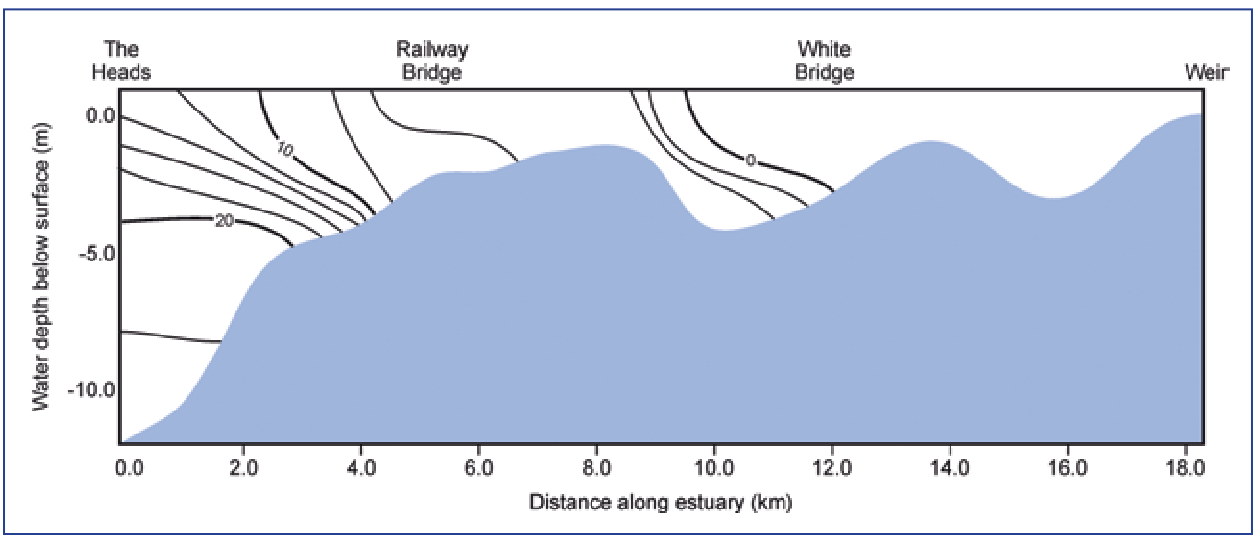

Figure 5.6 Salinity profiles along the Knysna Estuary on the 25th October 1996 during a 50 m³ per second flood event. Note the absence of any saline water between 12 km and 18 km from the estuary mouth[5].

nuanced concept[8] and best calculated with a computer simulation model, rough estimates can be made by considering the volume of interest and the flow rate that could flush it. For example, if one expected that the whole estuary (volume 32 million m^3) was flushed by the river (average 3 m^3 per second), then the basin-wide residence time would be approximately four months.

However, if one focused on the inner estuary (volume landward of White Bridge is 2.7 million m^3), the residence time is just 10 days — and if one considers that estuarine circulation rate can be several times larger than river flow rate, then residence times may be just a few days. At the same time, the outer estuary is readily flushed by tidal flows: during spring tides the 18.5 million m^3 tidal prism[9] (intertidal volume) can fill the basin from The Heads to just beyond the Railway Bridge so that the outer estuary residence time is less than a day during spring tides, being rapidly flushed by tidal action. Between the river-flushed inner estuary and the ocean-flushed outer estuary, however, waters in the mid-estuary may be resident for longer periods. Long residence is also found in dead-end or constricted channels like Ashmead Channel.

While the tidal volume between Railway Bridge and White Bridge (12 million m^3) is comparable with the tidal prism volume that passes Railway Bridge, waters moved seaward on ebb tide are not exported to the ocean and likely returned to mid-estuary on the next flood tide with little loss. The long residence of waters in the mid-estuary are evident in the high temperatures (discussed below). However, there are reports of only marginal hypersalinity in open-water[10], which is expected to occur with residence times of about 10 days during periods of low river flow[7]. When river flows are below 0.5 m^3 per second, evaporation can remove this freshwater in the upper estuary, thus resulting in negligible freshwater input to the mid- or lower estuary.

5.3 Salinity and temperature

The primary water property in an estuary is salinity, which is conservative (i.e. is not changed by biological or chemical processes) and thus tracks the interplay of zero-salinity freshwater flowing from the river and high-salinity seawater flowing in from the sea (ocean salinity about 35 ppt). In most estuaries, variations in salinity account for variations in density and thus for density-driven estuarine hydrodynamics, specifically estuarine circulation. However, in Knysna and other low-inflow estuaries adjacent to marine upwelling regions, water temperature differences may also be important in accounting for density differences that influence circulation patterns within the estuary.

Differences in water density account for stratification (layers of different density with limited mixing). Stratification can develop where stirring is weak enough, but where tidal currents (or winds) stir strongly enough, mixing precludes the formation of layers. In Knysna, the presence and importance of stratification changes spatially and temporally, in response to changes in river inflow and tidal flow speeds[5]. Knysna Estuary exhibits all stratification types on the continuum from completely mixed to highly stratified (Figure 5.5). Stratification tends to increase with increases in river flow during the rainy season and decreases during drought and other times of weak inflow — or rather the spatial extent of the stratified estuary portion shrinks towards the freshwater source at Charlesford Weir.

Stratifcation also changes with the tides, being stronger during neap tides with weaker currents and thus weaker mixing , and weaker during spring tides. The sweet spot for estuaries is when layers form but stratification is mild enough to allow cross-layer mixing; in this case, one gets 'estuarine circulation' with a tidal-mean inflow of dense seawater in the bottom layer and a tidal-mean outflow of low-density estuarine water in the upper layer. The cross-layer mixing pulls the dense water upward into the outward flowing upper layer, completing a conveyor-belt-like circulation in the vertical plane. This is what ventilates estuaries, continuously importing nutrients and other biogenic material from land and ocean watersheds and continuously flushing out material derived from biological production and decomposition.

During low inflows, Knysna is well mixed and the longest residence times are expected in the inner/mid-estuary, however for average inflow (Figure 5.5) the inner estuary is classified as partially mixed (i.e. modest stratification) and a robust estuarine circulation is expected (notably the circulation flow rate is several times larger than the river inflow rate). Estuarine circulation extends into mid-estuary during higher inflows, but highly stratified conditions (no mixing) can occur in the inner estuary during these periods, as the inflowing freshwater 'lifts off' and flows over a long-residence bottom layer. During highest flows, all saline water is flushed from the inner estuary (e.g. 25 October 1996, Figure 5.6), although stratification may be observed in the mid- and outer estuary.

Water temperature varies seasonally in Knysna Estuary (even more so in Knysna River), yielding significant estuary-ocean temperature differences.

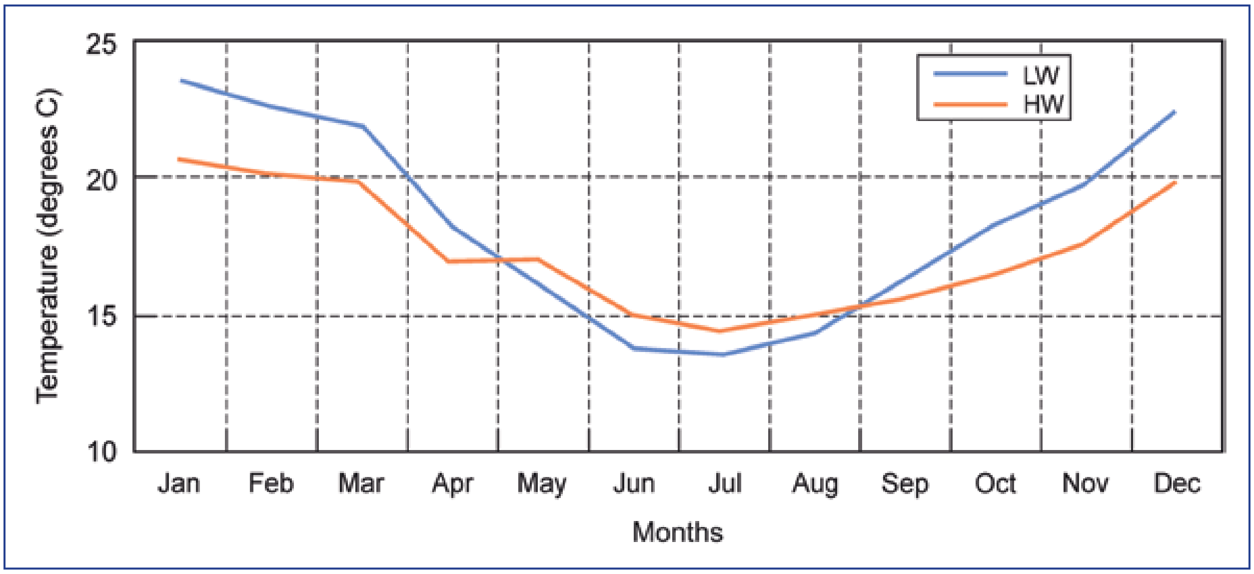

Figure 5.7 Mean monthly water temperature at low tide and at high tide in the outer estuary[10]. Temperatures were measured at Thesens Island Quay (Figure 1.4). River and inner estuary waters are colder than ocean and outer estuary waters during winter (June-August). In summer estuary waters are warm, typically over 20°C (December-March).

Summer temperatures are generally above 20°C in the estuary with lower temperature near the mouth owing to the influence of the sea, while winter temperature ranges from 12 to 15°C throughout the estuary (Figure 5.7). The estuary-ocean temperature difference is maximal in summer when ocean waters are coldest during coastal upwelling events, while estuary waters are warm[5,6]. Cold, upwelled water intrudes as a dense lower layer, analogous to a salt wedge, and may drive a thermal estuarine circulation in the outer estuary. Detailed descriptions of temperature fluctuations, and specifically of seawater intrusions as cold as 10°C extending as far as Railway Bridge, have been published[5,6]. Not only does temperature change dramatically in the outer estuary during these intrusions, but also oxygen, pH, nutrients and other water properties which can stress benthic organisms. In addition, dense fog sometimes develops over the coast and outer estuary as warm air moves over cool ocean waters entering the estuary during periods of upwelling along the coast (Figure 5.8).

The three zones identified in Knysna Estuary exhibit distinctively different thermohaline character and stratification. The outer estuary (bay regime) is characterized by high salinity, cool waters that are generally mixed and only stratify transiently during cold-water intrusions following coastal upwelling or during very high river flow rates. The inner estuary (estuary regime) is characterized by low salinity and stratification, with temperature that varies strongly between winter and summer. The mid-estuary (lagoon regime) is partially mixed with moderately high salinity and temperatures that are often higher than elsewhere in the estuary, particularly during summer. Fringing marshes may exhibit hypersalinity during dry periods with high evaporation, but residence time in the channel is typically insufficient for this to develop. However, residence in mid-estuary is sufficient for substantial warming of the waters. In summer, mid-estuary water can be more than 10°C warmer than one would expect from a simple mixing of river and ocean waters. Expecting a warming rate of about 1°C per day in waters a few meters deep, this indicates residence times of order 10 days.

5.4 Nutrients

The concentration of nutrients in the water controls photosynthesis (primary production), including phytoplankton, drift algae, fixed algae and submerged aquatic vegetation. New nutrients are brought into Knysna Estuary by inflowing river waters and inflowing ocean waters, with the importance of the ocean input being more significant in Knysna Estuary than in textbook estuaries (specifically during intrusions of cold, nutrient-rich water upwelled along the open coast).

In recent decades, the discharge of nutrient-rich wastewater and stormwater has become a third source of new nutrients for Knysna Estuary, especially in side-channels that were previously well removed from ocean or river nutrient inputs. While

Figure 5.8 The Heads shrouded in fog which develops as warm air moves over cool ocean waters entering the estuary during periods of upwelling along the coast (Photograph: © Vladimira Pufflarova).

Figure 5.9 Note the dense intertidal filamentous algal mats (upper half of the picture) that have developed in the Ashmead Channel as a result of nutrient pollution in this region of the Knysna Estuary (Photograph: © Alan Whitfield).

the supply of nitrate exerts overall control on productivity, nutrients are also recycled within the estuary and localized high concentrations of ammonium may result in filamentous algal blooms (Figure 5.9). Accumulated organic material in the sediment results in an important sediment-to-water flux of remineralized nutrients, including outwelling from marshes and shallow, muddy littoral habitats. The anthropogenic accumulation of organic material in Ashmead Channel over the last few decades (i.e. legacy pollution) ensures a continuous supply of nutrients to the water column even in the absence of discharge events, thus sustaining high concentrations of phytoplankton and benthic algae[4].

Nutrient concentrations at a given location depend on the transport and mixing of nutrient-bearing waters as well as biogeochemical reactions in the water and sediment-water nutrient fluxes. The essential nutrients required for primary producer growth are inorganic nitrogen and phosphorus, with nitrogen typically the limiting nutrient for algal growth in Knysna Estuary and other coastal waters.

Mixing diagrams have been used to describe nutrient cycling in the Knysna Estuary[3,9]. These are scatter-plot diagrams in which nutrient concentration is plotted as a function of salinity (Figure 5.10). If the nutrient is conservative, as is salinity, data points fall on a straight line between river and ocean source waters, i.e. nutrient reactions are negligible, and concentration is controlled by the physical processes of transport and mixing. Deviations from the 'mixing line' can be used to quantify nutrient uptake (downward curvature) or nutrient production (upward curvature). During high river inflow through the Knysna Estuary, nutrients behave conservatively — they are rapidly flushed from the upper and middle estuary via freshwater throughflow, and a combination of high flow and tidal flushing quickly removes these nutrients from the outer estuary. The short residence time in the estuary also limits the biogeochemical influence of nutrients on benthic, littoral, and pelagic primary producers. This rapid mixing and removal of high-nitrate river water from the estuary before it could fuel phytoplankton blooms is illustrated by data collected during high river flow on 16 November 2000 (Figure 5.10): data points fall along a mixing line between freshwater inflow with concentration 350 µg per litre and seawater with concentration 100 µg per litre.

In contrast, during periods of low river flow estuarine waters are resident long enough for nutrients to be taken up, contributing to significant photosynthesis and algal growth in the upper/mid-estuary. However, nutrient influx is low during low river flows, influencing only the inner estuary, and ocean-derived nutrients are more important in the

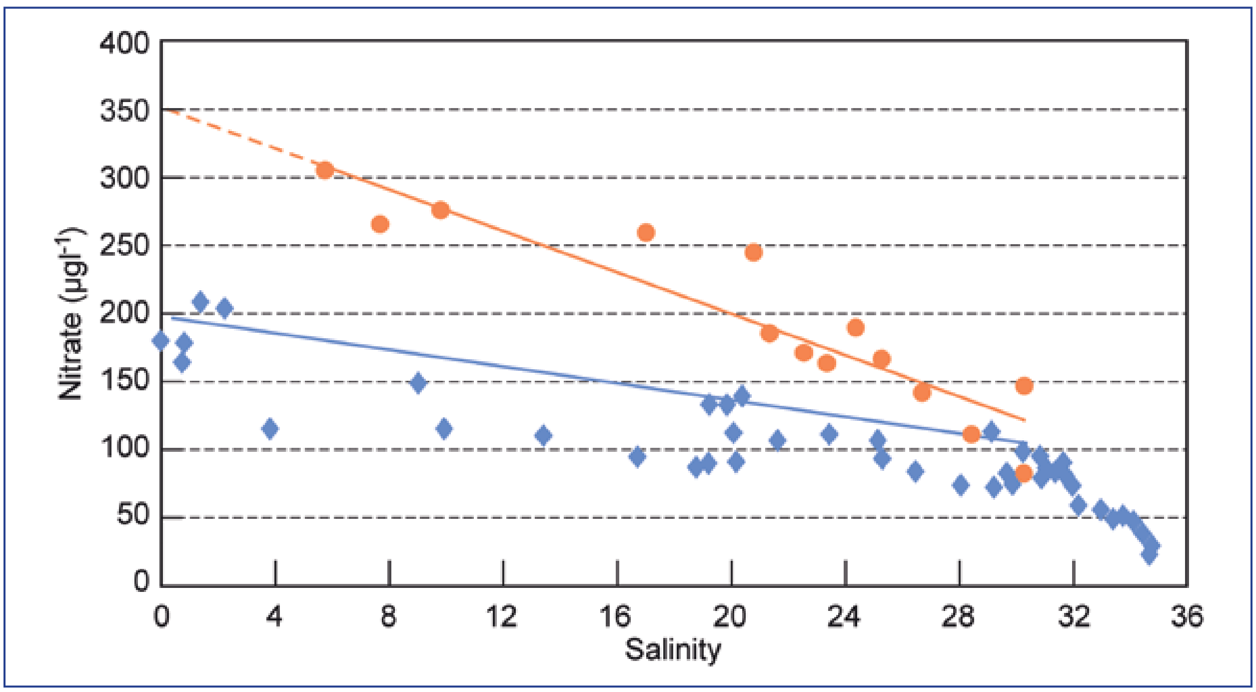

Figure 5.10 Mixing diagram for nitrate and salinity data from November 2000[9]. Blue symbols are for 13-14th November when water residence time is longer and nitrate values are lower than expected, i.e. biological uptake is important. Orange symbols are for 16th November during a high river flow event when elevated nitrate concentrations were transported through the estuary with weak uptake.

Figure 5.11 Nutrient rich effluent from the Knysna Waste Water Treatment Plant entering a reed bed prior to discharge into the estuary (Photograph: © Alan Whitfield).

outer and mid-estuary. Most commonly, the mixing diagram for nitrate in Knysna Estuary shows downward curvature corresponding to lower than expected concentrations in the mid-estuary between higher concentrations associated with both ocean and river inflows[3,11]. This shown in data collected on 13 - 14 November, when river flow was lower and flushing was slower relative to a few days later (Figure 5.10): while mixing alone would yield nitrate concentrations between freshwater values of 200 μg per litre and outer estuary values of 100 μg per litre, observed values remain around 100 μg per litre in waters with salinity between 2 and 32 (i.e., inner and mid-estuary), implying that 50 to 100 μg per litre nitrate has been taken up by photosynthesizing plants and plankton in the estuary.

In summer, pulses of cold high-nitrate ocean water associated with upwelling can intrude into the estuary[9]. For example, an upwelling event that began on 27th February 2002 resulted in a 7-fold increase in nitrate concentration as estuarine waters with concentration 2.5 μmol per litre were replaced by ocean waters with concentration 17.5 μmol per litre. When conditions are rapidly changing, data collected at multiple locations within the basin may not exhibit a single mixing-line relationship between nutrient concentration and salinity, as found for the dry winter of 1996/7 when concentrations of NH_4 and NO_xN in the estuary were generally below 3 μg per litre[3].

In addition to ocean inputs, nutrient influx via the Ashmead Channel explains higher concentrations of NH_4 and NO_x nitrogen in the outer estuary. A wastewater treatment plant that discharges into this channel (Figure 5.11) has experienced multiple failures over the years, which has led to excessive algal growth and hypoxia, i.e. eutrophication[4]. The long residence time in this channel allows for remineralization of legacy organic matter (i.e. accumulated material from prior inputs), resulting in the persistently high NH_4 concentration recorded in the Ashmead area. Conditions are amplified during dry periods (e.g. 2016-2017) when flushing events are minimal.

Dissolved reactive phosphate (DRP) concentrations in the estuary remain low (<30 μg per litre) for both high and low inflow periods. However, once again, higher concentrations are recorded in the Ashmead Channel area due to wastewater inputs and remineralization of legacy organic matter[4]. High concentrations of DRP are also found in the upper estuary during dry phases, derived from desorption of P from fluvial particulate phases[9].

5.5 Phytoplankton levels

Primary production in estuaries occurs through phytoplankton, benthic algae, seagrass meadows, and littoral marshes. While primary production is generally controlled by the availability of nutrients (described above) and the availability of light, the accumulation of phytoplankton biomass also depends on residence time in the estuary as a phytoplankton bloom (and floating macro-algae) can be flushed out of the estuary before it fully develops. Thus, in either low-nutrient systems and/or rapidly flushed systems, phytoplankton can be low, and waters can be clear, as in Knysna. This allows light to reach the bottom and promotes the growth of benthic algae and seagrasses that are fixed in place. Extensive seagrass meadows are documented for the Knysna Estuary (see Chapter 6 for details). However, if insufficient light reaches the bottom, these bottom-fixed plants and algae do not fare as well.

In general, phytoplankton biomass is tracked by measuring water-column concentration of chlorophyll a (Chl-*a*), the photosynthetic pigment in microalgae. Higher phytoplankton bio-mass is expected in more nutrient-enriched estuaries where dense phytoplankton blooms may exhibit concentrations over 20 µg per litre. In Knysna Estuary, Chl-*a* is generally below 3 µg per litre[3,12,] which is low compared with other South African estuaries[12]. While DWA documented typical low levels of 3.5 µg per litre in July 2007[10], high-concentration phytoplankton blooms can develop following intrusion of nutrient-rich upwelled waters or inflow of nutrient-rich river waters, as in August 2008 when DWA found localized peaks over 15 µg per litre in the vicinity of White Bridge. This was a period characterized by high nutrient availability, low turbidity, and favorable residence time. Phytoplankton biomass can also be high in the inner estuary during summer, such as in February 2008 when moderately high chlorophyll concentrations of 7.5 µg per litre were recorded.

It is likely that localized high-phytoplankton events will become more frequent in the estuary with increasing nutrient loading[9] — in specific areas with long residence times (e.g. side channels). In the inner estuary, a reduction in river flow (reduced flushing) or an increase in nutrient loading will result in the formation of denser phytoplankton blooms, which in turn are likely to lead to anoxic conditions in the lower layer of the upper estuary. In the canals in Knysna Quay, extreme Chl-*a* (over 100 µg per litre) and Secchi disk readings less than 0.5 m have already been measured. Rather than a broad increase in the average algal biomass throughout the estuary, it is expected that high-concentration events will occur more frequently, with high-concentration 'hot spots' becoming more widespread.

Phytoplankton levels may also change if river flow is reduced for Knysna Estuary, resulting in longer residence times in mid-estuary. In low-inflow estuarine bays in California, phytoplankton production is driven by ocean-derived nutrients, exhibiting peak Chl-*a* concentrations mid-estuary in the dry season as the outer bay has insufficient retention and the inner bay has insufficient nutrients[14]. Knysna Estuary is shorter than the California bays and river inflows are sufficient to preclude sufficient retention time in the inner estuary — however, if retention time increases in Knysna, a similar phytoplankton maximum may develop mid-estuary. In addition, further work is needed to quantify the rate of nutrient removal by seagrass meadows in the outer/mid-estuary as seagrass-mediated depletion of ocean derived nutrients may preclude this scenario in Knysna Estuary.

Elevated water turbidity is an important control on light availability for submerged aquatic plants. Turbidity may be due to high concentrations of phytoplankton or due to suspended sediments resulting from turbid river inflows, wave-driven sediment resuspension at the mouth, or resuspension of bottom material by tidal currents. While there are occasional turbid events, in general light can reach the bottom across most of Knysna Estuary (Figure 5.4). Traditionally, the Secchi-disk depth has been used to estimate the depth of light penetration (i.e. a measure of turbidity), which varies both spatially and seasonally. Light penetrates deepest in the outer estuary (Secchi depth ~2.3 m) while the middle and inner estuary are characterized by Secchi depths of ~1.5 and ~1.7 m, respectively. During marine dominated states, estuary waters are clearest with Secchi depths of ~2.5 m, ~2.0 m and ~2.25 m in the outer, middle, and inner estuary, respectively. In contrast, transparency decreases markedly during strong river inflow, with Secchi depth averages of ~2 m, ~1.5 m and ~1 m in the outer, middle, and inner estuary, respectively.

When light does not penetrate the entire water column, benthic primary production cannot occur, but phytoplankton can still photosynthesize if trapped near-surface by stratification. So, while seagrass in the outer/mid-estuary may deplete nutrients and limit phytoplankton concentrations, it is also possible that if phytoplankton concentration increases, it will limit growth of new seagrass plants and thus remove this nutrient control, resulting in a positive feedback and phytoplankton blooms with even higher concentrations, i.e. there is likely a tipping point in relation to anthropogenic nutrient inputs to the Knysna Estuary which would result in conversion from the present seagrass-dominated, clear-water state, to a future turbid-water state dominated by phytoplankton and macro-algae.

5.6 Oxygen and pH

Aquatic organisms require sufficient levels of dissolved oxygen (DO) to survive. For this reason, it is often used as an indicator of estuary health. In the Knysna Estuary, typical saturated DO values vary between 7 and 11 mg per litre and most commonly are between 8 and 10 mg per litre. Where there is a net biological oxygen demand (BOD) owing to uptake by respiration (dominant at night) and decomposition of organic material, oxygen levels can fall below 100% saturation. Conversely, where photosynthesis exceeds respiration and decomposition (common during the day), oxygen levels can be above 100% saturation, with small bubbles of oxygen from seagrass beds floating to the surface.

In South Africa, oxygen concentrations below 3 mg per litre are considered hypoxic, signaling the need for management intervention. The Knysna Estuary is well flushed and there is therefore insufficient time for severely deoxygenated waters to develop. However, just as anoxic levels occur naturally in the bottom waters of Swartvlei lake, so too can lower DO levels occur in the trapped, high-salinity lower layer in the upper Knysna Estuary (when stratification persists). This exacerbates a spatial trend of lower DO values with distance from the ocean; with lower DO recorded at Red Bridge than at Old Bridge, which in turn had lower levels than White Bridge, which were like those in the well-mixed water column closer to the ocean[3,11]. Lower DO in the inner estuary (above White Bridge) is attributed to higher BOD in this section of the estuary, as well as vertical stratification preventing effective re-aeration of the lower layer.

Seasonal differences in DO are primarily related to seasonal changes in water temperature, with higher DO levels occurring when waters are colder in winter (cooler waters have higher DO saturation values). While warm ocean water in summer may have a lower DO, these waters are seldom deoxygenated and tidal intrusions of ocean water bring well-oxygenated waters into the outer estuary and even the outer parts of the mid-estuary, with significantly higher DO when cold upwelled waters intrude during summer.

Net photosynthesis in seagrass beds can be a local source of oxygen-rich waters to the estuary, as recorded by Allanson et al.[3] in the Ashmead Channel at a time when photosynthesis in these beds was enhanced by nutrients from stormwater and wastewater inflows. However, more recently there has been a decline in DO in Ashmead Channel[14], particularly where wastewater delivers a high load of organic matter that accounts for BOD high enough to exceed local photosynthesis — resulting in a net uptake of oxygen and the observation of low DO values (hypoxic events). As outlined in sections 5.4 and 5.5 above, wastewater also delivers excess nutrients that lead to phytoplankton blooms, which contribute to additional BOD and lower DO as the bloom decays in a classical example of cultural eutrophication (see section 5.8 below).

As with salinity, the pH in the estuary is a function of its receiving waters — lower pH is associated with greater freshwater influence during low tides and higher pH is associated with greater seawater influence during high tides. Although pH levels also may rise in response to net photosynthesis or fall in response to net respiration, this effect is dominated by the large difference in the pH of source waters for the Knysna Estuary. Freshwater properties are determined by both the catchment geology and vegetation. The Knysna River drains Table Mountain Sandstone, which has a low carbonate content and contains acidic colloidal material, resulting in pH levels of about 5. Decomposed fynbos and forest plants contribute to the formation of humic acid, with the dissolved humates also giving rise to tannin-stained water (Figure 5.12).

In contrast to the Knysna River water, seawater is alkaline with pH levels about 8.5 due to the presence and buffering capacity of bicarbonate and carbonate compounds. This difference results in a pH gradient from the top of the estuary to the mouth, with values typically ranging between 5.5 and 8.3, and the lowest pH recorded in the freshwater-dominated waters in the upper estuary. During high river flow, low-pH waters can extend through much of the estuary, e.g. during the major 1996/97 flood the pH dropped below 7.0 (salinity <5 ppt), only increasing to 8.2 near the mouth (where seawater salinity was recorded).

5.7 Human modifications

Knysna Estuary has not only changed over geological time scales (Chapter 4), but also historically as humans have gathered on its shores and developed

Figure 5.12 Humate stained estuarine water adjacent to an eelgrass bed near the White Bridge. When salinities are above 17 ppt and the pH is above 8, the dissolved humic material precipitates out of the water column and the estuary then loses its tannin stain (Photograph: © Alan Whitfield).

the watersheds that drain into the lagoon. Two primary effects of socio-economic development are changing water quality (i.e. pollution) and the changing landscape (e.g. bridges, causeways and seawalls). The estuary is also changing in response to global climate change.

Pollution of estuaries is a global problem and there are many forms, including toxigenic pollution (pollutants that are toxic), pathogenic pollution (pollutants that spread disease), and biogenic pollution (pollutants that stimulate algal growth and oxygen depletion). There are few data on toxigenic pollution for Knysna Estuary, however past studies concluded that Knysna was not polluted at that time[12,15]. While there is no long-term record of metal data in the estuary, more recent data show elevated copper and zinc levels in stormwater[16] (above detection limits of 5 and 25 μg per litre, respectively), suggesting that more attention is needed. Similarly, there are few data on polyaromatic hydrocarbons and other toxic organics which are produced during processing of timber, including creosote seeping[3]. In addition, there is a need for data on pathogen concentrations in Knysna Estuary, specifically in locations where people have contact with the water.

Biogenic pollution of Knysna Estuary is better known, primarily in the form of nutrient pollution originating in river catchments and in wastewater from adjacent urban areas. In the Knysna catchment, indigenous Afromontane forest has been replaced with plantations over a third of the total area (133 km^2). During the last two decades there has been a marked increase in the use of fertilizers in the forestry industry and on cattle farms in the area. Fertilizer is transported to the estuary by runoff following heavy rains[9]. In addition, high-nutrient wastewater is discharged into the estuary -via the Ashmead Channel, accounting for algal blooms in this poorly flushed channel[14,17]. In the summer of 2014/2015 a bloom of green macroalgae covered the water column and mudflats of the channel — a clear sign of eutrophication[18,19]. When the filamentous or foliose green algae genera *Ulva* and *Cladophora* accumulate in such large abundance, it is known as a 'green tide'. Legacy sediment and organic matter which has accumulated in the channel are also a contributing factor, with high fluxes of nutrients from the sediment into the water column of 100-300 μmol per m^2 per day nitrogen and 15 μmol per m^2 per day phosphorous[20]. Water column concentrations of NH_4 and DRP in the Ashmead Channel are significantly higher where wastewater enters the channel (145 μmol NH_4; 5 μmol DRP) than where the channel joins the main body of the estuary (20 μmol NH_4; 1 μmol DRP). This is a significant change from concentrations recorded 20 years ago[4,9] and may be partially attributed to lower oxygen levels.

During periods of hypoxia, remineralization results in higher benthic flux of nutrients from sediment to water[17]. While such eutrophication is only currently recorded in the Ashmead Channel, it is unclear how much longer dilution by tidal flushing can maintain the oligotrophic/clear waters that characterize the outer estuary. Indeed, the green waters and low oxygen levels in Ashmead Channel are a forewarning of changes that could happen elsewhere if a more concerted effort is not made to manage biogenic pollution and maintain the ecological health of the estuary. Such changes would lead to a loss of seagrass habitats and a wholesale transformation of the ecosystem, including fish and bird populations.

Knysna Estuary is crossed by multiple bridges and causeways, including roads to Thesen Island and Leisure Isle and other smaller alterations have also been made through small-scale channel dredging and seawalls. The most significant change to the morphology of the estuary is the railway crossing that serves to demarcate the outer and mid-estuary (Figure 1.4), although impact studies on the

Figure 5.13 Historical aerial photograph from 1936 showing the railway bridge several years after construction. A long bridge section straddles the main channel in the upper left of the photograph while a narrow culvert-bridge straddles a secondary channel below it.

functioning of the system are lacking. Built in the mid-1920s, the railway crossing is a combination of embankments and short-span bridges that together constrain the flow of water in the estuary (Figure 5.13). During large river floods the constriction is likely to account for elevated water levels in the mid- and inner estuary, which may contribute to flooding of low-lying lands. And if the bridge blocks outflow during river floods it also reduces peak flow velocities in both the mid-estuary and the outer estuary where peak-velocity events are critical for scouring the channel through the flood-tide shoals. Also, by controlling outflow it slows the draining of high marshes that scours channels and maintains marsh-estuary connectivity.

Perhaps more significantly is the alteration of tidal flows that pass through narrow breaks in the embankment, specifically on the south west side where the railway crosses intertidal flats and marshes. On the north east side, the bridge constriction is likely to speed up tidal currents in the main channel, increasing scour of the channel in the vicinity of the bridge and accounting for more mixing that reduces stratification. Although the constricted flow will result in enhanced along-estuary exchange and reduced residence in the mid-estuary due to tidal pumping[1], this is countered by a reduction in the conveyor-belt-like estuarine circulation related to stratification. Most evident is the effect of the bridge on increased sedimentation on either side of the channels, accounting for shoals and precluding small channels that would feed the marshes adjacent to Brenton-on-Lake.

Climate change effects on Knysna Estuary are addressed in Chapter 10. In relation to estuary hydrology, the foremost change is the rise in sea level that will make high tides higher, increasing flooding of low-lying lands and slowly drowning shoals and marshes that cannot build up fast enough through sedimentation. Shoals in the outer estuary are supplied with marine sediments, worked by tides, and it is expected that they will elevate as sea level rises, but marshes and mudflats in the mid-estuary are unlikely to receive sufficient sediment given the low sediment loading and small inflowing rivers. With little low-lying space for landward expansion of intertidal marshes (and mostly already occupied by humans), it is expected that there will be a loss of marsh habitat in the estuary. Climate change will also result in warmer waters and potential for stronger estuary-ocean thermal gradients that could enhance stratified intrusion of high-nutrient seawater. In addition, climate change is expected to change precipitation patterns, which in turn impact the pulses of freshwater inflow to the estuary and therefore the hydrodynamics of the system.

5.8 Conclusions

Knysna Estuary is characterized by low freshwater inflow and a large tidal prism, which account for the water column being generally well mixed and extensive sand shoals in the outer estuary. Significant stratification is only found in the inner estuary or during events when there is high river inflow or intrusions of cold upwelled water from the ocean. Similarly, phytoplankton blooms occur as events separated by periods of low concentration and clear water that have allowed extensive seagrass meadows to form. Comparable with other low-inflow estuaries connected to coastal upwelling, the Knysna Estuary is primarily driven by the ocean. It is an unusual estuary in South Africa due to the combination of a permanently open mouth and low nutrient input from the land.

Knysna Estuary is threatened by increasing nutrient input through wastewater/stormwater discharges and the accumulation of organic-rich sediments in Ashmead Channel and other poorly flushed side channels. The Knysna Estuary offers direct value to humans, as well as being an important habitat for wildlife — all of which is founded on the present ecological state that is derived from its open-mouth, low-nutrient status.

Dedication

We dedicate this chapter to Brian Allanson, our mentor, colleague, and friend who passed away as we were writing this chapter. We will miss him deeply. Not only did we gain many insights into Knysna Estuary from Brian, but he is responsible for recruiting both of us to work on this special estuary. We enjoyed many hours talking about Knysna, learning from him and developing a common purpose of understanding the estuary and sustaining it.

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Low tide view over intertidal flats towards The Heads (Photograph: © Dreamstime.com).

Chapter 6 : The Role of Plants and Algae in the Functioning of the Knysna Estuary

Johan Wasserman, Janine Adams & Lucienne Human

6.1 Introduction

Knysna's large estuarine bay supports a rich flora that is fundamental to the functioning of the ecosystem. Diverse communities of algae and aquatic plants (or 'macrophytes') fuel the complex estuarine food web through photosynthesis. Vegetation within and adjacent to the estuary acts as invaluable habitat to invertebrates, fish and birds. In addition to the ecological benefits, the 'ecosystem services' provided by the Knysna Estuary's primary producers are also a socio-economic asset. Submerged macrophytes form nursery areas for fish and bait organisms which are indispensable to the livelihoods of many subsistence fisherman and to the estuary's value as a site for recreational fishing.

The plants that fringe the estuary and lie hidden beneath the surface filter the water of pollutants, thus maintaining the vital balance of nutrients within the system. In addition, both emergent and submerged plants are a valuable natural aesthetic for residents and visitors alike. Knysna's renowned beauty is inextricably connected to the health of the estuary, which is in turn dependent on the state of the estuary's flora. The proper management of these habitats is of utmost importance for conserving the invaluable ecosystem services provided by the estuary.

Primary producer communities in estuaries are shaped by the dynamic conditions presented by the estuarine environment at the interface of rivers and oceans. Only species that can tolerate the physiological stresses presented by frequent tidal inundation by saltwater will be found in the lower reaches of estuaries, while those less tolerant to such stress occur in the fresher upper reaches. In addition to these environmental stresses, biotic factors such as competition and herbivory also shape primary producer communities, albeit to a lesser degree. Furthermore, estuaries are susceptible to the impacts of all anthropogenic activities that occur in catchments and along the coastline; areas that have been historically developed and intensively utilised by humans. Primary producers are often the first to respond to changes in environmental conditions, thereby acting as useful indicators for monitoring and managing estuary health.

Unlike most South African estuaries, which are closed to the sea for varying periods of time, the Knysna Estuary is classified as an estuarine bay.The estuary is permanently connected to the sea via the deep channel that runs through the famous Knysna Heads. This permanent connection to the sea maintainsthe estuary in a marine-dominated state with a large tidal range of 1.8 m and spring-tide prism volume of 19×10^6 m^3. The large tidal gradient maintains the well-established eelgrass beds, as well as the intertidal and supratidal salt marsh habitats. The influence of freshwater inflows, predominantly from the Knysna River, is generally limited to the upper reaches above the N2 bridge. As a result, the Knysna Estuary presents a relatively stable environment for flora to thrive.

The Knysna Estuary boasts the third largest area of vegetated habitats of all South African estuaries, only surpassed by St Lucia on the east coast and the Groot Berg Estuary on the west coast. Seagrass beds, salt marshes, reeds, and sedges cover approximately 2 400 ha within the estuarine functional zone of the Knysna Estuary[1]. This is the largest estuarine habitat area in South Africa's warm temperate biogeographic region, which spans from Cape Agulhas in the southwest to the Mdumbi Estuary in the Transkei. Furthermore, Knysna is one of just two naturally formed estuarine bays in South Africa (the other being Durban Bay, which has been highly modified and degraded), and the only estuary of this type in the warm temperate region. The zonal rarity, size, and diversity of plant habitats give the Knysna Estuary high botanical importance and are thus responsible for its number one biodiversity importance conservation ranking among all South African estuaries[2].

6.2 Algae

Various types of algae, from tiny organisms invisible to the naked eye (microalgae) to larger plant-like seaweeds (macroalgae), are found throughout the Knysna Estuary. Algae are not considered plants, but instead belong to the Kingdom Protista. This is because, unlike plants, most algae are unicellular, and all are nonvascular, meaning they do not form tissues like roots, stems and leaves. However, they share a similar ecological role to plants as fundamental primary producers as they are also capable of photosynthesis. The photosynthetic activity of algae is essential in oxygenating the water column and introducing energy into the estuarine food web. They are also responsible for important processes in the biogeochemical cycles of estuaries, such as the uptake and transformation of nutrients and carbon.

6.3 Microalgae

Although microalgae are largely not visible to the naked eye, they are often the most important primary producers in estuarine ecosystems. These microscopic unicellular organisms can exist in the water column and be attached to sand grains and bottom sediments, rocks, and even growing on submerged plants. Microalgae are represented by a diversity of functional groups — estuarine communities are typically comprised of chlorophytes, cyanobacteria, diatoms, dinoflagellates, and flagellates, although other groups may also be found. The composition of microalgal communities is governed by many factors, including but not limited to; freshwater inflow, salinity, nutrient availability, temperature, and hydrodynamics[3]. These communities are extremely important to estuarine productivity and act as useful ecological indicators.

Benthic microalgae, those that grow on the bottom sediments, are often the most productive microalgal component in estuaries. This high productivity makes them important as a food source to grazers and as a nutrient sink. These benthic communities are found on intertidal sediments and in shallow subtidal areas where light penetration is sufficient. They often form extensive biofilms that bind and stabilise sediments, thereby having the potential to influence estuarine morphology. Benthic microalgal communities are highly heterogenous in time and space. Community structure and biomass typically change along the estuarine salinity gradient, and communities respond rapidly to environmental changes[3]. In the Knysna Estuary, diatoms are the dominant functional group (as is typical in estuaries), with species richness as well as biomass generally increasing with distance from the mouth. Temporal changes in biomass and species dominance have also been noted, with an overall increase in biomass in response to nutrient enrichment[4]. However, no long-term monitoring data exist for the Knysna Estuary from which a baseline for benthic microalgae could be established.

Microalgae that occur in the water column of estuaries are collectively referred to as phytoplankton. Although some species are somewhat motile, most are not, and their vertical and horizontal position in the estuarine water column is controlled by the flow and turbulence of the water. Because of the estuary's large permanently open mouth, several species of phytoplankton can be found in the water column ranging from diatoms to a variety of dinoflagellates and marine-influenced species such as coccolithophores and some freshwater blue-green algae. Phytoplankton biomass, however, is generally low throughout the Knysna Estuary, indicative of an oligotrophic, well flushed water column[5]. Phytoplankton are commonly more abundant in the warmer summer months, particularly in the upper reaches where there is greater nutrient availability, vertical stratification of the water column, and ideal flushing rates for the proliferation of dinoflagellates. However, localised peaks in biomass have been recorded under different circumstances of nutrient enrichment. High phytoplankton biomass has been reported in the estuary's upper reaches following winter floods, which introduce nutrients from the catchment[4].

Substantial increases in nutrients and plankton 'blooms' have also been recorded during periods of marine upwelling[5], when winds displace the surface waters in coastal areas and the cold, nutrient-rich bottom water rises to the top and fuels phytoplankton production. In the past, such upwelling events along the southern Cape have caused long-lasting and widespread dinoflagellate blooms that colour the water a deep red, making them known as 'red tides'. The red tides entered the Knysna Estuary on several occasions between 2014 and 2016, prompting local authorities to warn residents to not harvest any shellfish, which can be toxic to humans if contaminated by phytoplankton blooms. These blooms are concerning for several other reasons — they deplete oxygen from the water column, decrease biodiversity, and can cause fish kills, among others[6]. Fortunately, the Knysna Estuary is well flushed by the tides; however, the threat of eutrophication should not be underestimated as localised phytoplankton blooms are likely to become more frequent if better nutrient management strategies are not adopted in the catchment and estuary functional zone[4]. A key bloom forming species, *Heterocapsa* sp., recently found in the estuary, is cause for concern. This microalga is a well known bloom-forming red tide species occurring in the Sundays and Swartkops estuaries in the Eastern Cape.

The greatest potential impact to the estuary's microalgal communities is likely related to changes in freshwater inflow, which has been decreasing due to abstraction[7]. Although recent microalgal monitoring has been limited, decreased freshwater inflows has likely caused changes in abundance and community composition. This is especially pertinent to the estuary's upper reaches, which would present more stable conditions with longer water residence times that allow for the proliferation of dinoflagellates. The nutrient concentrations in the estuary are also intrinsically linked to river inflow, and any changes to incoming nutrient levels can cause shifts in microalgal species composition. Also related to low river input is a clear water column and a more marine-dominated state due to greater tidal penetration by seawater — these factors would facilitate an increase in benthic microalgal biomass[4].

6.4 Macroalgae

Various species of macroalgae are found throughout the Knysna Estuary, growing from the bottom sediment, floating in the water column, or attached to rocks and other hard surfaces. Much of the estuary's channel bottoms, particularly around the middle reaches, are covered by dense beds of bright green *Caulerpa filiformis* and the feathery red *Asparagopsis taxiformis* (Figure 6.1). *Asparagopsis taxiformis* is an extremely successful invasive species in many parts of the world, including Knysna, where it was first discovered in the Leisure Isle boat harbour in 2008[8]. The species is thought to have been introduced by the transport of oysters for commercial aquaculture. Recent underwater surveys found the species to be widely distributed throughout the Knysna Estuary[9]. *Caulerpa filiformis* itself is a highly competitive species, and together with *A. taxiformis*, is likely placing competitive pressures on the important subtidal eelgrass beds of *Zostera capensis* in the estuary. Nonetheless, these benthic macroalgal beds provide a valuable habitat for invertebrates and nursery areas for juvenile fish.

In areas that would be otherwise barren, seaweeds provide habitats for a diverse array of fish species that find food and shelter within the fronds of these plants. For example, the rocky areas around The Heads have been colonised by numerous macroalgae including species of the green seaweeds *Bryopsis*, *Chaetomorpha*, *Codium*, *Enteromorpha* and *Ulva*, the brown seaweeds *Splachnidium rugosum* and *Zonaria tourneforti*, and the red seaweed *Gelidium pristoides*. Macroalgae found in the marinas and harbours of the estuary create natural habitats in unnatural settings. Around Thesen Island, dense free-floating beds of *Codium tenue* gather in quiet inlets and dead ends in the canals, where they are an important habitat for the endangered Knysna seahorse[10]. Mixed beds of *C. filiformis*, *A. taxiformis*, *Polysiphonia* sp. and seagrass also form habitats within the marina[11].

Seaweeds have also been a nuisance in the Knysna Estuary. Like red tides, the term 'green tide' is given extent that they cover the surface of the water in sheets. Common bloom forming species belong to the foliose or uniseriate filamentous

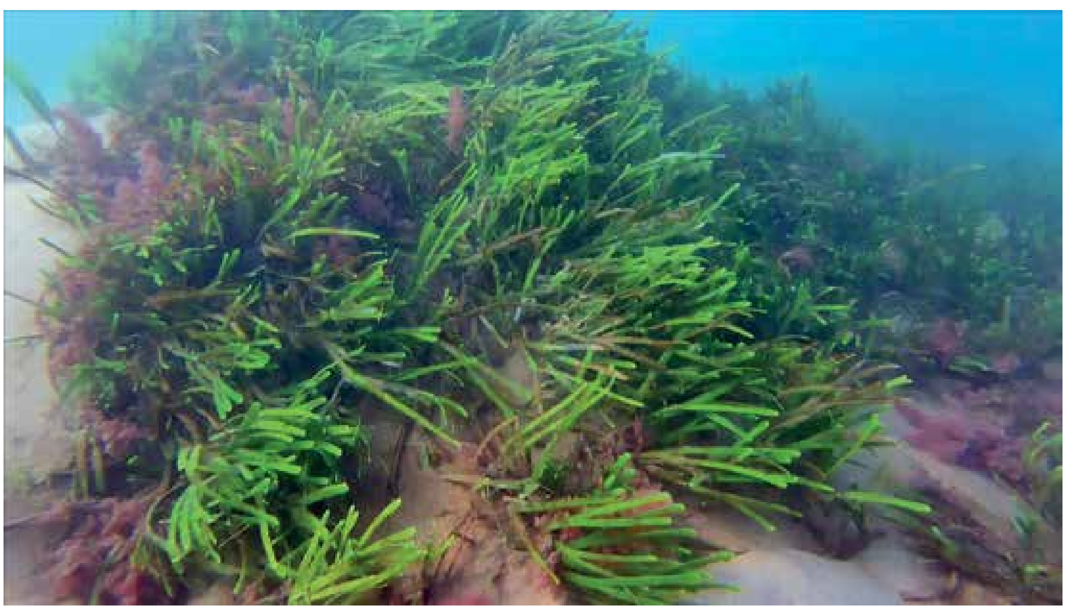

Figure 6.1 A subtidal bed of the green seaweed *Caulerpa filiformis* and the invasive red alga *Asparagopsis taxiformis* visible in the top left and bottom right of the picture (Photograph: © Johan Wasserman).

green algae genera *Ulva*, *Enteromorpha* and *Cladophora*. Successful occupancy by green tides in a water body undergoing nutrient enrichment is attributable to their successful uptake and storage of inorganic nutrients, high growth rates, and high tolerance to a wide range of temperatures and salinity. In the summer of 2014/2015, the estuary's first green tide was recorded[12,13]. Large decaying algal mats were deposited along various parts of the estuary's shore, raising concerns among residents with the unappealing resemblance of toilet paper and off-putting odours. This was a macroalgal bloom comprised mostly of the sea lettuce *Ulva lactuca* (Figure 6.2) which forms thin green mats, but a filamentous green *Chaetomorpha* species was also present. Winds and tides washed these mats onto intertidal areas, where they covered mudflats and smothered *Z. capensis* beds. *Ulva* blooms not only impact seagrass beds, but also cause major reductions in the abundance of invertebrates in unvegetated sediments, which has knock-on effects on higher trophic levels. The green tide resulted in a significant decrease in fish diversity and abundance over both bare sediments and *Z. capensis* beds[14]. The bloom was a symptom of eutrophication fuelled by the recycling of nutrients in the anoxic

Figure 6.2 A mat of filamentous *Ulva lactuca* associated with a *Zostera capensis* bed (Photograph: © Johan Wasserman).

sediment of the warm, shallow Ashmead Channel and discharge from the nearby wastewater treatment works[13]. Concerningly, *Ulva* blooms appear to be recurring in the estuary's bait reserve, with bright green algal mats still apparent in the Ashmead Channel and around Leisure Isle during 2018 and 2021 (Figure 6.3a & b). Eutrophication and algal blooms will remain a threat to biota in the Knysna Estuary, particularly in the Ashmead Channel region, if the anoxic conditions and wastewater discharge continues[15].

Although there are nuisance macroalgae in the estuary, innovative solutions exist to minimise their ecological impact. Tissue samples of *Ulva* that caused the green tide were found to have a high macronutrient content and low concentrations of selected heavy metals, leading to Human et al.[13] recommending that the species be harvested and used for compost or fertilizer. Additionally, recent studies have shown that *Asparagopsis* seaweeds, including the invasive species in the Knysna Estuary, can be used to supplement cattle feed and effectively decrease livestock methane emissions by over 80%[16]. Dairy farming is a major economic activity in the Garden Route, and the use of *Asparagopsis* in cattle feed presents an opportunity to lower the greenhouse gas emissions of these farms while simultaneously removing an invasive species from the country's most important estuary. Capitalising on such innovations will be essential in moving toward a sustainable 'blue economy' in the face of global change.

Figure 6.3a Bright green mats of *Ulva lactuca* cover much of the *Zostera capensis* bed area in the Knysna Estuary's bait reserve; June 2021 (Photograph: © Johan Wasserman).

Figure 6.3b *Ulva lactuca* smothering *Zostera capensis*; view towards Leisure Isle; March 2018 (Photograph: © Janine Adams).

Table 6.1 Area cover of the different subtidal habitats within the study area.

Description	Habitat	Area (ha)	Total area (ha)
Submerged macrophytes	*Zostera capensis*	130.4	316
	Zostera capensis mixed	185.6	
Macroalgae	*Asparagopsis taxiformis* mixed	41.3	315.9
	Caulerpa filliformis	12.3	
	Caulerpa filliformis mixed	262.3	
Unvegetated areas	Unvegetated sediment	218.5	221.9
	Natural rocky areas	3.4	
Other	Sponge and soft corals	2.6	2.6
			856.4

6.5 Seagrass

Expansive beds of seagrass form a particularly special habitat in the Knysna Estuary. Here, the largest, most stable beds of the endangered Cape dwarf eelgrass *Zostera capensis* are found[17] (Figure 6.4). This is the dominant seagrass species along our coastline. In shallow subtidal areas where light penetration is sufficient, dense canopies of long leaved *Z. capensis* can be found. However, eelgrass has great morphological plasticity and is tolerant of desiccation, and extensive beds of *Z. capensis* with shorter and narrower leaves can be found in intertidal areas that are exposed during low tides. The latest assessment of *Z. capensis* in Knysna determined that the estuary accommodates at least 317 ha in intertidal areas and 130 ha in subtidal areas that had not been accounted for in previous surveys[9] (Table 6.1, Figures 6.5 and 6.6). The true area cover is greater, as this assessment also recorded a further 130 ha of *Z. capensis* as the dominant vegetation in beds mixed with macroalgae and did not account for the areas extending above the N2

Figure 6.4 An intertidal eelgrass bed in the Knysna no-bait exploitation area that flourishes due to the lack of bait harvesting activities and absence of smothering macroalgae (Photograph: © Alan Whitfield).

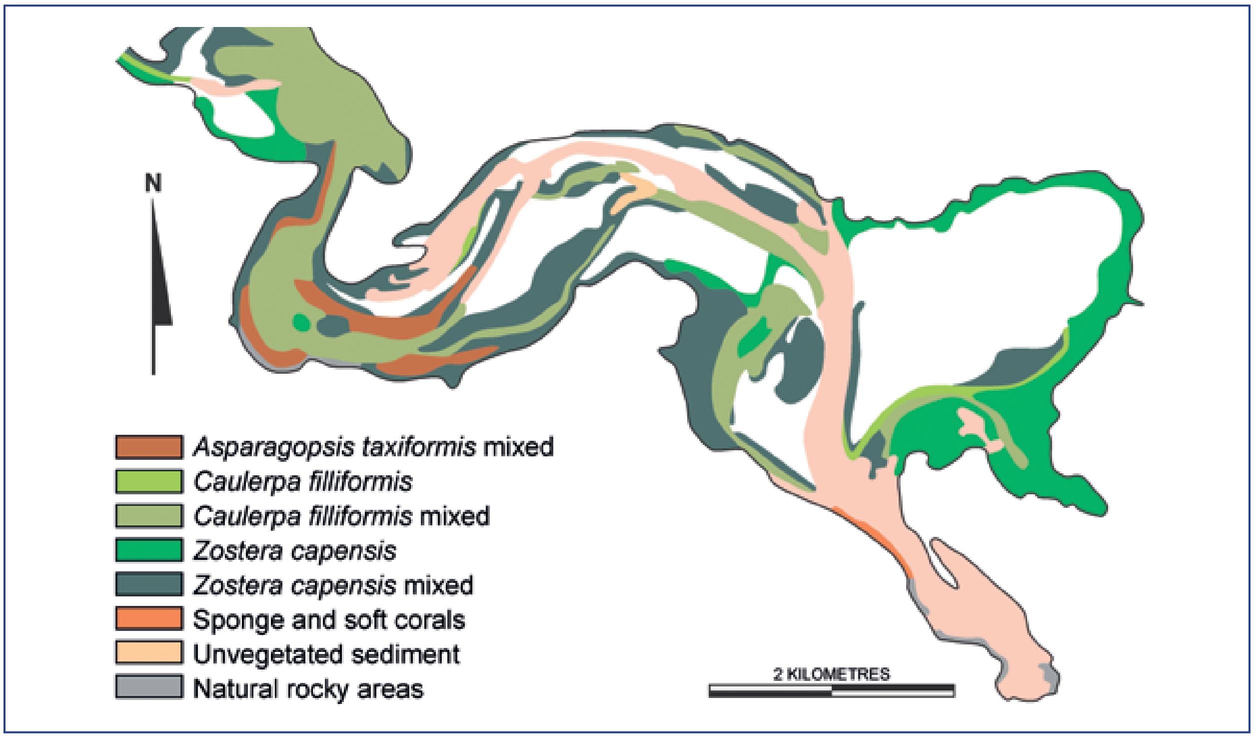

Figure 6.5 Distribution and area cover of macroalgae and eelgrass *Zostera capensis* in the Knysna Estuary (adapted from Wasserman[40]).

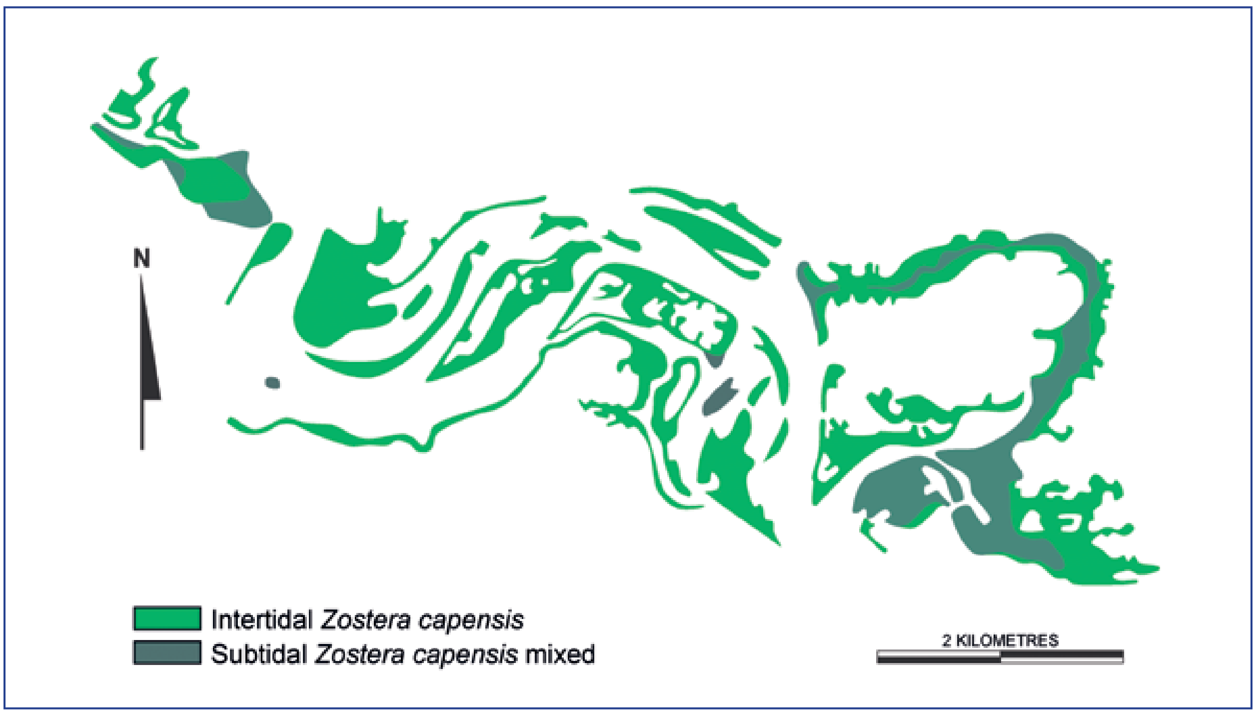

Figure 6.6 Distribution of intertidal and subtidal eelgrass *Zostera capensis* in the Knysna Estuary (adapted from Wasserman[40] and Wasserman et al[9]).

Figure 6.7 The small spoon grass *Halophila ovalis* among eelgrass *Zostera capensis* in shallow subtidal areas. In deeper subtidal areas the spoon grass can occur as pure stands (Photograph: © Janine Adams).

bridge and into the Salt River. Another seagrass, the small spoon grass *Halophila ovalis* is also often hidden amongst the estuary's subtidal *Z. capensis* beds (Figure 6.7).

Seagrass beds have long been recognized as some of Earth's most productive and valuable ecosystems but have, unfortunately, been rapidly declining around the world. In South Africa, local extinctions of *Z. capensis* have occurred at Durban Bay and St Lucia[17]. Seagrass beds are sensitive to extreme weather events such as floods and heat waves. Floods can temporarily remove *Z. capensis* beds from estuaries, as has occurred in the Swartkops Estuary. The impact of marine heat waves on estuaries has not yet been recorded in South Africa, but such events have caused large-scale seagrass diebacks in Australia. Seagrasses can recover from such events, but this may take several years. However, the expected increase in extreme weather events associated with global climate change is concerning and presents a major challenge in conserving these valuable habitats.

The important seagrass beds of the Knysna Estuary face their own unique threats. The greatest threat is the deterioration of water quality and eutrophication. Resultant *Ulva lactuca* blooms in the Ashmead Channel have displaced *Z. capensis* beds in the past and continue to wash up and smother these beds (Figure 6.3). Heavy growth of epiphytic microalgae is also apparent on *Z. capensis* leaves in the Ashmead Channel, a symptom of nutrient enrichment which is problematic as it reduces the amount of light available to the eelgrasses. However, another cause in the decline of *Z. capensis* in Ashmead Channel may arise from the anoxic sediment itself. Studies have shown that high sulphide concentrations linked to anoxia lead to sulphide intrusion into the meristematic tissue of seagrass. This results in decreased photosynthetic rates and leaf growth, and even mortality.

Other pressures on *Z. capensis* seagrass beds include boating-related damage anchoring and propellor damage, trampling by bait collectors, illegal bait digging (Figure 6.8), and siltation due to stream and stormwater runoff[7]. There is also erosion along the banks in the upper reaches of the estuary that could limit the distribution of eelgrass in these areas (Figure 6.9). These are all anthropogenic threats

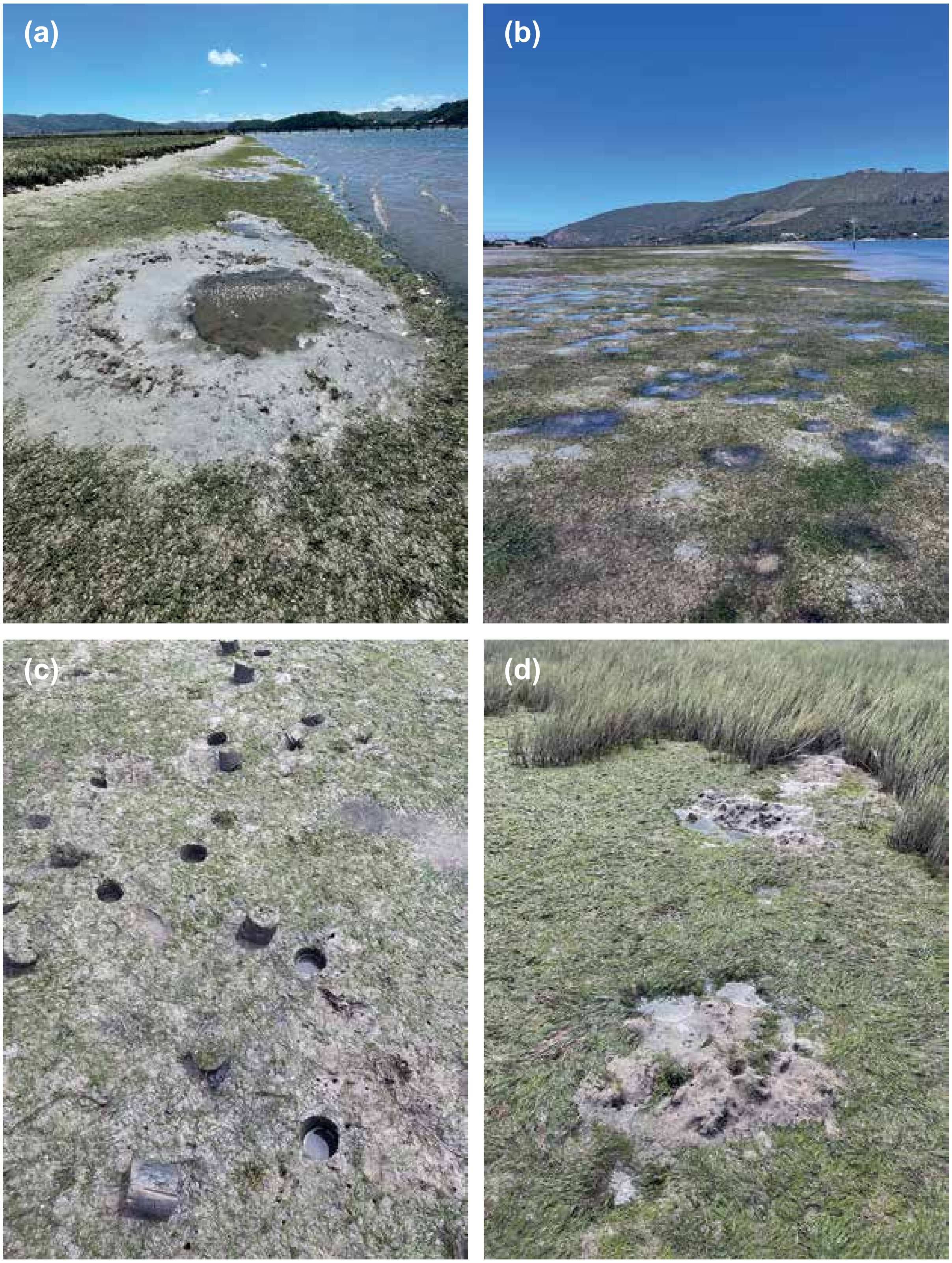

Figure 6.8 Effect of crab and bait collection on intertidal *Zostera capensis* beds in the Knysna Estuary; February 2022 (Photographs: © Riaan Weitz).

Figure 6.9 No eelgrass habitat present in the area above the N2 bridge, possibly due to severe bank erosion; February 2021 (Photograph: © Janine Adams).

that need to be addressed through management actions to ensure the conservation of the estuary's eelgrass habitats; the largest in South Africa.

6.6 Salt marsh

The gently sloping banks of the Knysna Estuary are covered with colourful salt marshes. These are among the largest salt marshes in the country, covering approximately 685 ha, with the third-largest area of intertidal salt marsh following the Groot Berg and Langebaan estuaries[18]. Salt marsh plant communities are comprised of a variety of small succulent herbs, grasses, and low shrubs that can withstand the physiologically stressful conditions associated with the dynamic coastal zone.

Salt marsh habitats can typically be defined into distinct zones, each characterised by a different dominant plant species. The shoreward limit of each zone is determined by the dominant plant's tolerance to tidal inundation and salinity, while the landward limit is influenced by competition with other plants. Tidal inundation and salinity are related to the elevation — the lower-lying areas on an estuary bank are submerged by high tides more frequently and for longer periods of time and are generally more saline (Figure 6.10). As a result, salt marsh zonation can be easily distinguished on estuary banks with a constant incline from the water's edge toward the land (Figures 6.11a & b), but difficult to see in areas with an uneven terrain where the plants form mosaics (Figure 6.12). Knysna's salt marsh zonation is generally well developed due to the estuary's large tidal range and gentle slopes that eventually grade into terrestrial vegetation on the landward side of the salt marsh (Figure 6.13).

Intertidal salt marsh

Intertidal salt marsh is found on the lowest-lying parts of estuary banks that are frequently inundated during high tides. In the lower and middle reaches of the Knysna Estuary, the lowest portion of intertidal salt marsh is dominated by dense stands of small cordgrass *Sporobolus maritimus*, often protruding above a layer of short-leaved eelgrass. The top of the cordgrass zone blends into stands of the small arrowgrass *Triglochin buchenaui*, which in turn transitions into a rich mosaic of various small herbaceous plants that is mostly inundated only during spring high tides. The dominant species in this zone belong to the tufty sea-lavender (*Limonium*) and fleshy segmented glasswort (*Salicornia*, previously *Sarcocornia*) genera. Of the glassworts, *Salicornia*

Figure 6.10 Spring high tide and submergence of the salt marsh grass *Sporobolus maritimus* and succulent *Salicornia tegetaria*; March 2018 (Photograph: © Janine Adams).

tegetaria is dominant. Other species that can be seen in this zone include the deep green succulent *Plantago crassifolia*, *Cotula coronopifolia* with its bright yellow button-like flowerheads and the small succulent creeper *Poecilolepis ficoidea*. In the upper reaches of the estuary, above the N2 bridge, the salt marshes have a visibly different community structure due to the diminished tidal influence and freshwater input from the Knysna River. Intertidal salt marshes here are comprised mostly of extensive stands of the incema rush *Juncus kraussii* lying among networks of creeks (Figure 6.14). Most of the previously mentioned succulent herb species lie hidden among these stands, often among shallow brackish creeks, but zonation is difficult to discern.

Supratidal salt marsh

Just landward of the intertidal zone lie the colourful supratidal salt marshes, which are submerged during only the highest of spring tides. The succulent leaves of several species are often a bright pinkish-red; a physiological response to the stressfully high salinity resulting from the high concentration of salts in the sediment due to evaporation in between infrequent tidal flooding. The most widespread species in this zone is *Chenolea diffusa*, which often forms sprawling mats of whitish-green and pink from above the high water mark (Figure 6.15). At a slightly higher elevation, blankets of *Disphyma crassifolium* can often be seen, characterised by bright violet pink flowers amongst fleshy green clavate leaves that are triangular in cross-section. Patches of *Salicornia pillansii* may also occur here (Figure 6.16), although this species is more common in the estuary's upper reaches where it often forms sprawling monospecific blankets in areas where salt has accumulated in the sediment. The uppermost fringe of supratidal salt marsh is often lined with the grasses *Stenotaphrum secundatum* and *Sporobolus virginicus*. In some areas in the estuary's lower and middle reaches, stands of *J. kraussii* can also be found at the top of the supratidal zone, with these stands being more common further upstream from the mouth. *Spergularia glandulosa* (common name sandspurry) often grows in the supratidal salt marsh areas in the ecotone with terrestrial vegetation, although it is a halophyte tolerant of salty conditions (Figure 6.17).

Figure 6.18 shows the distribution of salt marsh species along a tidal gradient situated east of the Old Belvidere residential areas[19]. This transect was 140 m in length and showed clear zonation of different species along an elevation/tidal inundation

Figure 6.11a Salt marsh zonation along the tidal inundation/elevation gradient as seen at Belvidere (Photograph: © Janine Adams 2020).

Figure 6.11b Three distinct salt marsh zones visible along an elevation gradient opposite Thesen Island (Photograph: © Alan Whitfield).

Figure 6.12 A mosaic of different salt marsh plants near The Point (Photograph: © Alan Whitfield).

gradient. *Juncus kraussii* was dominant at the top of the transect and gave way at 20 m to moderate patches of *D. crassifolium* interspersed with *S. pillansii* which was dominant between 30 to 90 m. *Chenolea diffusa* grew in a distinct band with some *S. tegetaria*, *Limonium*, *P. ficoidea* and *P. crassifolia* growing in between. As the profile started dropping at approximately 100 m, a band of *T. buchenai* became dominant, shortly followed by *S. maritima* as the profile dropped steeply at 120 m. Thereafter intertidal eelgrass *Z. capensis* became exclusively dominant at the estuary water channel.

Salt marsh loss

As in many estuaries around the world, Knysna has lost extensive areas of salt marsh due to development. In the last century, the respective loss of intertidal and supratidal salt marshes has been approximately 30% and 65%[18]. Fortunately, development in coastal zones has become more regulated by legislation such as the National Environmental Management Act and the National Water Act introduced in 1998 and the National Environmental Integrated Coastal Management Act promulgated in 2008. Now, developments within the 5 m contour boundary of estuaries, known as the estuarine functional zone, require environmental impact assessments and authorisation. Despite this, historic developments have already led to the substantial irreversible loss of salt marsh and will continue to impact Knysna's salt marshes into the future. The construction of bridges, roads, causeways and seawalls have restricted tidal movement, impacting plant zonation and limiting the deposition of detritus that provides the nutrients necessary for plants to survive, ultimately degrading some areas of salt marsh[20].

As sea levels rise continually with climate change, peripheral developments will act as a barrier preventing salt marshes from moving landwards in a phenomenon known as 'coastal squeeze'. Recent modelling has estimated that coastal squeeze will result in further loss of large areas of intertidal salt marsh from Knysna during this century[21]. Because of hard infrastructure (e.g. Figure 6.19), Knysna has not been identified as a priority site for salt marsh restoration in South Africa[22]. This highlights the importance of conserving the existing salt marshes and preventing future development within the estuarine functional zone. There are salt marsh areas that are allotted for future development within the South African cadastre that should be set aside for future salt marsh expansion with sea level rise (Figure 6.20).

Figure 6.13 An intertidal salt marsh on Leisure Isle, showing the transition or ecotone from an aquatic to a terrestrial environment (Photograph: © Johan Wasserman).

Figure 6.14 Stands of sharp rush *Juncus kraussii* close to water in the upper reaches of the Knysna Estuary; June 2018 (Photograph: © Janine Adams).

Sea-level rise and sediment surface elevation changes

Ongoing long-term monitoring using Rod Surface Elevation Tables (RSETs) is being carried out to investigate the response of Knysna's salt marshes to sea level rise (Figure 6.21). This is the globally standardized method for measuring coastal wetland responses to sea-level rise. The RSET is used to measure changes in sediment surface elevation in comparison to a perm-anent reference point or benchmark which is levelled relative to mean sea level[21]. RSET benchmarks are installed by first driving solid, 15 mm stainless steel rods into the sediment until refusal. A PVC pipe (30 cm length) is inserted to be level with the surface of the sediment. The receiving end of the benchmark is placed last, so that is protrudes from the surface of the sediment. The PVC pipe is then filled with cement to secure the benchmark. The first measurements are taken at least six months later to allow time for the benchmark to stabilise. The measuring arm is secured into the receiving end, the arm is levelled, and measurements are taken from the nine vertical pins (Figure 6.21).

There are seven existing permanent RSET stations in the Knysna Estuary; all located in the lower intertidal zone in the salt marsh grass, *S. maritima*. This would be the first area to be affected by increases in sea level. The *S. maritima* zone is also known to trap sediment from tidal flows as the vegetation dissipates the flow of water, allowing suspended sediment to settle out[19]. Measurements taken over the past decade have shown that surface elevation change is variable through the length of the estuary, with some sites showing surface elevation gains (increasing in height), while others showing deficits (subsidence, or loss of elevation). These trends are associated with different hydrodynamic conditions and sediment availability in different areas of the estuary[21].

Future threats

In addition to development, Knysna's salt marshes have been impacted by several other anthropogenic activities[20]. In some places, vegetation bordering salt marshes has been removed, allowing silt-laden and nutrient-rich stormwater to flow directly onto the salt marsh and strong outflows have directly

Figure 6.15 The whitish-green and pink *Chenolea diffusa*, sprawling amongst the slender deep green *Triglochin buchenai* and the bright green *Salicornia tegetaria*; February 2018 (Photograph: © Janine Adams).

Figure 6.16 A mat of bright green *Disphyma crassifolium* adjacent to the pink finger-like *Salicornia pillansii*; February 2018 (Photograph: © Janine Adams).

Figure 6.17 *Spergularia glandulosa* (common name sandspurry) often grows in the supratidal salt marsh areas in the ecotone with terrestrial vegetation; it is a halophyte tolrant of salty conditions (Photograph: © Janine Adams).

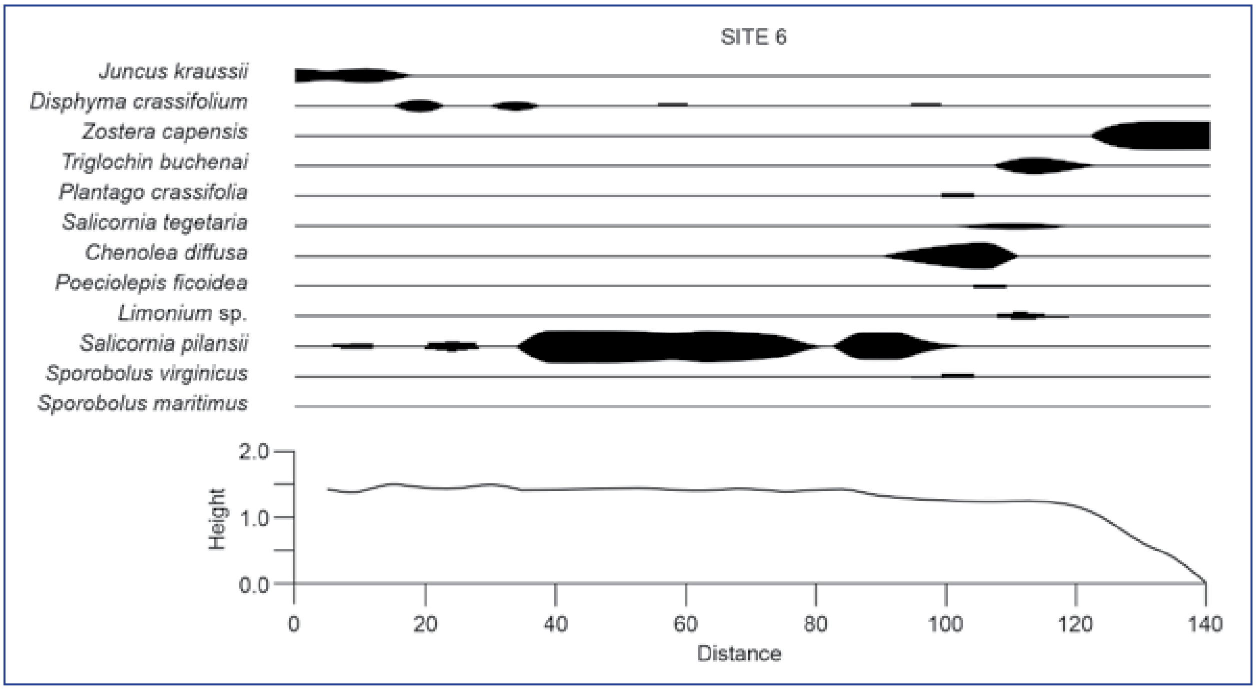

Figure 6.18 Distribution of eelgrass and salt marsh species along an elevation gradient (estimate of height above mean sea level in m) at a site near the Old Belvidere residential area.

damaged the habitat in some cases. Some areas that have been disturbed during development have been colonised by invasive or terrestrial plants. Boats are often left moored on salt marshes, shading out and killing underlying plants. Fishermen and recreational users have formed footpaths throughout the estuary's salt marshes; although they tend to use the same paths preventing further damage. The wake from boats also causes salt marsh erosion.

An additional immediate threat to Knysna's salt marshes is likely the decrease in fresh-water inflow[7], which can impact the composition and distribution of salt marsh communities through changing the salinity regime that influences salt marsh zonation. When Thesen Island was developed (2000 - 2007) it was stipulated that there should be no net loss of salt marsh. This was achieved by planting supratidal salt marsh above the rip rap of the marina canals. However, there are now signs of erosion (Figure 6.22) as survival of this habitat is dependent on a sediment supply. The salt marshes at Knysna Estuary are nationally important and need to be prioritized for protection.

6.7 Reeds and sedges

Dense stands of the common reed *Phragmites australis* fringe parts of the Knysna Estuary. This reed species is cosmopolitan and found in wetlands around the world. *Phragmites australis* is sensitive to salinity, so in estuaries, it only occurs in brackish waters or in areas of freshwater seepage, where its roots are submerged in relatively fresh water[23]. Reeds cover approximately 24 ha in the Knysna Estuary, with the largest stands occurring to the east of George Rex Drive and in several stands north of the N2 bridge[7]. The estuary's reed beds have remained relatively stable over time, although some area has been lost around George Rex Drive.

Sedimentation in the estuary's upper reaches has been noted, which may allow for the spread of reeds[4]. The spread of reeds may be problematic as they can choke up channels and cause anaerobic conditions through organic loading which occurs with an accumulation of leaf litter[24]. However, this is unlikely to occur in Knysna as the saline conditions throughout most of the estuary will limit reed growth and dispersal, especially as freshwater inflow has been decreasing[7]. The existing reed beds can be expected to remain stable on the fringes of the estuary where there is runoff or freshwater seepage (Figure 6.23).

6.8 Ecosystem services

Through their various ecological roles, estuarine flora provide a multitude of ecosystem services (Figure 6.24). Primary producers configure the estuarine

Figure 6.19 Hard infrastructure near Brenton-on-Lake showing the inability of any salt marsh establishment landward of the vertical concrete wall (Photograph: © Alan Whitfield).

environment through their ecological functions. Algae and submerged macrophytes oxygenate the water column and regulate the acidity of the water through their photosynthetic activity. Seagrasses are considered particularly efficient 'ecosystem engineers' due to their ability to manipulate the surrounding environment. Their dense canopies reduce current velocity and wave energy thereby increasing sedimentation, while the below ground roots and rhizomes stabilise sediments[25]. This makes these beds important in protecting coastlines against erosion as well as improving water clarity, thus facilitating the photosynthetic activity of other estuarine primary producers. On the banks of estuaries, reed beds and salt marshes provide a natural defence against coastal flooding and erosion.

Through forming physical habitats, vegetation also maintains estuarine biodiversity. Invertebrate burrows are formed in the salt marsh (Figure 6.25). Vegetated habitats like seagrasses and salt marshes are widely referred to as 'nursery areas' that provide fauna with refuge from predation and the arduous estuarine environment and are crucial to the growth and survival of juvenile fish and invertebrates. Salt marshes also provide important habitats for a variety of bird species (Figure 6.26) and serve as roosting and feeding sites. Seagrass beds are particularly important nursery areas—many South African studies have shown how important our *Z. capensis* beds are as sites for foraging and shelter that support abundant and diverse communities of fish and invertebrates, including numerous studies conducted in the Knysna Estuary[26,27]. Knysna's eelgrass beds are also important habitats for highly endemic and threatened species like the Endangered Knysna seahorse *Hippocampus capensis* and the Critically Endangered limpet *Siphonaria compressa*[28,29]. During high tides, salt marshes and reed beds also serve as valuable shelter and feeding grounds for fish[30].

The role of primary producers in biogeochemical cycles maintains the health of estuaries. As they take up nutrients necessary for their growth, they alleviate nutrient pollution from anthropogenic activities in the surroundings of estuaries, thereby limiting eutrophication. Salt marshes and reed beds

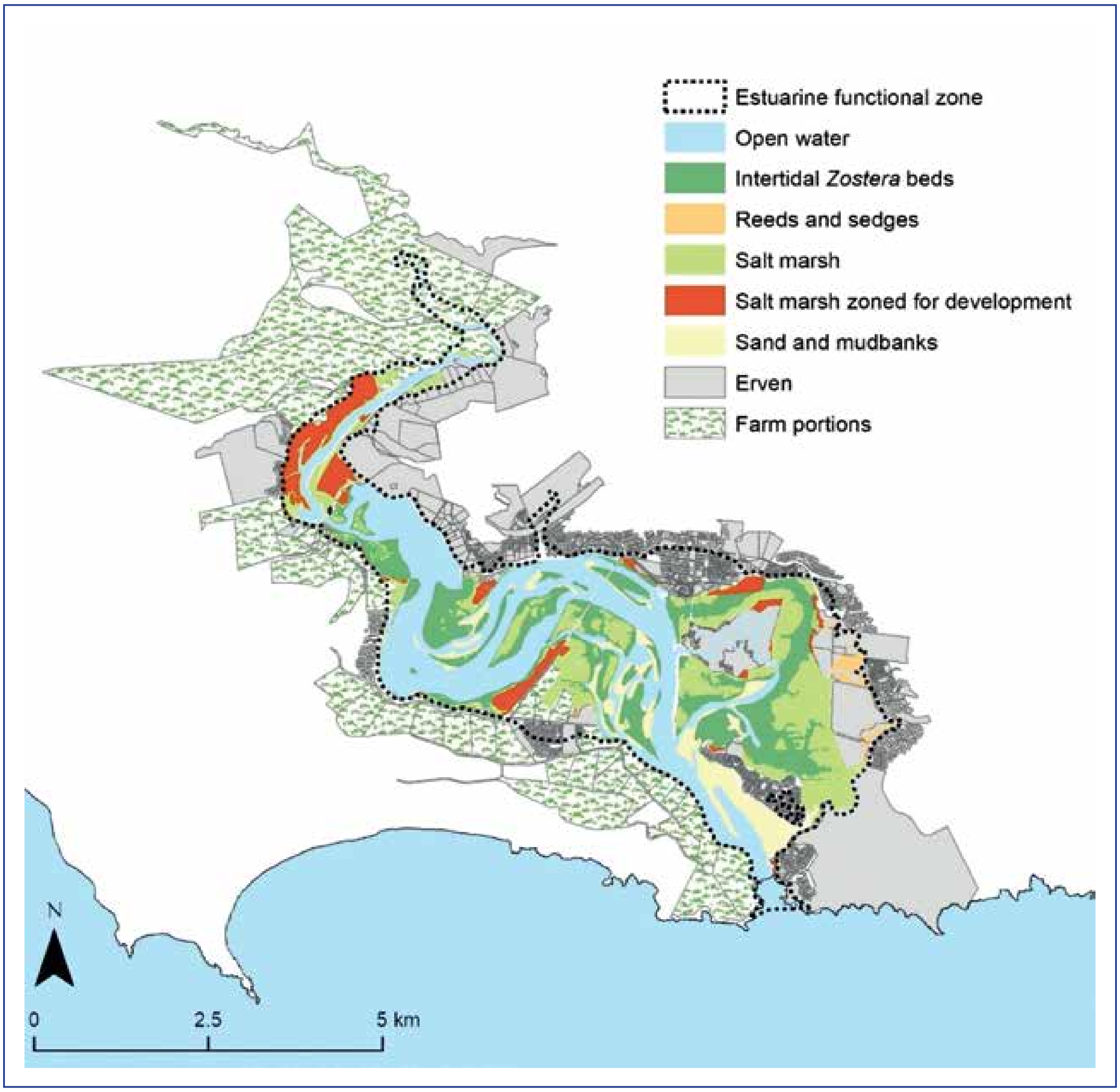

Figure 6.20 Distribution of habitats and developed areas around the Knysna Estuary. Salt marshes shaded red are those that are allotted for future development within the South African cadastre (adapted from Raw et al. 2020). These areas should be set aside for future salt marsh expansion in response to sea level rise.

Figure 6.21 The RSET levelling arm that is attached to a receiver is used to measure surface elevations and can therefore monitor salt marsh level changes (Photograph: © Janine Adams).

act as natural buffers that can filter nutrients from terrestrial water sources (like agricultural runoff and septic tanks) and groundwater that enters estuaries. Reed beds are particularly useful indicators of nutrient enrichment[31]. Salt marshes also act as a filter for other contaminants like heavy metals that are detrimental to estuarine biota[32]. Microalgae and seaweeds effectively take up nutrients from within the water column, and seagrasses take up nutrients from both the sediment and the water column, forming a link in the nutrient cycles of the sediment and the overlying water. While growing, seagrasses assimilate nutrients (particularly substantial amounts of nitrogen) until they senesce and release inorganic forms of nutrients during decomposition, which can then be easily taken up by other primary producers[33,34]. As dead seaweeds and *Z. capensis* wrack float away, they transport large amounts of nutrients to other areas of the estuary or nearby coast, or onto salt marshes if deposited onto the shoreline (Figure 6.27). This is an important source of detritus for the estuary.

Salt marshes and seagrasses also play a crucial role in the global carbon cycle. These habitats, referred to as 'blue carbon habitats' are able to sequester large amounts of organic carbon in their biomass and underlying sediment and store them over millennial timescales. This is a particularly important ecosystem service in the face of ever-increasing anthropogenic carbon emissions, and along with the abovementioned ecosystem services, highlights the value of conserving estuarine habitats for their ability to mitigate the impacts of global climate change. Blue carbon science has emerged in the last decade as an exciting new field of research that is continually expanding, including in South African estuarine research[35,36,37].

All of these ecosystem services provided by the Knysna Estuary's flora are truly appreciable socioeconomic and cultural assets. The estuary's habitats keep the estuary clean and healthy, maintaining the amenity value for residents and attracting thousands of visitors each year. It is estimated that tourism associated with the estuary generates

Figure 6.22 Supratidal salt marsh established at Thesen Island showing erosion and loss of sediment; February 2021 (Photograph: © Janine Adams).

Figure 6.23 Reeds (*Phragmites australis*) form an important buffer for the estuary at freshwater seepage sites (Photograph: © Alan Whitfield).

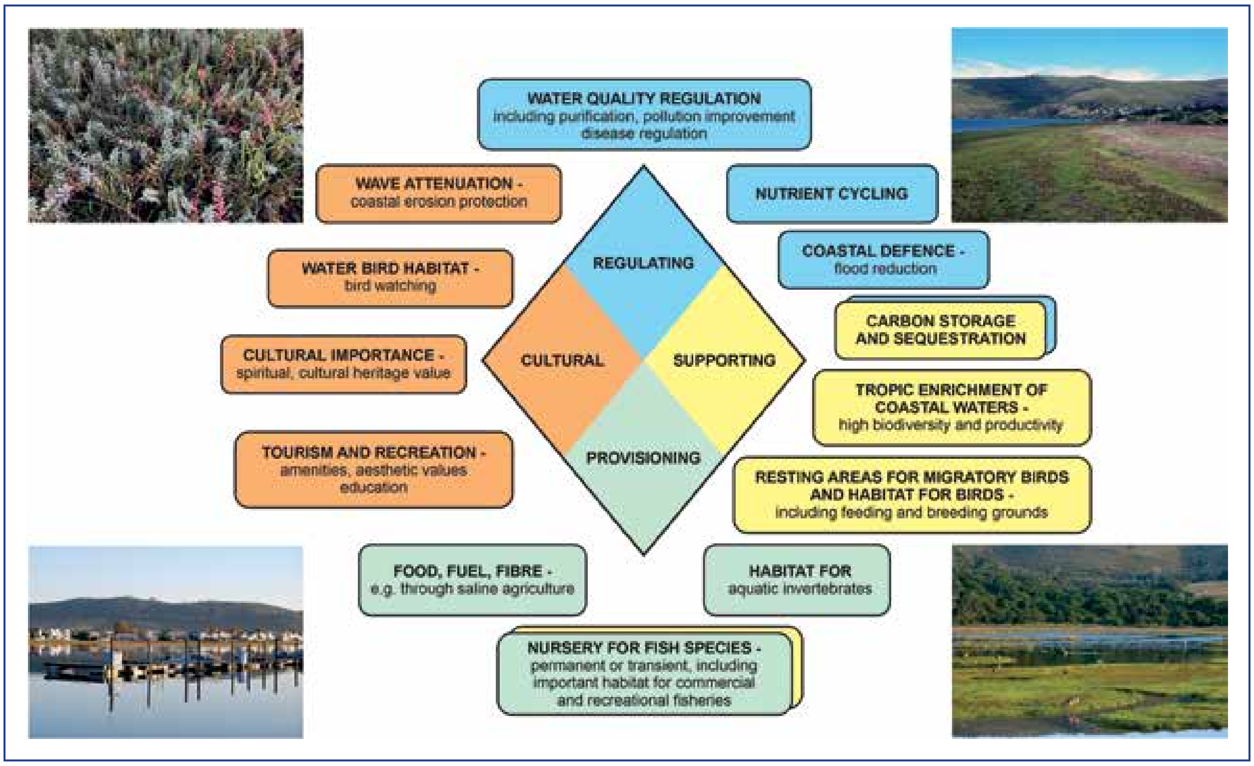

Figure 6.24 Ecosystem services provided by estuarine plants[22].

Figure 6.25 Giant mud crab (*Scylla serrata*) burrow and pincer in the lower intertidal salt marsh area in the upper estuary reaches; May 2021 (Photograph: © Janine Adams).

R1 billon each year[38]. The estuary is also crucial to the livelihoods of resident subsistence fishers. The economic value of the estuary's function as a nursery habitat for fish and invertebrates is estimated at nearly R170 million annually, while subsistence use generates nearly R700 000 to R1 million per annum[38,39]. The scenic views of the Knysna Estuary and its picturesque salt marshes hold high aesthetic values—the highly sought-after properties with a view of the estuary are valued at a total of between R1.4 to R2 billion. In addition to this economic value, the estuary provides a site for recreation and contributes to human wellbeing, which is invaluable to residents and visitors alike.

6.9 Looking forward

The diverse plant and algal communities of the Knysna Estuary fulfil a variety of ecological roles that provide environmental as well as societal benefits. Although these habitats have already been impacted in several ways, it is important to manage and mitigate existing impacts and to avoid emerging ones. However, the conservation of the estuary's habitats cannot be at the expense of their subsistence and recreational value that is so important to the livelihood of Knysna. Maintaining a harmonious relationship between the environment and society presents a major management challenge that requires innovative and adaptive approaches.

Several impacts can be directly addressed by means of management action. Firstly, no further saltmarsh should be lost or degraded to allow for new developments. Surrounding land needs to be protected to allow for landward salt marsh migration as a result of sea-level rise. Currently there are limited policies and planning mechanisms to address this. Protection of sensitive plant habitats at Knysna Estuary is essential as there are few opportunities for restoration or recreation of habitat due to coastal squeeze and hard infrastructure surrounding much of the estuary edge.

Eutrophication and the associated algal blooms pose a major threat to the integrity of the estuary's habitats, especially the important seagrass beds. Regular water quality monitoring and the prevention of non-compliant discharges is necessary, particularly from the wastewater treatment works near the Ashmead Channel. Illegal bait digging and trampling of seagrass beds must be limited as much as possible through policing the designated bait reserve areas. Invasive species such as the red seaweed *Asparagopsis taxiformis* must be monitored and actions to remove, or to prevent further spreading at the very least, need to be identified and then implemented.

The most challenging pressures to address will be those related to climate change. Freshwater inflow, which has already decreased, may continue to decline with decreases in rainfall and prolonged droughts. This will increase salinity levels in the estuary, with direct physiological impacts on plants and algae. Consequently, the composition and distribution of habitats may be altered, particularly in the fresher upper reaches of the estuary. It is crucial that no dams, weirs, or other structures that may impede inflow from the Knysna River be constructed. Furthermore, developments fringing the estuary will restrict the ability of the important salt marshes to migrate landwards in response to rising sea level. The existing areas of salt marsh need to be conserved and, where possible, structures acting as a barrier for salt marsh migration should be removed.

Figure 6.26a The salt marsh as a roosting habitat for birds such as the blacksmith plover shown here (Photograph: © Janine Adams).

Figure 6.26b Egyptian geese goslings resting in the succulent *Salicornia tegetaria* salt marsh (Photograph: © Alan Whitfield).

Figure 6.26c A sacred ibis feeding in an intertidal salt marsh (Photograph: © Alan Whitfield).

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Crown crab *Hymenosoma orbiculare* in an eelgrass bed (Photograph: © George Branch).

Chapter 7 : Benthic and Planktonic Invertebrates of the Knysna Estuary

Richard Barnes, Tris Wooldridge & Alan Hodgson

7.1 Introduction

As pointed out in Chapter 1, the invertebrates of the Knysna Estuary have been under investigation since the late 1940s when Professor John Day and his colleagues Naomi Millard and Arthur Harrison from the University of Cape Town visited the area as part of a much wider study of the ecology of all South Africa's major estuaries. They concluded that Knysna "has the richest fauna we have seen", both in terms of individual animals and of numbers of species, recording over 350 different types of invertebrate on and in Knysna's rocky and soft-sediment shores[1]. Fifty years later their surveys were repeated by a team led by Professor Brian Allanson of Rhodes University[2], and high values of species richness were again observed. It is in part this abundant and rich invertebrate biodiversity that has, through to the 21st Century, given Knysna the distinction of being the estuary of highest overall conservation importance amongst the 290 possible South African contenders[3].

In the last decade, research has attempted to build on these foundations in order to understand the nature of the faunal patterns that can be observed across the estuary and to comprehend the processes that may have given rise to these patterns. This work has been led by two of the authors of this chapter, also from Rhodes University, and has resulted in the zoobenthic community of the Knysna Estuary having one of the most intensively studied invertebrate components of any South African system[4,5]. This has confirmed the opinion of John Day's team that Knysna supports the largest number of invertebrate species of any South African estuary[6]. The size of species lists is usually proportional to the magnitude of the area studied and to the amount of time spent studying it. The large size of the Knysna Estuary and the unusually high man-hours devoted to faunal surveys there may in considerable measure account for the very impressive invertebrate fauna list contained in the Appendix, but there are several other processes that have contributed to the high biodiversity.

The estuary is permanently open, an unusual condition in South Africa[7], and it experiences a large flux of Indian Ocean water twice daily. This permits large numbers of otherwise fully marine species to occur in the system and creates clearwater conditions. Because the mouth of the estuary is a gap carved through the sandstone of The Heads, and because of the extent of the fringing shallows of the drowned river valley and the marshland that has developed there, the usual soft sediments of an estuary are here also augmented by rocky shores and saltmarsh so that the diversity of Knysna habitat types is also unusually large, only mangroves are missing. Today, many animals are moved around the planet intentionally or accidentally by humans, and Knysna has more than its fair share of these too[8]; other essentially subtropical species are arriving because of our warming oceans[7]. Knysna's geographical position is also relevant. The South African coastal marine fauna is itself particularly rich, located as it is at the interface between the Atlantic and Indo-Pacific biogeographical realms[9], and within that coastline Knysna is sited in the warm-temperate interface between the cool-temperate zone and Benguela Current to the west and the subtropical region and Agulhas Current to the east. Elements of its fauna can derive from all these sources.

Like all estuaries, that at Knysna basically provides aquatic animals with three main categories of habitat: muds and sands, with or without a covering of seagrass or tidal-marsh vegetation; hard surfaces, much increased by relatively recent human engineering (seawalls, pilings, jetties, bridges, causeways, etc.); and the tidally-pulsing overlying water mass. We consider these in turn below.

7.2 Bare and vegetation-covered soft sediments

Introduction

Submerged and emergent vegetation is an extremely important component of estuaries, forming a habitat for many benthic invertebrates and providing food resources that support the higher trophic levels such as fishes and birds (Figure 7.1). Estimates of the extent of submerged plants in Knysna vary, but based on recent subtidal surveys and reviews of its ecology[10,11,] the seagrass *Zostera capensis* covers

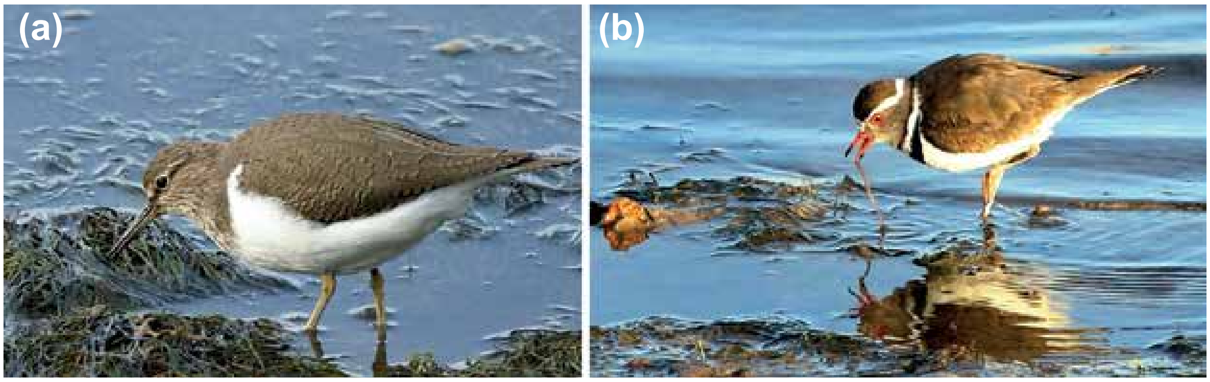

Figure 7.1 (a) Common sandpiper and (b) Three-banded plover feeding on eelgrass associated invertebrates (Photographs: © Tris Wooldridge).

30% of the system, just over half of it below the low water mark[12]. The total eelgrass area for all other South African estuaries and bays is currently only some 700 ha[10], so Knysna supports half of the country's total area of this vulnerable and declining habitat forming plant. To place this in context, seagrass plays one of the planet's most important ecosystem-service roles. Amongst other services, seagrasses (i) stabilise coastal sediments and prevent erosion, (ii) reduce water velocities, (iii) trap nutrients and organic molecules, (iv) shelter and/or feed juvenile nektonic prawns and fish of commercial importance and the adults of iconic species such as the vulnerable dugong and syngnathid fish like seahorses; and (v) sequester carbon from the atmosphere. Indeed, per annum, 1 ha of seagrass can sequester carbon equivalent to that emitted by a car travelling 3 350 km, making it a globally significant carbon stock with an average of some 14 kg of buried carbon per square metre, and a unit hectare can absorb the nutrients released in the treated effluent of 200 people[13,14].

Economic assessment of all the services provided by seagrass beds is still incomplete, but just their value to local fisheries has been estimated to be worth US$ 50 000–180 000 per hectare per year at places as far apart as Borneo, temperate Australia and the Canary Isles; and in 2020 those of the Agulhas Current region (from the Cape of Good Hope to Tanzania) were estimated in total to be worth US$30 345 million per year[15]. In spite of these known benefits to humanity, however, deliberate destruction of seagrass beds and their loss via unrestrained eutrophication continue at a very high rate, i.e. a global loss of 7% per year since 1990[16], and this could be releasing 300 trillion grammes of blue carbon annually to contribute to global warming[17]. Knysna is a jewel in South Africa's estuarine crown, partially as a consequence of its flourishing beds of seagrass.

In several areas of the world, the animals inhabiting seagrass beds are considerably more numerous and more diverse than those found in adjacent areas of mud or sand that do not support such a plant cover. Many reasons why this should be so have been put forward, including that prey species can more successfully hide away from their fish predators in the myriad of seagrass leaves which also provide an abundance of detrital and microalgal food resources for invertebrates. Knysna, however, is one of several exceptions to this generality. Here, conversely, animals may be more numerous in and on the bare sediment than in the seagrass, although the number of species present in the bare areas is often somewhat less[18]. Be that as it may, the faunas in the two habitat types are very similar at Knysna and can all be treated under the same heading.

So far, the animals living in most intertidal beds of Knysna seagrass and adjacent areas of bare sediment have been investigated but we still know relatively little of those below low tide level. Even so, more than 200 types of invertebrates have been recorded.

Seagrass fauna and ecology

At first glance, seagrass beds may appear devoid of animals (Figure 7.2a) although the large sea-hares *Bursatella leachii* are seasonally evident (see below) and the lucky may spot a giant mud crab, *Scylla serrata*, before it disappears into a cooking pot (Figure 7.3). This is because most invertebrates are very small (i.e. less than 5 mm). You have specifically to

Figure 7.2 (a) Dense mass of subtidal *Zostera capensis* leaves floating at the surface. Note the apparent absence of animals: most are hidden within or below the mat and in any event are usually very small in size. (b) Relatively large tick shells visible on the leaves (Photographs: © Richard Barnes).

look for them to find them, and even when found they usually require examination under a microscope for successful identification. At least in part, this may account for the fact that, for some of the smallest ones, Knysna is the only place in the whole of Africa that they are known to occur.

Close inspection of the surface of the sand, mud or seagrass may reveal some of the relatively large species such as the tick shell (*Nassarius kraussanus*) (Figures 7.2b and 7.8), and in quiet backwaters the burrow systems of the mudprawn (*Upogebia africana*) visibly dominate the landscape and, for many, provide the main reason for visiting the shores (see below). Nine of the local species commemorate the estuary as part of their scientific name, as *knysnaensis*, *knysnaense* or *knysna* (see Appendix 1) and several others were originally described with that name but have since been synonymised and have lost it (two such now being *capensis* instead). Two more even bear the names of particular Knysna features or districts, having the specific names *westfordensis* and *railbridgensis*.

Generally, the fauna is that typically occurring in a large, permanently open South African estuary[19,20], but six distinct spatial variants have been distinguished[4]. The sheltered backwater creeks and channels in the saltmarsh that separate the large Thesen and Leisure islands from the eastern (mainland) shore (Figure 7.5a) support a fauna that differs quite considerably from that along the main longitudinal axis of the estuarine bay (Figure 7.5b). Along this axial channel, the different faunal variants are arranged like beads on a string, with those in the sandy region adjacent to the mouth then being most different to those upstream in markedly muddier areas.

Estuarine faunas are basically marine in nature[21]; a subset characterising sheltered coastal areas rather than specifically regions of low salinity[22]. Therefore, as might be expected, at Knysna numbers of species per unit area decrease on progression upstream, although the decline is not necessarily uniform. A step change appears to occur at the junction of the lagoonal and middle estuary region, perhaps marking the point at which essentially seawater-only ('stenohaline marine') species drop out of the fauna (see Figure 7.6); 45% of Knysna's species have been estimated to fall into this category[23]. Although numbers of species decrease, number of individual animals per unit area remains remarkably constant upstream at a density of some 4 000 per square metre, considerably smaller than that supported by the eastern backwater regions (see Figure 7.7).

Significantly different variants of the intertidal mud- and sand-flat fauna occur in different areas, but the more characteristic Knysna species almost all occur throughout the whole estuary, so that regional differentiation is largely due to different relative abundances of a common suite of species rather than to different species being confined to different areas. Relative importance does vary widely, and a few of the most abundant species are only locally dominant. The tiny mudsnail '*Hydrobia*' *knysnaensis* and the burrowing shrimp-like crustacean *Halmyrapseudes cooperi*, for example, are mainly confined to the backwaters, whilst the cushion star *Parvulastra exigua* is dominant only in the lagoonal zone.

In a nutshell, the shores of the bay's main axial channel, lagoon and middle-estuary regions are dominated by burrowing worms (polychaetes there forming 47% of all animals); the backwaters and to a lesser extent the upper estuary are dominated by a group of surface-living sea-snails known zoologically as the truncatelloids (forming 77% and 38% respectively), with polychaetes only comprising 30% of the upper-estuarine fauna; whilst the sandflats near the mouth are dominated jointly by polychaetes (42%) and another type of surface-living snail, the cerithioids or 'creepers' (33%), the same group of gastropod molluscs being even more important subtidally in the regions more influenced by seawater (84%).

The most characteristic, numerous and widespread members of the intertidal soft-sediment fauna (those with an overall abundance >50 per square metre) are illustrated in Figure 7.8. Readers may note that two of this suite of common species are given generic names in apostrophes: '*Hydrobia*' *knysnaensis* and '*Assiminea*' *capensis* (either, or both of which is presumably the mysterious '*Assiminea* c.f. *ponsonbyi*' that John Day[24] described as being "abundant in Knysna Lagoon on sandy mud"). Both these endemic South African species are awaiting new genera to be described for them[25] (see below) and until such time as these are published they languish under names of convenience. Such is probably true of other species as well which further investigation may show to be South African specialities.

Two intertidal invertebrates are particularly associated with Knysna. One is the critically-endangered seagrass false-limpet *Siphonaria compressa* (Figure 7.3) that lives on the seagrass leaves, scraping off their biofilm coating for food. It is otherwise only known in the world from Langebaan on the west coast — although recent research suggests that animals from the two localities differ both morphologically and genetically. The other is the pansy shell, *Echinodiscus bisperforatus* (Figure 7.3),

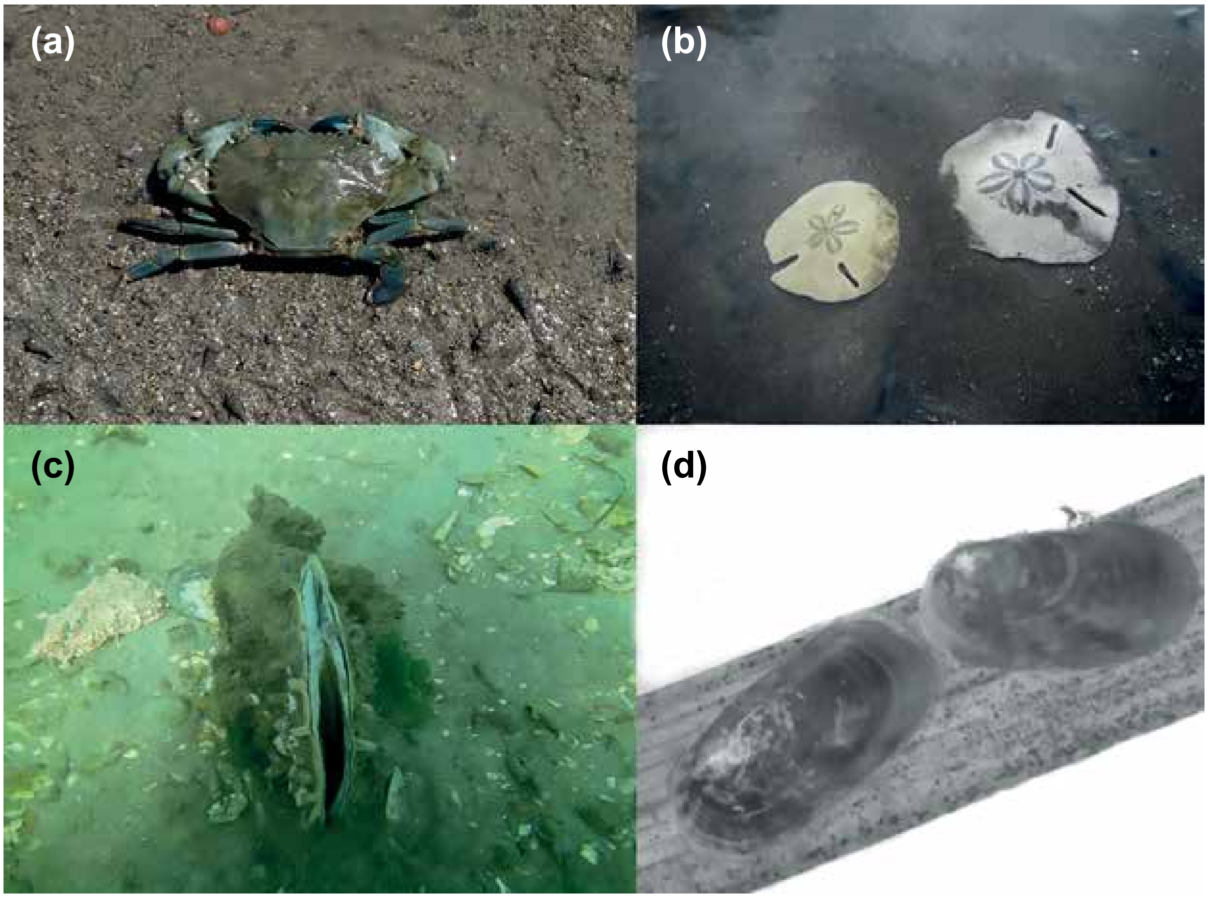

Figure 7.3 Animals particularly associated with the Knysna Estuary
(a) *Scylla serrata*, (b) *Echinodiscus bisperforatus*, (c) *Atrina squamifera*, (d) *Siphonaria compressa*.
(Photographs: *Atrina*, © Louw Claassens, *Echinodiscus* © Frédéric Ducarme, *Scylla* Bishnu Sarangi, *Siphonaria* © Brian Allanson).

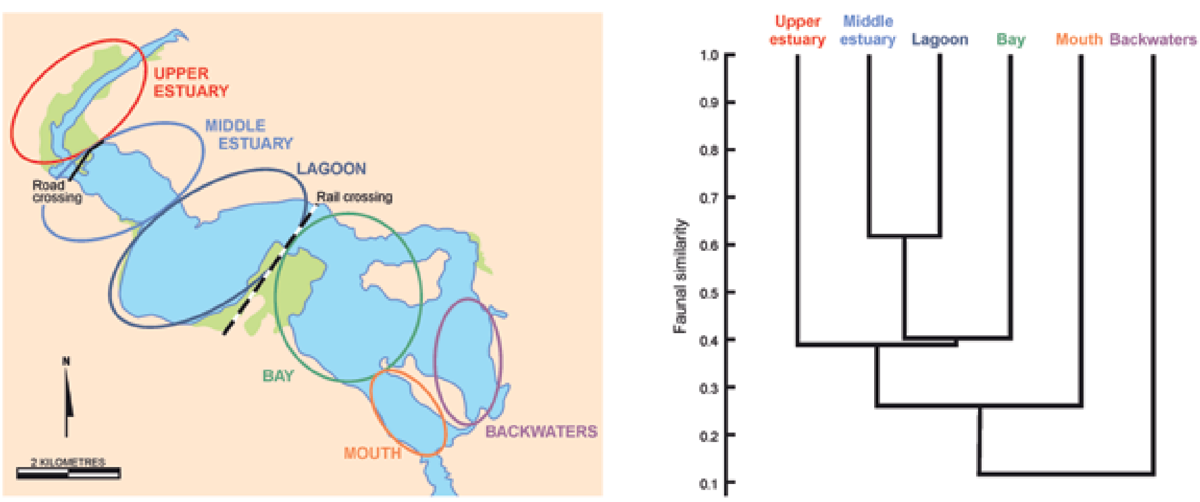

Figure 7.4 Faunistic divisions of the Knysna Estuary based on the intertidal soft-sediment invertebrate macrofauna, and the pattern of similarity between these different divisions.
All spatial variants to seaward of the middle estuary together constitute the lower estuary.

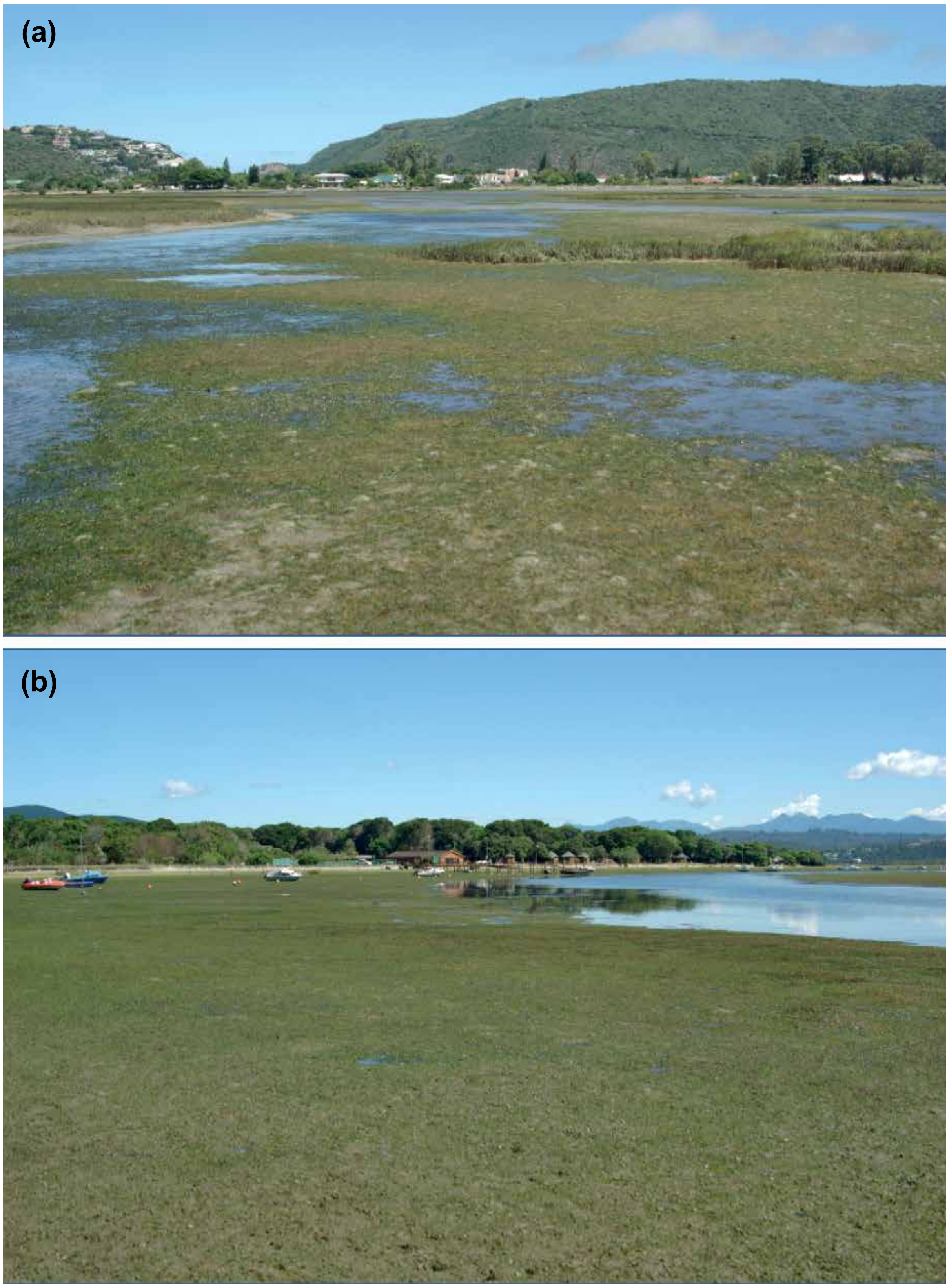

Figure 7.5 Knysna intertidal seagrass meadows at low tide: (a) in a backwater channel in the eastern block of saltmarsh; (b) along the main axial channel at Brenton-on-Lake (Photographs: © Richard Barnes).

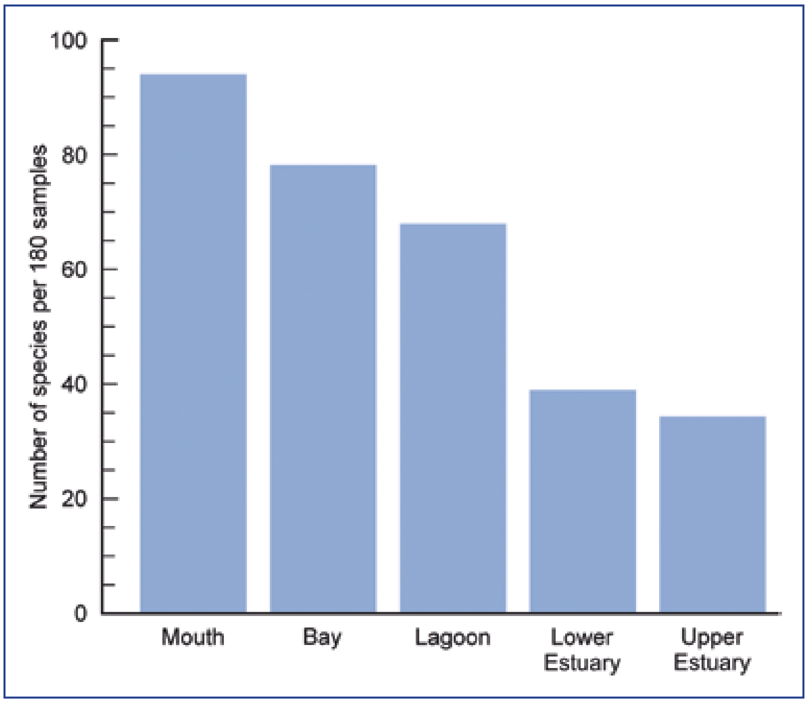

Figure 7.6 Number of animal species in intertidal seagrass per unit sampled area along the main axial channel of the Knysna Estuary. Note the progressive decline in the number of species moving upstream towards the upper estuary, with a particularly large step between the lagoon and middle estuary regions.

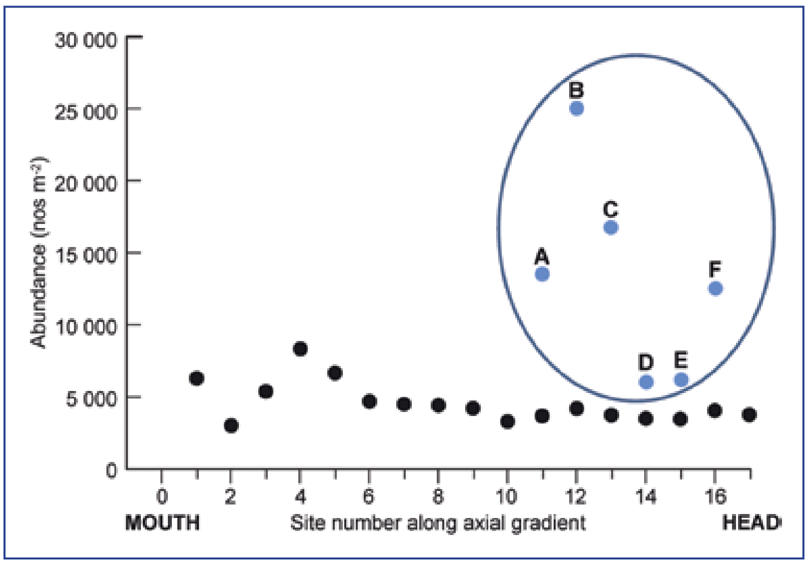

Figure 7.7 Number of animals per unit area in the seagrass beds of the Knynsa Estuary at 17 sampling sites positioned along its axis. Equivalent numbers at six sites in the eastern backwaters are shown within an envelope (Site A-F) for comparison.

a greatly flattened, burrowing sea-urchin, which is now probably more abundant in Knysna souvenier shops than in its natural habitat on the 'pansy bank' sand flats near the mouth. The same is true of the fan shell or horse mussel *Atrina squamifera* (Figure 7.3). Although popularly termed the 'Knysna' pansy shell (at least in or near Knysna!), *Echinodiscus* occurs all along the South African south and east coasts, and indeed beyond, throughout the Indian and west Pacific Oceans. The giant mud crab is also known locally as the 'Knysna crab', although it too has a similar range to the pansy shell and is relatively rare in Knysna!

Unfortunately, relatively little is known of the ecology of many of the seagrass and sandflat invertebrates, but by reference to similar species that have been investigated on other shores it is possible to deduce the likely workings of the whole Knysna estuarine system. Several ecological categories of animal are present. The tiny but abundant snails '*Hydrobia*', '*Assiminea*' and *Alaba*, and the cushion star *Parvulastra* live on or above the sediment and consume the thin biofilm of bacteria and microalgae that coats the seagrass leaf surfaces and sand grains, scraping it off with their various tooth-like systems; *Alaba pinnae* seems much more abundant in the Knysna Estuary than at any other known place — it is a real, though unheralded, Knysna speciality.

The worms *Prionospio* and *Caulleriella* live in burrows but feed in a similar fashion using a pair of long tentacles to capture their food particles on or above the surface and to convey them back to the mouth; the bivalve *Salmacoma* uses a long siphon to achieve the same end. Other worms probably feed on similar material but obtain organic material that has already been incorporated into the substratum by eating the sediment itself (e.g. *Capitella*, *Orbinia* and *Paradoneis*). They are joined by other animals that hide beneath the surface during high tide but emerge from their burrows at low tide to consume the surface biofilm (e.g. the *Danielella* crab)—presumably they are at greater risk from fish than they are from birds. All such species are termed deposit feeders because they feed on material that coats surfaces. A parallel suite of consumers feeds on similar-sized particles but obtains them from the water column itself using some form of filtration system, the suspension feeders. They may live below the surface (e.g. *Turritella*, *Solen* and *Arcuatula*) or above it (e.g. ?*Cylindroleberis*). The mudprawn (*Upogebia*) is one such and is considered in more detail below.

Most of the small crustaceans are generally regarded as being omnivorous, eating whatever particulate organic material is available on or above the surface (e.g. *Halmyrapseudes*, *Exosphaeroma* and *Melita*). The ragworm *Simplisetia* which lives in burrows below the surface and the tick shell *Nassarius* that lives on or above the surface are the epitome of opportunistic omnivores, including feeding as predators when the opportunity presents itself; the giant mud crab *Scylla* is also an opportunist and scavenger, with predation probably being more important than currently estimated. The small crown crab *Hymenosoma* is a fulltime predator and specialises in feeding on worms and small crustaceans, as indeed does the non-native moonshine worm *Diopatra aciculata* (see Figure 7.10) which is sought by bait collectors with hooked wires inserted into their tubes on the sandflats.

It should be noted that none of the invertebrates living in the seagrass beds actually feeds on the eelgrass itself; only one such species is present in the estuarine bay, namely the tiny snail *Smaragdia* (Figure 7.9); but this recent arrival, probably courtesy of global warming, is so uncommon as to have no potential ecological effect on the estuary. Some consumers may eat the small saltweed *Halophila*, but the food source most targeted by invertebrates is really the microalgae growing on the leaf blades or on the sediment particles, i.e. the associated 'microphytobenthos' (MPB) and non-photosynthetic bacteria that they support. The common invertebrates mentioned above then form the link between these basal algal and bacterial food sources and the crabs, octopuses, cuttlefish and fish that are the higher level consumers in the estuarine food web[6].

Several lines of evidence suggest that the numbers of all these invertebrate consumers of the microscopic diatoms and flagellates are held well below the level that could be supported by the available primary productivity at Knysna[4]. This evidence includes observations that the distribution and abundance of individual species show no evidence of negative interaction such as would result from competition for food or space, and that the 4 000 individuals typically present per square metre is 10 or even 20 times less than the numbers of equivalent animals supported by some other less productive systems in higher latitudes. It seems most likely that their numbers are kept at low levels by 'top-down control', especially the predation pressure exerted by the many carnivorous fish that occupy the Knysna Estuary, but also by the other equivalent top invertebrate consumers such as predatory crabs, molluscs, squid and octopus.

Four characteristic species illustrating particularly interesting biological features

The 4 mm long '*Hydrobia*' *knysnaensis* (see Figure 7.8) is a member of the spring-snail family (Hydrobiidae) of which 99% of species live in freshwaters or inland salt lakes. One small subgroup of them (the 15 or so species of 'mudsnail'), however, includes coastal-marine and brackish-water forms. In densities of up to 300 000 per square metre, these species dominate muddy shores and subtidal zones in estuaries, lagoons, inland seas and sheltered coastal bays on both sides of the North Atlantic. Indeed, mudsnails may comprise 80% of all the animals present at a site. All but one species in the entire family, however, only occur in the northern hemisphere (north of some 20ºN).

In the southern hemisphere, hydrobiid snails are replaced by members of other, superficially similar but not particularly closely related families. Many types of small snail possess very different bodies but almost identical shells, and they are therefore often confused by people only interested in features of shells. The only known southern-hemisphere hydrobiid is '*H.*' *knysnaensis* which seems to have a similar body form and ecology to the North Atlantic mudsnail *Peringia*, though the eggs of '*H.*' *knysnaensis* hatch to release young snails whereas those of *Peringia* release larvae. Granted its differences to all

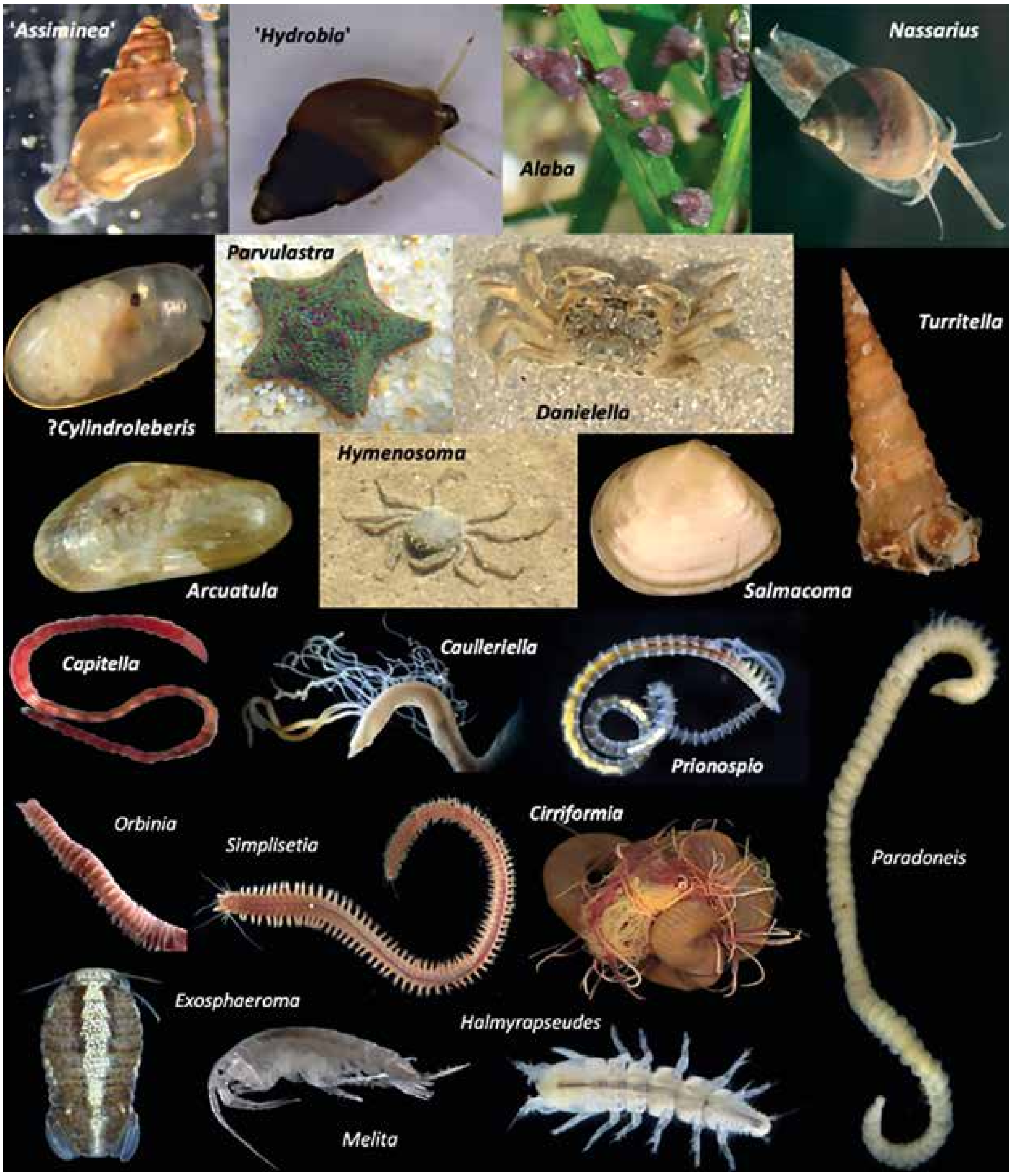

Figure 7.8 Thumb-nail pictures of the most numerous and widely distributed animal genera in the soft-sediment habitat (Photographs: *Alaba* © Ria Tan; *Arcuatula* and *Salmacoma* © Natural History Museum Rotterdam, '*Assiminea*' © Nelson Miranda, *Capitella* © Carol Simon, *Caulleriella* © Letizia Tassinari, *Cirriformia* and ?*Cylindroleberis* © David Fenwick, *Danielella* and *Hymenosoma* © Frances Smith, *Exosphaeroma* © Leslie Harris Natural History Museum of Los Angeles County, *Halmyrapseudes* © Keiichi Kakui, '*Hydrobia*' © Richard Barnes, *Melita* and *Orbinia* © Hans Hillewaert. *Nassarius* © George Branch, *Paradoneis* © Katrine Kongshavn University Museum of Bergen; *Parvulastra*, © Simon Grove / TMAG; *Prionospio* © Gustav Paulay © 2010 Moorea Biocode, *Simplisetia* © Chris Meyer © 2010 Moorea Biocode, *Turritella* © Gustav Paulay / TMAG).

known northern hemisphere mudsnails, it would seem not to be an accidental alien introduction (although there are several alien species now part of the Knysna fauna[26], see Figure 7.9), but why it alone of the multitude of hydrobiids should occur south of the equator is a mysery. Appropriately enough granted its name, its main stronghold seems to be Knysna, although '*H.*' *knysnaensis* is known from the Great Berg Estuary on the Atlantic coast to the Kleinemonde estuaries in the Eastern Cape.

In southern Africa, hydrobiids are generally replaced by vlei snails (tomichiids) inland and by sentinel snails (assimineids) intertidally. The snail with which '*Hydrobia*' is usually associated at Knysna, '*Assiminea*' *capensis*, is also a most aberrant member of its group, by virtue of both its morphology and its ecology; indeed its relationships have only been established very recently by molecular sequence analyses[27]. Coastal assimineids characteristically live amphibiously, high up on the shore in salt-marshes or mangroves, but '*A.*' *capensis* is much more thoroughly aquatic, even extending into the subtidal zone. It may represent a whole new indigenous subfamily or even family of snails[28]. It is known (insofar as it is known!) from Still Bay in the west to the St Lucia system in the east.

Anyone walking past a sheltered high-level mudflat (e.g. that along the southern side of the causeway onto Leisure Island) at low tide cannot fail to have noticed the hordes of tiny crabs on the surface of the exposed sediment. These are the 8 mm or so *Danielella edwardsii* (confusingly at various times in the past also known as *Cleistostoma*, *Paratylodiplax* and *Danielita*; see Figure 7.8), that take the place of their close relatives, the sand-bubbler crabs, and their not-so-close ones, the hordes of soldier, sentinel and fiddler crab species that are such diverse and important elements of tropical and subtropical

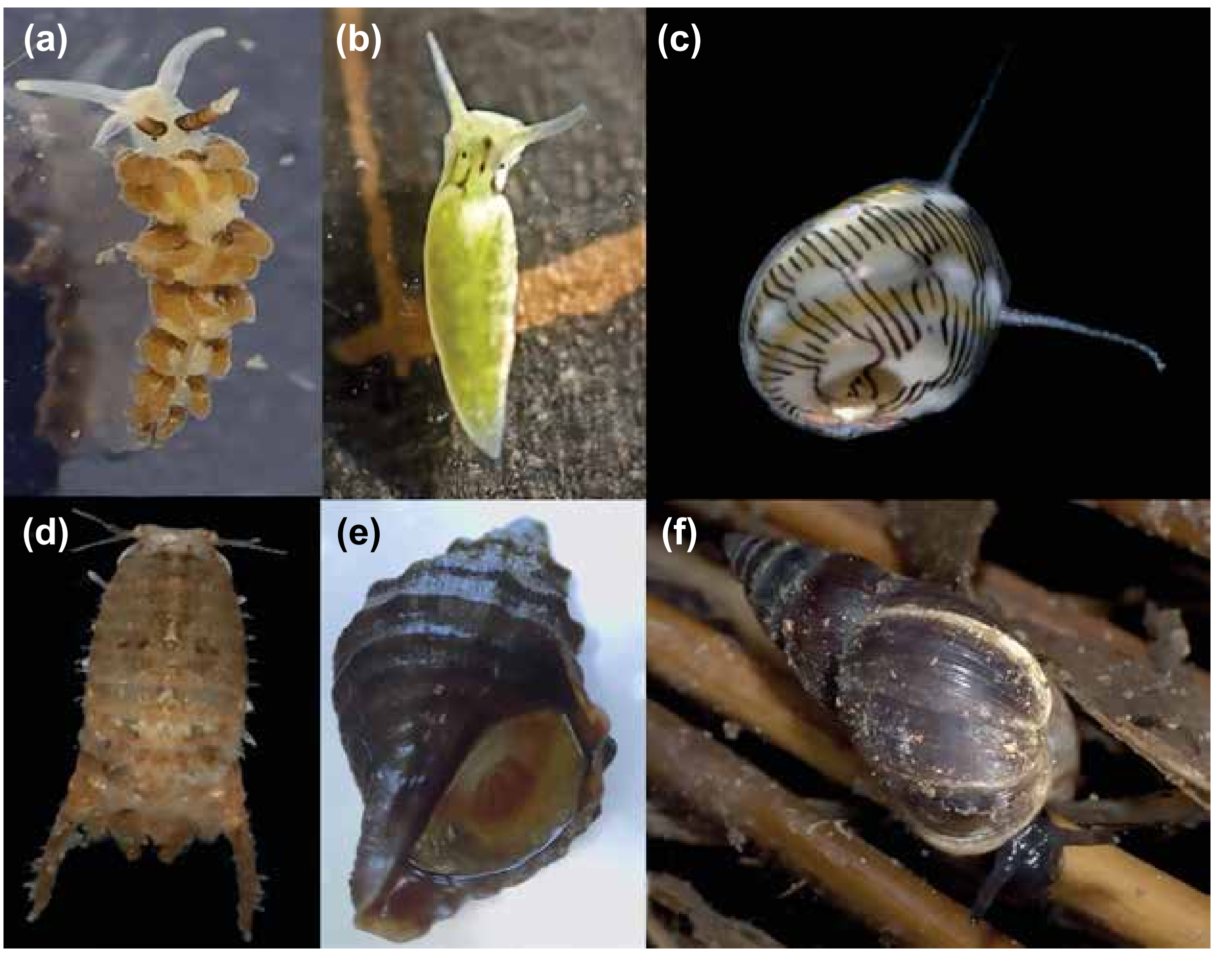

Figure 7.9 Non-native species that have arrived in the Knysna Estuary via shipping or as a result of global warming, etc. (a) *Favorinus ghanenesis*, (b) *Elysia hirasei*, (c) *Smarogdia souverbiana*, (d) *Paracerseis sculpta*, (e) *Indothais dubia*, (f) *Myosotella myostis* (Photographs: *Elysia Favorinus* and *Indothais* © Richard Barnes, *Myosotella* © A. Bertrand, *Paracerceis* © Yue Hu, *Smaragdia* © Denis Riek).

shores. Like them, *Danielella* emerges from below the surface during low tide to spoon up the surface sediment with the more or less spatulate 'fingers' of their claws and deliver it to their mouths which bear multiple sets of jaw-like paired appendages ('maxillipeds'). Collected sand particles are rubbed between the lower surface of one pair of these and the outer surface of another pair, and the relatively light bacteria, diatoms and other organic flakes that are brushed off, or strained out by setae, are swallowed with the aid of a current of water; the rejected heavier particles being deposited back on the ground as pellets.

Amongst true crabs, this is a way of life extremely common between some 43ºN and 43ºS, but very rare outside this range (although hermit-crabs like *Diogenes brevirostris*, often seen scuttling over the sediment, can feed in an essentially similar fashion). Unlike its larger relatives, *Danielella* does not build a permanent burrow, it just 'shuffles' below the surface when not feeding[29]. Lower down the shore it is replaced by a very close relative, the somewhat bigger (10 mm), much hairier and pale-blue carapaced *Paratylodiplax algoense*. Both are restricted to southern Africa and therefore endemic to the region.

For many, the Knysna system is synonymous with an opportunity to collect bait for fishing[30] (see Figure 7.10), and for most this means collecting the up to 6 cm long mudprawn, *Upogebia africana* (having of course first collected a permit from SANParks!), the presence of which is positively correlated with that of seagrass. It is in fact an oversimplification but in general *Upogebia* constructs a semi-permanent burrow in stable sediment in which it 'sits' and filterfeeds, straining out particles of food with a sieve formed by setae on its anterior limbs from a water current that it creates by beating fans on its abdominal ones. Almost 1 litre of water per hour can be filtered by a related and similarly sized *Upogebia* species. In contrast, its distant sandprawn cousin, *Kraussillichirus kraussi* (rarely encountered at Knysna, and more characteristic of temporarily closed estuaries) consumes the organic matter in or adjacent to its burrow, and is therefore a potent bioturbator or mover of sediment[31]. A further difference is that *U. africana* produces planktonic larvae, whilst those of *K. kraussi* remain within the parental burrow system from which they excavate their own side chambers. The mudprawn's burrow itself comprises two more or less vertical shafts, up to 60 cm or more deep, joined at their base by a horizontal passage. Collecting the mudprawns involves increasing water pressure in one shaft so that they shoot out of the other onto the surface. There is no evidence that bait collection is harming the mudprawn population[32], but the negative effect that it has on the habitat and direct trampling of the other species in the seagrass beds is a different matter (see Figure 7.11).

The final example that space permits is one of

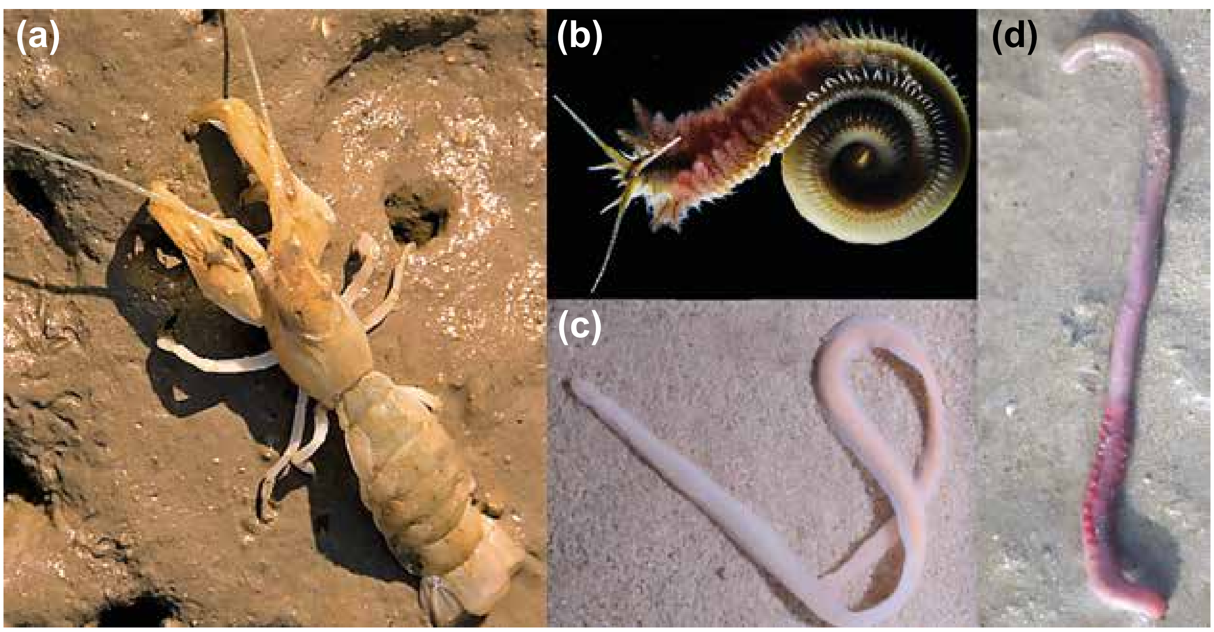

Figure 7.10 Invertebrates particularly sought after for bait (a) *Upogebia*, *(b) Diopatra*, *(c) Polybrachiorhynchus*, (d) *Arenicola* (Photographs: *Arenicola* © Shaun Swanepoel, *Diopatra* © Alvaro Migotto, *Polybrachiorhynchus* © George Branch, *Upogebia* © Chris & Tilde Stuart).

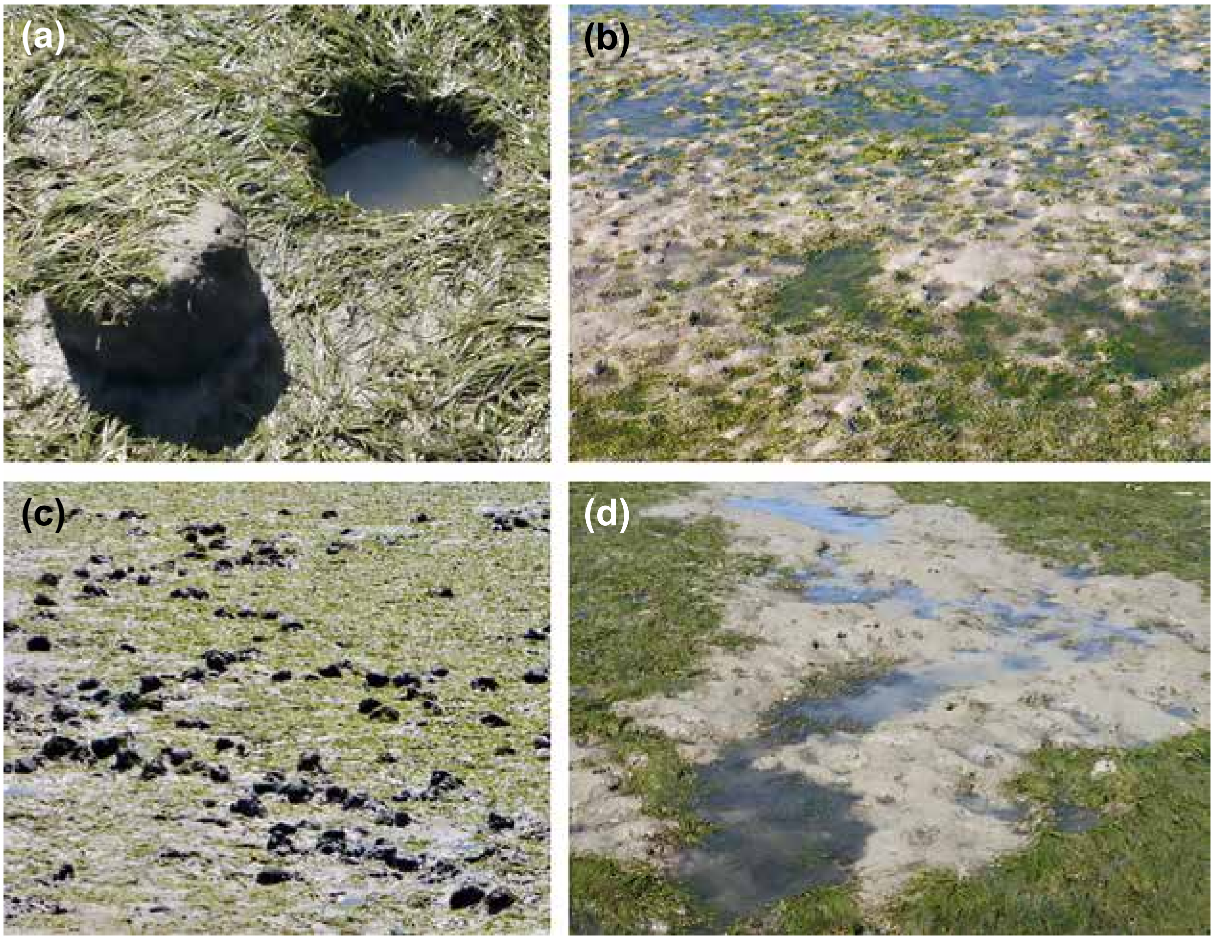

Figure 7.11 Destructive effects of bait-collecting activities on intertidal seagrass habitat in a 'no-take bait sanctuary' section of the Knysna Estuary: (a) The hole and jettisoned plug created by pushing for mudprawn; (b) A substratum pock-marked by such mudprawn pushing and (c) the resultant plugs scattered over the seagrass surface; (d) An area of seagrass destroyed by trenching for bait worms (Photographs: © Richard Barnes).

the largest and most noticeable animals, especially when it forms mating aggregations. This is the 10+ cm long, green, brown or purple, shaggy sea-hare, *Bursatella leachii* (Figure 7.12), often seen gliding slowly over the sediment surface whilst feeding on bacterial or algal films. It is hermaphrodite and, attracted by chemicals called attractins, sea-hares can form long mating chains in which animal B can fertilise animal A in front of it, whilst itself being fertilised by animal C behind it, and so on down the chain. The lead animal then can only function as a female and the last one as a male. Seemingly, breeding often takes priority over safety, and such aggregations may be overtaken by falling tides, the animals becoming overheated and desiccated, and the water becoming deoxygenated, resulting in mass mortality of the unfortunate animals. After mating, long, sticky, variably-coloured strings of eggs (Figure 7.12d) are deposited in the seagrass. from these hatch small, shelled, free-swimming larvae. Their shell, however, is lost before they become adult. *Bursatella leachii* was thought to have a world-wide distribution across the Atlantic, Indian and Pacific Oceans, but it is possible that it is one of a complex of morphologically very similar species. It has recently invaded and spread right across the Mediterranean.

Saltmarsh fauna

At higher shore levels, seagrass gives way to saltmarsh and/or to sedge or rush marshes, for which Knysna is also an important site, supporting >700 ha, the third largest area of any South African coastal

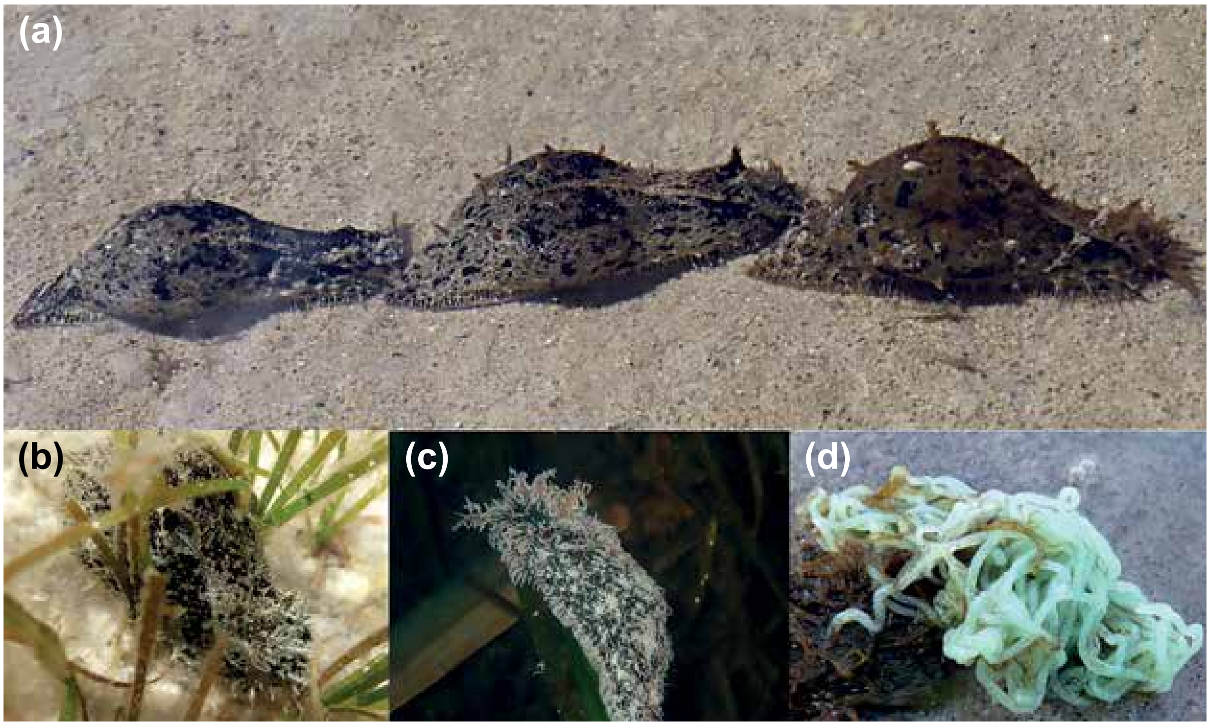

Figure 7.12 The shaggy sea-hare *Bursatella leachii*: (a) part of a mating chain (Photograph: ©Tangatawhenua); (b) and (c) the animal itself (Photographs: © Javier and Louw Claassens); and (d) with a newly laid egg string (Photograph: © Louw Claassens).

system. The two vegetation types interdigitate, however, in that seagrass often occurs along the beds of the creeks and channels within a marsh. The surface of such marshes are usually muddy and they support far fewer types of burrowing invertebrate than does seagrass, but, as throughout the tropical and warm-temperate zones, they are the home of sesarmid and related crabs. At Knysna these include the common omnivorous marsh crab, *Parasesarma catenatum*, whose burrows often riddle the sediment, and at even higher levels the rather less common shore crab *Cyclograpsus punctatus* (Figure 7.13). Several predominantly lower-level species that live on the sediment surface extend their range this far upshore, especially in small pools or pans and in the creeks. These include molluscs such as '*Hydrobia*' and crustaceans like *Exosphaeroma*. A few other species are particularly characteristic of these zones, including '*Assiminea*' *globulus* illustrated in Figure 7.13 and the introduced air-breathing snail *Myosotella myosotis* (one of a group of 'primitive' land snails that are semimarine in nature).

Of special note is the occurrence in the marshes of the larger, 3 cm long, marine cerithioid snail *Cerithidea decollata*. This is a tropical species, best known for climbing mangrove tree trunks during high tide (perhaps to escape potential fish predators), and then back down during low tide to feed on mud-surface biofilms and detritus. Global warming has resulted in a number of species extending their range southwards to Knysna, but there are no mangroves (yet). Where tall rushes (and wooden posts) occur, *Cerithidea* climbs them in an equivalent tidally-cyclical manner (see Figure 7.13), but over most of the saltmarsh it appears to have adopted a non-climbing lifestyle. Knysna is as far south as it occurs, and it seems to survive the cold non-tropical winters in a largely inactive state. *Cerithidea* was not recorded to have been present there in the late 1940s[1]. The animal was then found at a single site; now, however, it occurs virtually throughout the estuary's marshes[33].

Many of the animals of the saltmarsh have colonised it from the land, including beetles, homopteran bugs, and spiders. *Desis* (Figure 7.13), a nocturnal hunting spider, preys on intertidal marine crustaceans during low tide which it catches with its huge fangs, one-third of its body length. Another saltmarsh species of spider has been shown to survive inundation by seawater during high spring tides by the adaptation of falling into a temporary coma[34], in

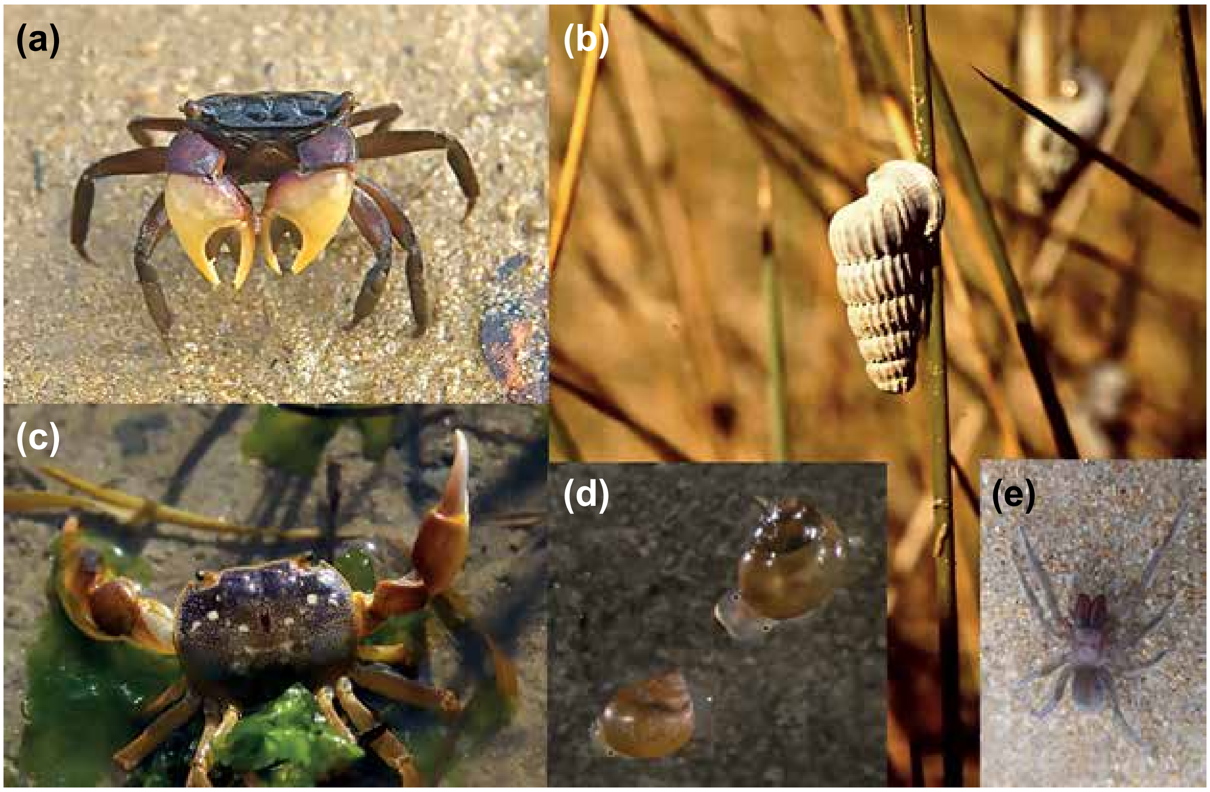

Figure 7.13 Selected invertebrates of the higher level salt– and rush marshes: (a) *Parasesarma*, (b) *Cerithidea,* (c) *Cyclograpsus*, (d) *Assiminea globulus* (e) *Desis* (Photographs: '*Assiminea*' © Nelson Miranda, *Desis* © Wendy Dewberry, *Cerithidea Cyclograpsus* and *Parasesarma* © Richard Barnes).

Figure 7.14 A green algal mat smothering the surface of a seagrass bed (Photograph: © Frances Smith).

a somewhat equivalent reaction to temporary periods of environmental hostility to that of *Cerithidea*.

Threats and the future

The current high loss rates of seagrass throughout the world, including of *Zostera capensis* in southern Africa[10], raises an important question as to the future of Knysna's significant seagrass and saltmarsh systems. The two threats that might particularly affect the seagrass and its inhabitants are uncontrolled bait harvesting by destructive means (Figure 7.11) and blooms of green algae (Figure 7.14). Bait harvesting by 'pushing' for mudprawns and trenching for worms is rife in Knysna[30], even in the formally protected bait-reserve area. Unfortunately, there are immense logistic and social problems associated with preventing illegal bait-harvesting in southern Africa, especially in areas of high unemployment where subsistence fishing provides the main or only source of protein and the local intertidal provides the only source of bait[35]. Subsistence harvesting at Knysna is worth approximately R1 million per annum[36]. It is, however, not only the underprivileged who cause this problem: at the other end of the wealth scale, some of the most privileged Knysna retirees/holiday-makers consider that such local regulations should not apply to them, and therefore direct their domestic employees to obtain the necessary local bait to sustain their passion for fishing regardless of local regulations.

The precise effect of bait collection on the seagrass macrofauna is unknown because the extent of harvesting means that a like-with-like, harvested versus unharvested, comparison is not possible, i.e. there is no comparative area of intertidal seagrass that remains un-pushed or un-pumped. At other localities, however, it and the associated trampling are known to have severe consequences for the plant habitat and associated zoobenthos[37].

The second major threat is excessive nutrient loading or eutrophication, to which *Z. capensis* is known to be sensitive, and the consequent blooms of opportunistic green algae that can blanket the mud- and sandflats (Figure 7.14). At the moment these are only local in extent, affecting mainly the backwater channels into which the municipal sewage treatment plant discharges and in which there is a legacy of organic matter retention[38]. Knysna's large tidal prism proves invaluable insofar as minimising blooms in the main axial channel is concerned, although floating masses of torn-off algae may be a common sight after rough weather[39]. But the local effect of the green algal blanket is dramatic and destructive[40]. Animal numbers may recover on its seasonal dieback, except in the very local areas of anoxia, although this increase is almost entirely confined to densities of the dominant groups of worms[41]. Crustaceans do not bounce back so readily, and as they provide the food for zoobenthivorous fish (see Chapter 8), the fish populations may suffer the consequences. The problem of eutrophication is soluble but only at considerable financial cost.

A third very real threat is total loss consequent on reclamation for development, including of marinas. Marshes and other wetlands are all too often ignorantly perceived as 'wasteland'—useless, horribly muddy places to convert into good, solid dry land as soon as humanly possible. More than 30% of the saltmarsh has already gone and 25% of that remaining could be lost too[12]. Only changes in perceptions and attitudes, including wider appreciation of the true economic and ecological value of estuarine and sheltered coastal habitats, can really combat this threat.

Estuaries are naturally dynamic systems that are subject to dramatic changes across time scales from semi-diurnal to geological. Knysna seagrass waxes and wanes, particularly near the mouth region (Figure 7.15); so too do the populations of various animal species. Over the last few years, for example, densities of '*Hydrobia*' and '*Assiminea*' have been in decline in the Steenbok Channel and marsh creeks. Such fluctuations may be particularly characteristic of these tiny snails, though mass mortality of shaggy sea-hares was noted above and such also occurs in the burrowing 'sea-potato' urchin, *Echinocardium cordatum*[42], common in sandy areas near the mouth, but we still know very little of their causality. Indeed, although the outlines of the way in which the Knysna Estuary operates as an ecological system are broadly understood, more study will be required before we are in any position to appreciate many of its intricacies and to predict its reactions to external pressures, including sea-level rise, and changes in rainfall and temperature patterns.

7.3 Mussel beds and other hard substrata

South African estuaries typically have large intertidal sand and mud flats with few natural rocky shores. Whilst the intertidal in the Knysna Estuary is predominantly of soft substrata, important shorelines composed of rocks and other types of hard surfaces are also present. This diversity of habitats is one reason for the impressive richness of invertebrate species within the estuary (see Appendix).

Rocky shores are found on the east and west sides of the relatively narrow entrance (mouth) of the estuary at The Heads (Figure 7.16a). Inside the

Figure 7.15 The lower reaches of the Knysna Estuary at low spring tide, illustrating waxing and waning of its seagrass beds: (a) in 2009 when there was a luxurious carpet and (b) in 2021 when there was none (Photographs: © Richard Barnes).

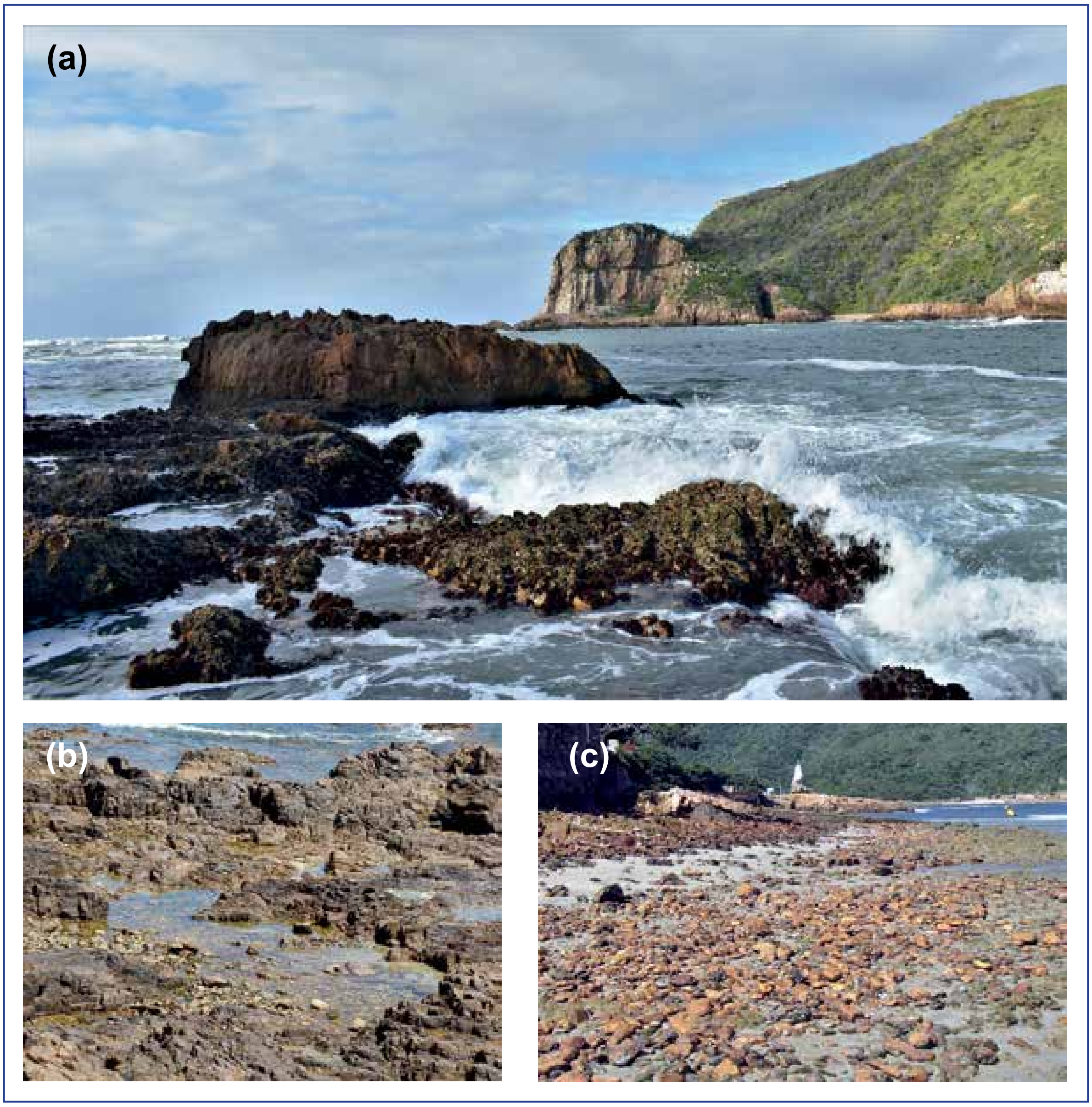

Figure 7.16 (a) Intertidal rocky shore at the Heads in the mouth region of the estuary. (b) Example of a rock pool at The Heads. (c) Example of a cobble shore close to The Heads with rocks embedded in sand (Photographs: a, © Alan Hodgson; b and c, © Peter & Frances Smith).

estuary in the bay region (see Figure 7.4), a cobble beach (Figure 7.17d) and shorelines in which rocks are embedded in sand (e.g. Figure 7.16c) or mud, as well as horizontal beds of soft rock are present. As the town of Knysna grew during the 20th century, a variety of man-made hard surfaces were introduced into all regions of the estuary, some of which replaced soft sediment shores. Introductions include the armouring of shorelines with seawalls made of concrete, cemented stones, loose rocks, or gabions (wire boxes filled with rocks) to prevent erosion, so protecting properties and roads. Examples include the seawall on Cearn Drive, Leisure Isle (Figure 7.17a,b), and a long section of the northern bank of the lagoon that was armoured during the horizontal widening of the N2 national road from the Railway Bridge to the White Bridge (Figure 7.18b). This latter development converted 14% of estuarine soft sediment shoreline to rock[43].

Because recreational boating is very popular within the estuary, one boat harbour (Leisure Isle) and three marinas (The Moorings, Knysna Quays and Thesen Islands Marina) were constructed. The construction of Thesen Islands Marina on Thesen Island (originally Paarden Island) within the bay region introduced 25 ha of seawater canals into the estuary in the early 2000s. The walls of the canals are constructed of gabions (Figure 7.17e) sitting on top of reno mattresses (rectangular mattress-shaped gabions), which means that there are now several kilometres of vertical 'rocky shoreline' in the marina. Associated with boating activities are numerous wooden jetties with wooden pilings that are present not only inside the marina and boat harbours, but also around the estuary.

Other large man-made structures include: (1) a reinforced concrete wharf on Thesen Island (Figure 7.17c); (2) a railway bridge that traverses the lagoon with its numerous large metal supports embedded into the estuary sediments (Figure 7.18a); (3) causeways to Leisure and Thesen islands. Finally, there are numerous channel marker poles and anchored buoys within the estuary. All these hard surfaces, along with other favourable environmental conditions, have enabled some marine invertebrates normally associated with rocky shores to move into the estuary. Compared to studies of the macrobenthos of soft sediments and eelgrass meadows, there have been fewer quantitative surveys of the invertebrates of hard substrata and no studies on their role in ecological processes. The first estuarine survey[1] revealed a rich invertebrate fauna (about 145 species, Figure 7.19) at Fountain Point (The Heads) that constituted about one third of invertebrate species they recorded. More recent published[5,43] and unpublished studies have updated species records and distributional information, and provided some quantitative assessments of species numbers on other hard substrata in other regions of the estuary.

Rocky shores of the mouth region — The Heads

The invertebrate fauna on the rocky shores at The Heads is typical of that found along the southern Cape coastline. Here the organisms that live there are subject to continuous and strong wave action and water flow during the rising and ebbing tides. The invertebrates at The Heads are marine (i.e. saltwater) species and have little tolerance to fluctuations in salinity. The most abundant species living on the rock in the mouth region are either grazers of micro- or macroalgae, or filter-feeders that use modified appendages to sieve phytoplankton and other organic particles from the water at high tide.

A major factor affecting where intertidal species are found is their position above the low water level, which influences how long they are exposed to air during low tide, and governs their tolerance to physical stresses such as heat and water loss. This results in zonation of organisms within the intertidal. Five zones are recognized on south coast shores[44]. These are from top to bottom, the Littorina, Upper Balanoid, Lower Balanoid, Cochlear, and Infratidal (only some of this region is exposed to the air on the lowest of spring tides). All these zones are not difficult to recognize at The Heads because of the presence of characteritic taxa. The Littorina zone is almost exclusively inhabited by the small southern (or Knysna) periwinkle *Afrolittorina knysnaensis*, and sea slaters (*Ligia natalensis*) (Figures 7.20a, 7.20b). These species are also present high in the intertidal on hard substrata throughout the estuary. The Upper Balanoid zone fauna (see Figure 7.20d-k for examples) is characterized by three species of barnacles (Crustacea), the volcano barnacle (*Tetraclita serrata*), the eight-shell barnacle (*Octomeris angulosa*), and the smaller toothed barnacle (*Chthamalus dentatus*). All these species can extend downshore into the Lower Balanoid zone. Common molluscs in the Upper Balanoid zone are the granular limpet (*Scutellastra granularis*), prickly limpet (*Helcion pectunculus*), the Cape false-limpet (*Siphonaria capensis*), the variegated topshell (*Oxystele antoni*), and the predatory common dogwhelk (*Nucella dubia*) that mainly feeds on barnacles and periwinkles[45]. This voracious predator can control population numbers of the volcano barnacle and is regarded as a keystone species on rocky shores[44]. Spiny chitons (*Acanthochitona garnoti*) are also common in crevices or amongst the larger barnacles. All these

Figure 7.17 (a and b) Armoured sea wall at Cearn Drive, Leisure Isle.
Note the band of the alien invasive Mediterranean mussel in b (arrowed) just above the sand.
(c) Mediterranean mussels attached to Thesen Wharf. (d) Cobble beach on the western shore of the bay region.
(e) Vertical wall of gabions lining a canal inside Thesen Islands Marina. Visible is a band of
the Mediterranean mussel (arrow 1) and below them a band of sea squirts (*Microcosmos squamiger*) (arrow 2)
both covered in silt. The gabion is placed on top of a reno mattress
(Photographs: a,b,d,e, © Peter & Frances Smith; c, © Alan Hodgson).

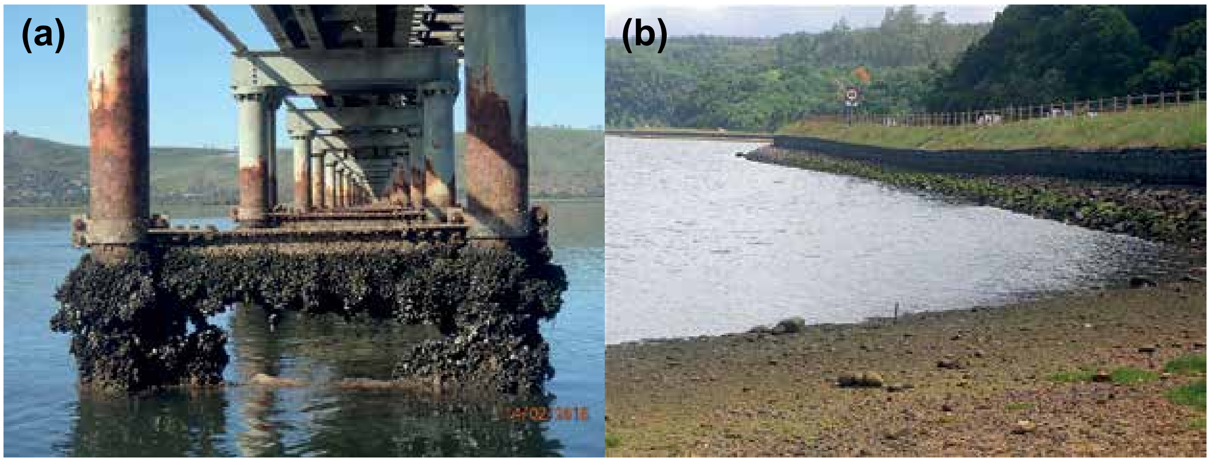

Figure 7.18 (a) Metal supports of the Railway Bridge viewed at low tide. Note the large numbers of exposed Mediterranean mussels attached to the supports. (b) Armoured shore line of gabions and rocks after horizontal widening of the national road (Lagoon Drive) (Photographs: © Peter & Frances Smith).

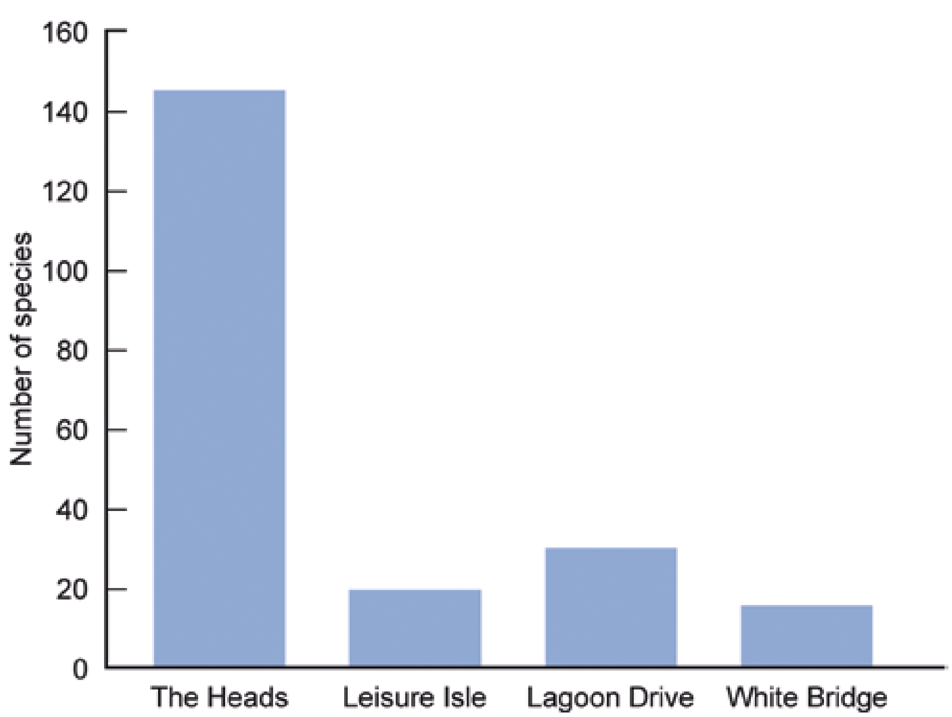

Figure 7.19 Number of invertebrate species recorded from intertidal rocky shore surveys in the Knysna Estuary. Data from Day et al.[1] and Allanson et al.[43].

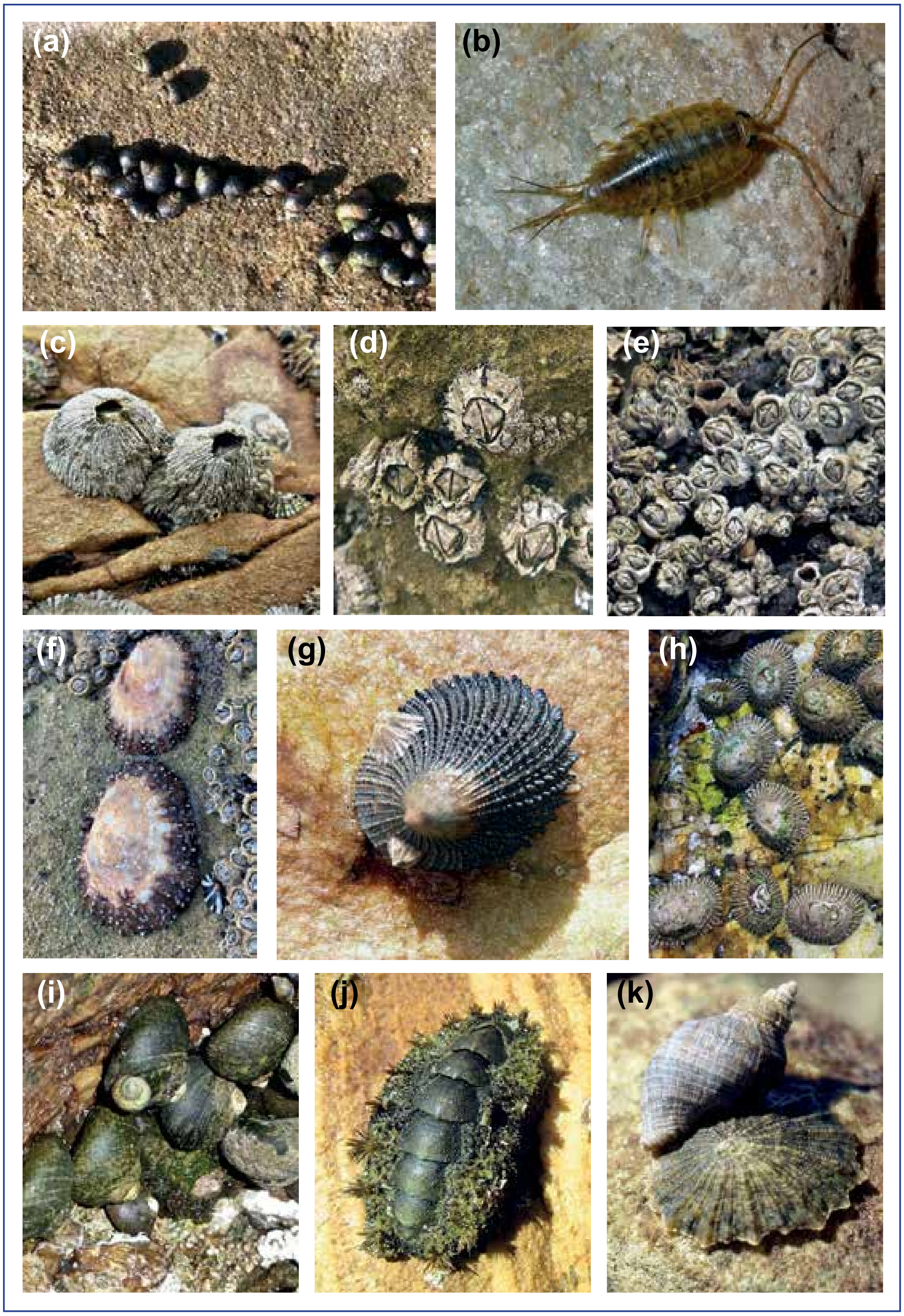

Figure 7.20 Common species from the Littorina (a, b) and Upper Balanoid (c to k) zones at The Heads. (a) *Afrolittorina knysnaensis*, (b) the sea slater *Ligia*, (c) Tetraclita serrata, (d) *Octomeris angulosa*, (e) *Chthamalus dentatus*, (f) *Scutellastra granularis*, (g) *Helcion pectunculus*, (h) *Siphonaria capensis*, (i) *Oxystele antoni*, (j) *Acanthochitona garnoti*, (k) *Nucella dubia* attacking *Cymbula oculus* (Photographs: a,c,h,i,j, © Peter & Frances Smith; b, © Charles Griffiths; k, © George Branch)

Figure 7.21 Common species from the Lower Balanoid zone at The Heads. (a) *Cymbula oculus*, (b) *Scutellastra longicosta*, (c) *Oxystele sinensis* (dorsal view), (d) *Spirobranchus krausii* tubes (with *Teteraclita serrata*), (e) *Mytilus galloprovincialis*, (f) *Oxystele tigrina* (ventral view), (g) *Burnupena cincta*, (h) *Pseudonereis podocirra* (Photographs: b, © George Branch; all others © Peter & Frances Smith.)

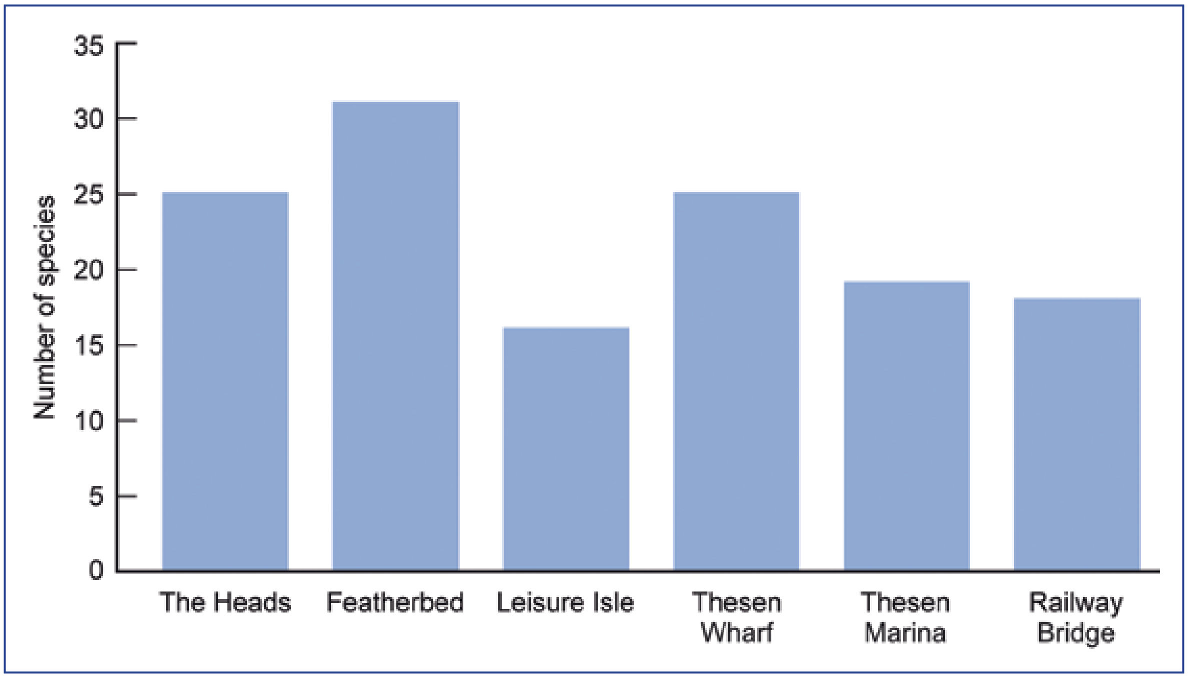

Figure 7.22 Total number of species found within mussel beds at different sites at the mouth and bay regions of the estuary. Data from Hodgson et al.[5].

molluscs, as well as the periwinkles and sea slaters in the Littorina zone, are mainly active on nocturnal low tides although they can be active on overcast or moist days.

Invertebrate fauna easily seen at low tide within the Lower Balanoid (Figure 7.21) include the goat's eye and long-spined limpets (*Cymbula oculus* and *Scutellastra longicosta*), the topshells *Oxystele sinensis* (pink-lipped topshell) and *O. tigrina* (tiger topshell), as well as several species of predatory whelk (e.g. *N. dubia*, and species of *Burnupena*). Also present is the blue coralworm (*Spirobranchus krausii*). A notable recent addition to this zone is the invasive Mediterranean mussel (*Mytilus galloprovincialis*), which probably arrived to the shores of Knysna the mid-2000s[46]. At The Heads, mean densities of the Mediterranean mussel can be as high as 9 000 per square metre and they can occupy up to 50% of the rock space within the Lower Balanoid[5]. Because mussels can significantly alter habitats they are known as ecosystem engineers or bioengineers.

Clumps of the Mediterranean mussel at The Heads provide shelter for up to 31 species of invertebrate (Figure 7.22), including the polychaete mussel worm *Pseudonereis podocirra* (previously named *variegata*) that is popular as fishing bait, as well as several species of scavenging isopod and amphipod (both types of crustaceans). An interesting and common inhabitant of the mussel beds is the intertidal spider *Desis formidabilis* (formidable shore spider) (Figure 7.13). This predator traps air in silk-lined empty mussel shells when covered by high tide, and constructs silk-lined nests in the intertidal. It emerges to hunt for small crustaceans at night when the tide is out. The spider is not only found at The Heads, but also in mussel beds throughout the Bay region and as far upstream as the White Bridge[43].

Lower down the shore in the Cochlear Zone (Figure 7.23) are a few small patches of the pear limpet *Scutellastra cochlear* with its garden of rhodophyte algae (Figure 7.23a). Here the Mediterranean mussel is replaced by the native brown mussel *Perna perna* (Figure 7.23b), which can cover 100% of the rock surface. When Professor Day and his colleagues undertook their survey in 1947, the Cape rock oyster (*Striostrea margaritacea*, Figure 7.23c) was common on the low shore. This species is now rare, probably a result of human exploitation. The brown mussel extends into the Infratidal Zone where the predatory spiny starfish *Marthasterias africana* (Figure 7.23d) is present as well as redbait (*Pyura stolonifera*, Figure 7.23e). These latter two species are usually only exposed to air on the lowest of spring tides in concert with very calm conditions and a high pressure system.

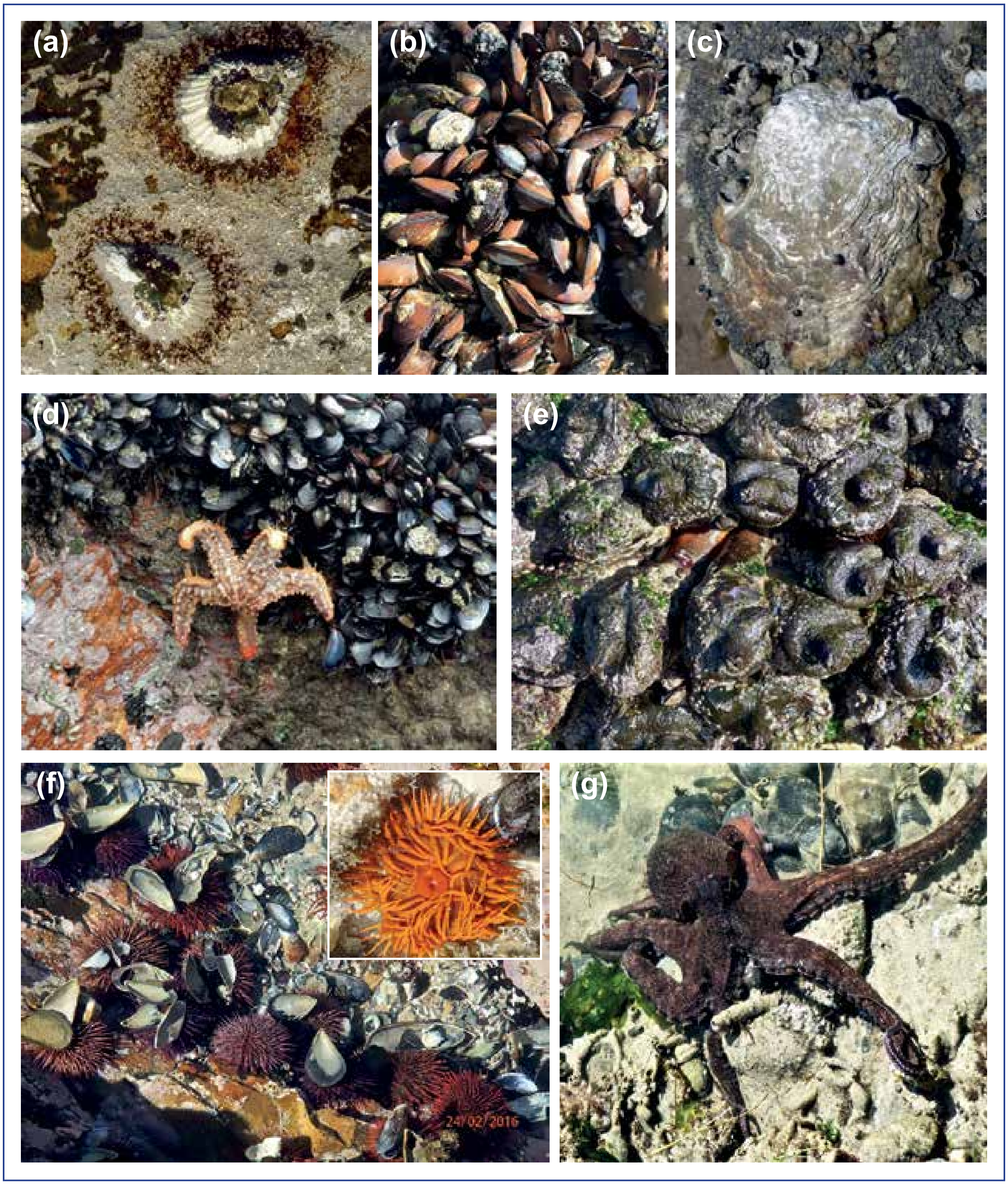

Figure 7.23 Common species from the Cochear and Infratidal zones at The Heads. (a) *Scutellastra cochlear*, (b) *Perna perna*, (c) *Striostrea margaritacea*, (d) *Marthasterias africana* below a bed of mussels (e) *Pyura stonlonifera*, (f) *Parechinus angulosus* in a low shore rock pool, with insert *Pseudactinia flagellifera*, (g) *Octopus vulgaris* (Photographs: a, © George Branch; b, d, © Alan Hodgson; c,e,f, g, © Peter & Frances Smith).

A feature of the rocky shore at The Heads is the numerous rock pools (Figures 7.16b, 7.23f). These enable species that are unable to tolerate exposure to air to exist in the intertidal, including sea anemones, chitons, brittle stars, the Cape sea urchin *Parechinus angulosus* and the dwarf cushion star *Parvulastra exigua* (Figure 7.8). This latter species feeds mainly on microalgae and is very common in high shore pools. They can be difficult to find because their body patterns and colours help them blend into their background. Low shore rock pools can also be home to the common octopus (*Octopus vulgaris*, Figure 7.23g) which forms dens and is found throughout the Bay region, including the canals of Thesen Island Marina where it probably feeds on mussels.

The rocky shore at The Heads extends into the subtidal. Whilst just inside The Heads is an area frequented by scuba divers, there is little information on the invertebrate community beneath the waves. However it is known that anemones, soft corals, sponges, basket stars, and sea squirts are all present (Figure 7.24).

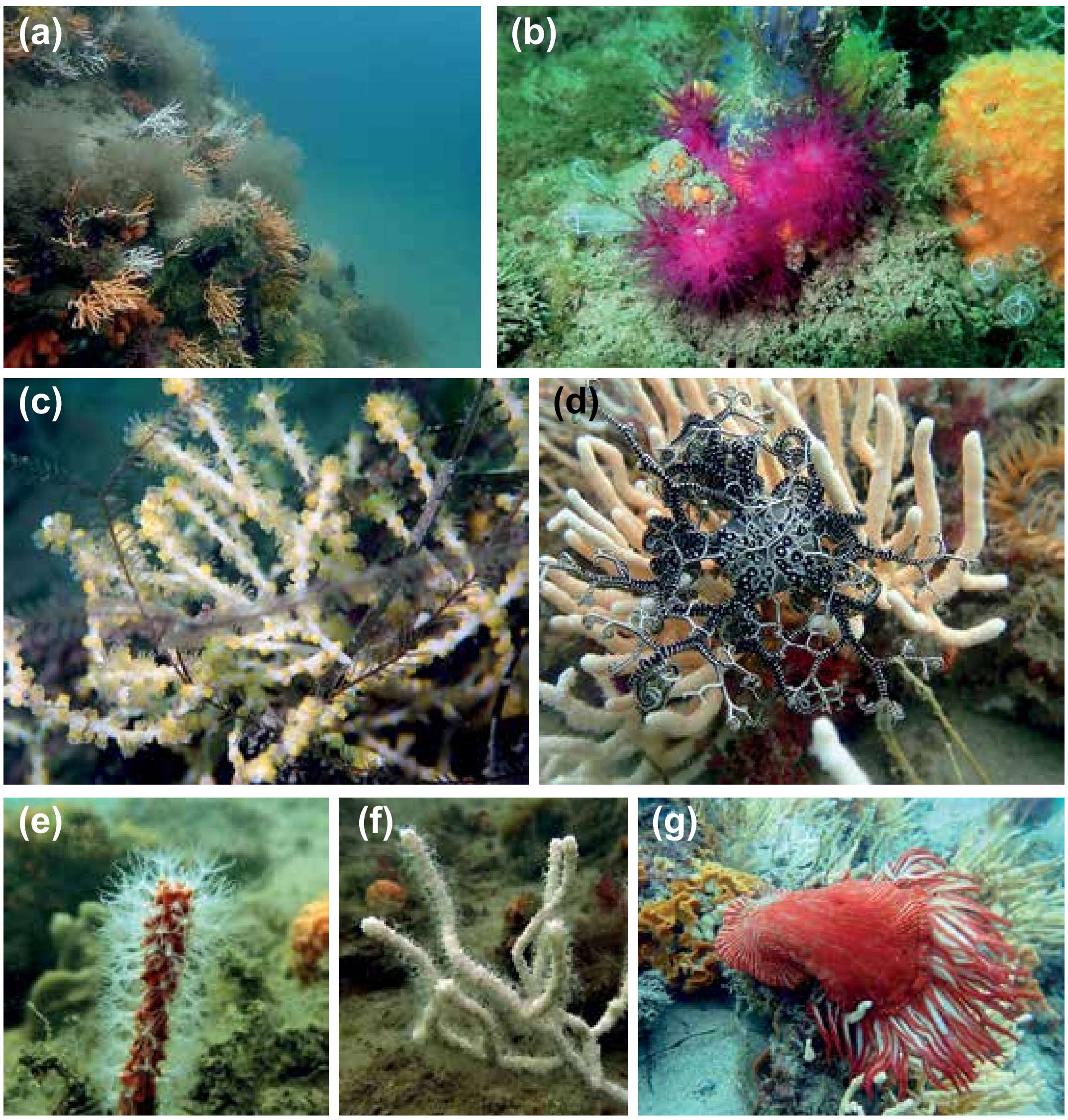

Figure 7.24 The subtidal with its abundant life (a), and examples of the fauna at The Heads: (b) *Alcyonium fauri* (soft coral), (c) *Melithaea* sp. (soft coral), (d) *Astrocladus euryale* (basket star), (e) *Parasphaerasclera* sp. (soft coral), (f) *Eunicella albicans* (soft coral) and (g) *Korsaranthus natalensis* (candy-striped anemone) (Photographs: © Louw Claassens).

The Bay Region

When compared to the invertebrate fauna of The Heads, the number of intertidal 'rocky shore' species decreases markedly within the estuarine bay (Figure 7.19). Species composition also changes. Away from the mouth wave action is greatly reduced and this results in silt deposition on intertidal rocks and other hard surfaces, as well as any organisms present.

Whilst silt benefits deposit-feeding species, it restricts the growth of algae and therefore most of the rocky shore invertebrate grazers present at The Heads are deprived of food and not present. Predatory whelks are also absent further into the bay area. Several different types of natural and artificial hard substrata are present in the Bay region. Unfortunately, quantitative faunistic surveys with confirmed species identifications are lacking for most of these habitats. On the western shoreline about 1 km from the mouth is a small area of soft flat rock covered in silt. Rock boring bivalve molluscs called piddocks have created their burrows here (Figure 7.25a,b). The identification of the species has still to be confirmed and it is not known whether it is a native species. These animals are now threatened by people who dig them out of the soft rock, perhaps for bait. Further upstream on the same side of the estuary is a cobble beach at Brenton-on-Lake (Figure 7.17d). This habitat is home (both on the cobbles and in the substratum beneath them) to over 40 small invertebrate taxa[47], many of which, such as small anemones living on the sides of the cobbles, are yet to be identified. On the eastern side of the bay, sections of shoreline are composed of rocks embedded in sand (e.g. Figure 7.16c) or mud. As with the cobble shore, little is known about the ecology of invertebrates within this habitat type.

Only 18 species were found on the artificial seawall of Cearn Drive on Leisure Isle[43], far fewer when compared to The Heads (Figure 7.19) which is less than 1 km away. The main reason for this is because the wall and rocks are only at the tidal height of the Littorina and Balanoid zones, much of the Lower Balanoid and the entire lower intertidal beng of sand flats. Grazers and filter-feeders dominate the Leisure Isle rocks. The fauna of the Littorina zone is as found at The Heads. Whilst *T. serrata* and *C. dentatus* are still present in the Upper Balanoid, the striped barnacle *Amphibalanus amphitrite* (Figure 7.26b) is now abundant. This species, which is found throughout South Africa, prefers habitats such as lagoons and estuaries where wave action is less intense. Most of the limpets present are species of *Siphonaria*, which are

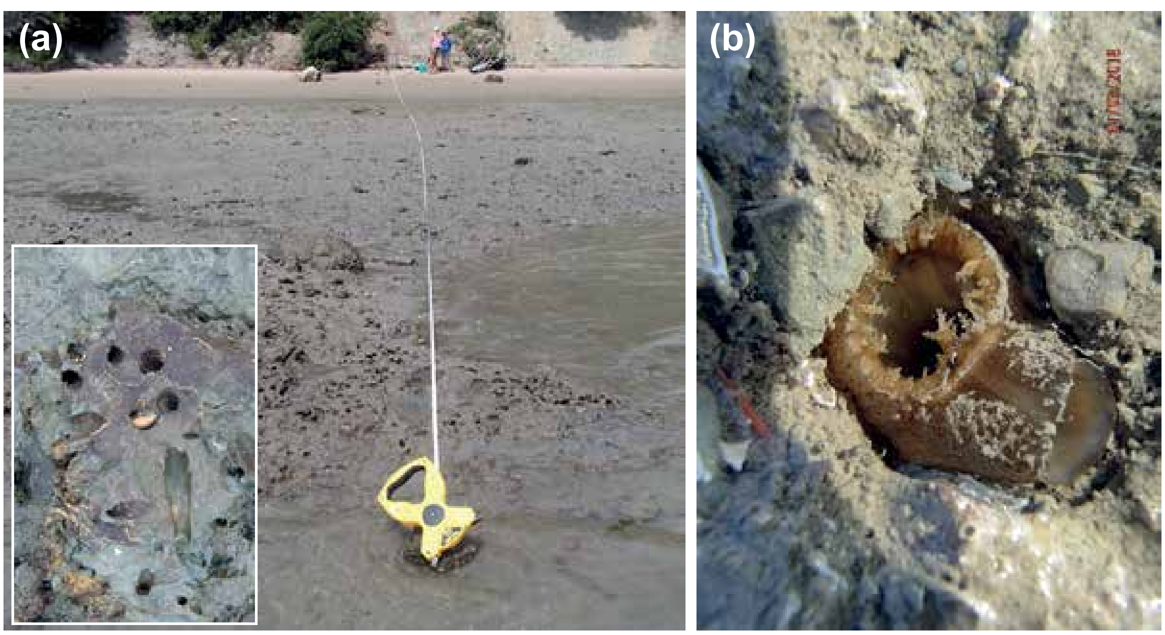

Figure 7.25 (a) Flat platform of soft rock on the west side of the bay region in which burrowing piddocks are found. Inset, small area of rock damaged by diggers showing piddock burrows. (b) The siphons of a piddock in situ (Photographs: © Peter & Frances Smith).

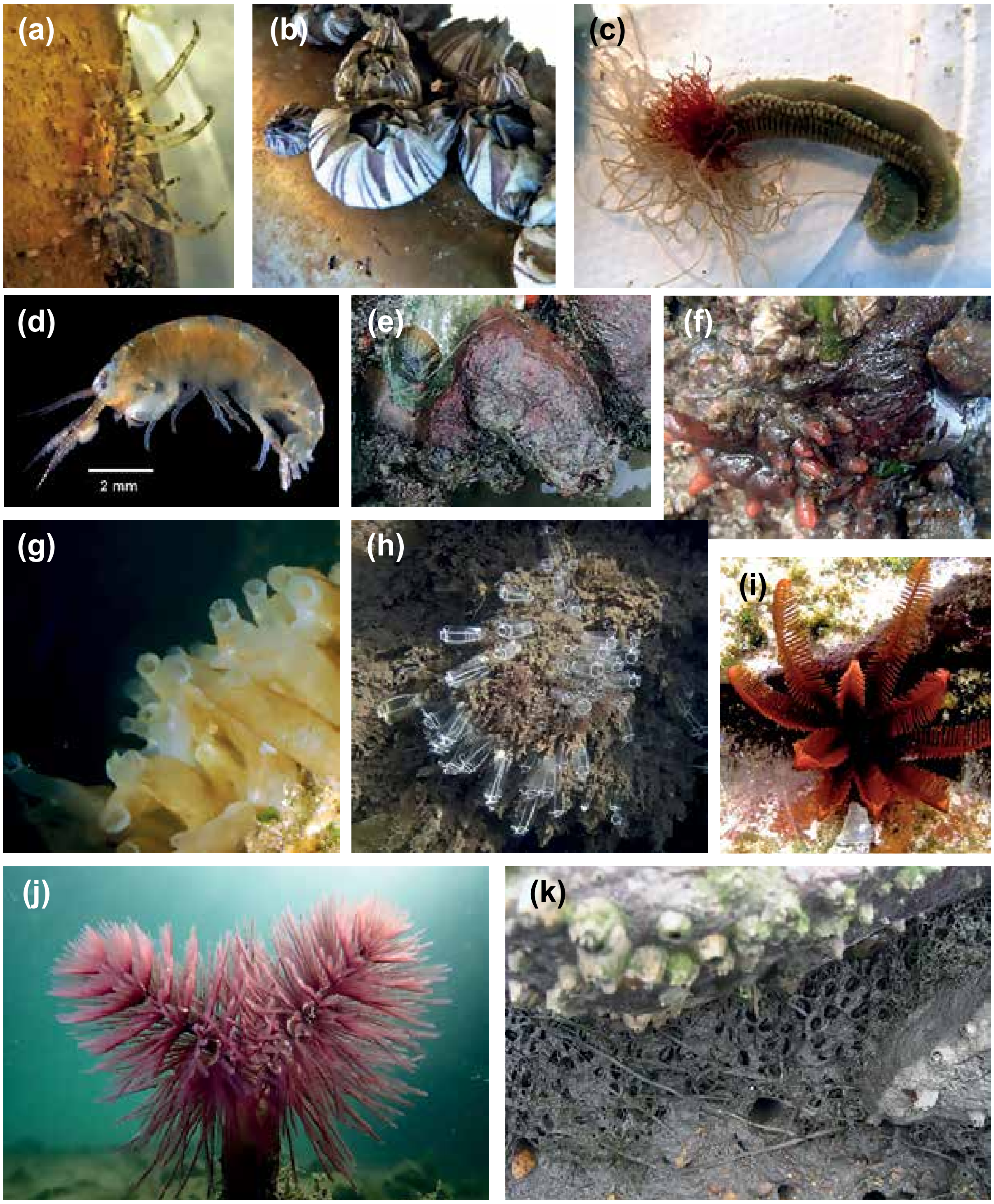

Figure 7.26 Invertebrates from the Bay and Lower Estuarine region. (a) Example of a small unknown anemone species on the side of a cobble from the bay region cobble beach, (b) *Amphibalanus amphitrite*, (c) Tangleworm extracted from its leathery tube. The feeding tentacles are arrowed. The smaller red filaments are the gills, (d) *Ptilohyale plumulosa*, (e) *Microcosmos squamiger*, (f) *Pyura herdmani*, (g) *Ciona robusta*, (h) *Clavelina lepadiformis*, (i) *Tropiometra carinata*, (j) *Pseudobranchiomma longa*, (k) Group of *Arcuatula capensis* sitting in 'chambers' created by a matrix of byssal threads (Photographs: a,b,c,e,f,h,i, © Peter & Frances Smith; d, © Yale Peabody Museum; g, © Charles Griffiths).

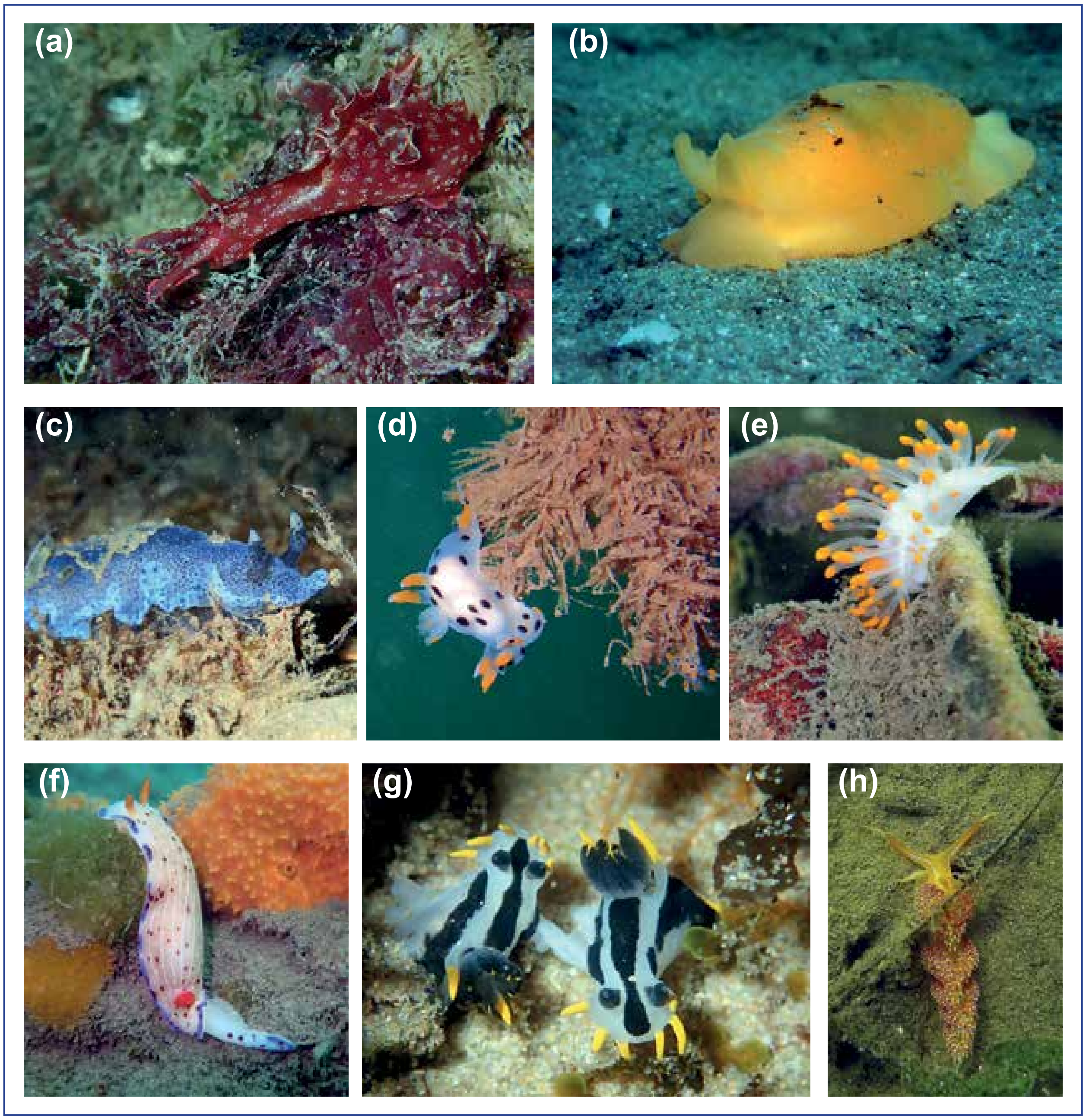

Figure 7.27 Examples of sea hares (a) and sea slugs (b-h) present in the Knysna Estuary. (a) *Aplysia parvula*, (b) *Berthellina granulata*, (c) *Dendrodoris caesia*, (d) *Thecacera pennigera*, (e) *Limacia lucida*, (f) *Hypselodoris capensis*, (g) *Polycera capensis* mating, (h) *Godiva quadricolor* (Photographs: © Louw Claassens).

pulmonate (false) limpets and more closely related to land snails than to the true limpets. Unlike true limpets (Patellidae), siphonariids can survive lengthy periods covered in sand[48]. This can happen on Leisure Isle because the sand bordering the rocks on the seaward side of the island shifts over time[49] and can cover rocks in the Balanoid zones. Also present just above the sand/rock interface is a 5 m wide band of *M. galloprovincialis* (Figure 7.17b). Compared to the native brown mussel, the Mediterranean mussel is more tolerant of sand inundation[50] which must in part, explain why it can live at the sand rock interface. When compared to other sites in the estuary, fewer species of invertebrate live in the Leisure Isle beds of the Mediterranean mussel[51] (Figure 7.22). However, some species found in amongst the mussels, such as the amphipod *Ptilohyale plumulosus* (Figure 7.26d), are very abundant and densities of all the invertebrates can exceed well over 6 000 per square metre.

Since its arrival, the Mediterranean mussel has spread throughout the bay region of the estuary where it forms multi-layered beds on the reinforced concrete frame of Thesen Wharf (Figure 7.17c), the Railway Bridge supports (Figure 7.18a), the gabions of the western section of Thesen Islands Marina (Figure 7.17e), channel marker poles and many jetties[46]. Mean mussel densities on these structures can be greater than 12 000 per square metre. Within the bay, the mussels grow much quicker and reach a larger size than those on wave exposed rocks[51]. For example, mussels of up to 94 mm shell length are found at the Railway Bridge compared to a maximum size of 79 mm at The Heads[46]. The mussels mainly breed in summer[46,52] and, because of their high fecundity, large numbers of juveniles settle within the mussel beds at this time of year[53], although only a few survive to become adults. The adult mussels are aggressive competitors for space and they have undoubtedly replaced some species previously recorded. For example, Day et al.[1] reported that oysters and red bait could be found on Thesen Wharf and the Railway Bridge, and that native brown mussels were present on the Wharf. All these are now absent or rare, having been smothered by *M. galloprovincialis*.

The mussel beds provide habitat for 25 invertebrate species at Thesen Wharf, 19 in Thesen Islands Marina and 18 on the Railway Bridge (Figure 7.22) although overall community composition differs among sites[5]. In addition to large numbers of the amphipod *P. plumulosus*, several species of deposit-feeding invertebrates, including peanut worms (Sipuncula) and tube-dwelling tangleworms (Polychaeta) (see Figure 7.26c) inhabit the space between mussels. The tangleworms feed on organic material in silt using numerous fine elongate tentacles that they extend over the substratum to shuttle small particles to the mouth. Often the only clue to their presence is their extended tentacles at high tide.

Filter feeders can also be found associated with the mussel beds. For example, in addition to the striped barnacle (*A. amphitrite*), blue coral-worm (*S. krausii*) and small spiral fanworms (*Spirorbis* species) all grow on the mussel shells. Another abundant species that lives in amongst the mud trapped at the base of the mussel bed, and in amongst the byssal threads (sometimes referred to as the 'beard') that attach mussels to the substratum and to each other, is the tiny dwarf rusty clam *Lasaea turtoni*. Little is known about the biology of these minute clams, but like their sister species they are probably hermaphrodites that brood their young. Filter-feeding species of sponge, including the crumb-of-bread sponge (*Hymeniacidon perlevis*) are common in the Lower Balanoid and infratidal, especially on the Railway Bridge supports.

The construction of Thesen Islands Marina in the Bay region introduced a large area of vertical intertidal rock walls (gabions) that line the canals. Detailed studies of the fauna attached to these silt-covered walls are lacking. However, zonation on the gabions is apparent (Figure 7.17e) and the presence of some species has been recorded. *Afrolittorina knysnaensis* and *Ligia natalensis* are abundant at the high water mark. The only barnacle species in the Upper Balanoid is *A. amphitrite* where it co-exists with siphonariid limpets. On the gabions close to the western entrance to the marina, the Lower Balanoid is occupied by a band of silt-covered *M. galloprovincialis*, with a band of the alien sea squirt *Microcosmos squamiger* (Figures 7.17e and 7.26e) living just below the mussels. In this region of the marina numerous spiny starfish are present where, at lowtide, they can be seen clinging to the gabions and on the reno mattresses. Here they are taking advantage of the abundance of food in the form of the Mediterranean mussel.

A feature of Thesen Island Marina are the numerous floating jetties. The underside of these jetties are rarely out of water and have a rich invertebrate community attached to them, especially those close to the marina's western entrance. Fauna of note include sea anemones and hydroids (both phylum Cnidaria), colonial bryozoans (moss or lace animals, some of which can be mistaken for brown or grey weed), as well as solitary and colonial sea squirts (ascidians). Ascidian species of note include Herdman's red-bait (*Pyura herdmani*), and two alien invasive species, the sea vase (*Ciona robusta*), and the bell ascidian (*Clavelina lepadiformis*) (Figure 7.26h). A few large mussels often with a shell length greater than 90 mm (both the Mediterranean and brown mussel) are also attached to the underside of the jetties.

The complex 3-dimensional mass of sea squirts and mussels create a habitat for many species of flatworm, polychaete worm, crustaceans and echinoderms. For example, several species of tube-dwelling fanworm are present including the feather-duster worm (*Pseudobranchiomma longa*, Figure 7.26j), the gregarious fanworm (*Pseudopotamilla reniformis*) and red fanworm (*Protula bispiralis*). Echinoderms of note include feather stars such as the elegant feather-star (T*ropiometra carinata*, Figure 7.26i), brittlestars, and the Cape sea urchin. Finally, numerous species of sea hare and sea slugs (all gastropods) have been recorded inside the marina, some of which are illustrated in Figure 7.27. Whilst the sea hares are grazers, many of the sea slugs are predators feeding on hydroids and bryozoans.

Most of the marine fauna in the marina, especially on the jetties, suffered severe mortality during the September 2015 floods when salinities in the shallow waters of the canals were very low (5-15% seawater) for several days (salinities recorded by the Knysna Environmental Monitoring Platform). However, re-colonization by most species had occurred within the next 6 months.

Lower Estuarine Regions

Prior to the widening of the N2 road in 2010, most of the eastern shoreline in the middle lagoon section of the estuary was composed of a soft sediment or muddy/pebble substratum. Reconstruction of nearly 5 km of the Lagoon Road section of the N2 resulted in a shoreline armoured by rocks. The hard shoreline close to The Point is now colonized by 29 species of invertebrate, whereas towards the White Bridge only 14 species are found[43] (Figure 7.19), some of which inhabit the mud beneath the rocks. Species that inhabit this region of the estuary not only have to tolerate deposition of silt, but also regular reductions and fluctuations in salinity that occur during times of greater freshwater inflow from the Knysna River. Therefore, many of the species found are true euryhaline estuarine species (tolerant to a wide range of salinities). The rocks in the mid to lower intertidal are mostly colonised by the barnacle *A. amphitrite* (maximum mean density 27 200 per square metre[43]), and siphonariid limpets. Although a few small Mediterranean mussels are present, by far the most abundant mussel in the Lower Balanoid is the filter-feeding estuarine mussel *Arcuatula capensis* (Figure 7.8), which can each a maximum mean density of 2 470 per square metre[43]. These mussels are attached to the underside or sides of rocks by byssal threads that form a complex 3-dimensional matrix that traps mud (Figure 7.26k). This in turn provides a habitat for some bryozoans, sipunculids, polychaete worms and sea squirts[43].

Some concluding remarks

Since the first rocky shore survey of the Knysna Estuary[1] there have been significant changes to the estuarine environment, especially the conversion of soft sediments shore-lines to hardened surfaces. Faunal surveys during the last 10 years, and studies on the recently established mussel beds[5], have revealed the presence of many previously un-recorded species (43% of taxa identified). We still have much to learn about the invertebrates inhabiting the estuary and their role in the ecology of the system, as well as community structure on shore types such as cobble shores, shores of mixed soft sediments and rocks, as well as the subtidal. Such studies are critically needed for sound conservation and management decisions. Investigations into the habitats listed above will undoubtedly reveal more invertebrate wonders.

7.4 Zooplankton

Although the Knysna estuary is considered one of the best researched estuaries in South Africa, published information on its zooplankton is surprisingly limited[54]. The first reference to the zooplankton community is provided by Day et al.[1], but samples were not analysed in detail. None-the-less, the zooplankton of the estuary was described as "rather poor". This broad conclusion was probably linked, at least in part, to the make-up of the sampling gear (a "medium plankton net" with no description of mesh size) or when samples were collected.

The only other available description of zooplankton present in the Knysna Estuary was provided by Grindley[55,56]. The list of species in both publications follows a general approach, with no reference to the density of the species present. In addition, the list of species originated from unpublished reports[57].Unfortunately, no further account of the estuarine zooplankton of the Knysna Estuary appears in the published literature. This conclusion is supported by accounts[58,59,] who both quote Grindley's[56] publication as a source of information on the zooplankton of the estuary. In a more recent review, Claassens et al.[12] provide no further reference to zooplankton research outputs from the estuary, although the need for research on the role of zooplankton in the Knysna Estuary was identified.

The term 'zooplankton' covers a wide range of species (Figure 7.28) that may be grouped into different size classes, each category requiring a specific sampling strategy that maximizes for sampling efficiency of the group. Many different phyla also occur in the zooplankton, adding to the complexity of the assemblage.

We have obviously come a long way since zooplankton investigations began in the 1950s in South Africa, but it must be noted that the earlier research was pioneering and initiated at a time when almost nothing was known about the zooplankton of our estuaries. Unfortunately, the status and composition of the estuarine zooplankton in the Knysna Estuary is poorly known and this has not changed significantly since those earlier studies.

Despite the lack of detailed information on zooplankton from the Knysna Estuary, Grindley's[56] list still provides opportunity to associate species with specific zones along the salinity gradient. Most of the species on this list are macrozooplanktonic, a size class of zooplankton retained by a net of 200 μm mesh aperture. Characteristically, the macrozooplankton in a tidal estuary having a full salinity gradient falls into three broad categories, as summarized in Figure 7.29. The same horizontal patterns are likely to be present between The Heads (marine dominated) and the Charlesford Rapids (freshwater dominated), but subsets or pockets of the euryhaline and freshwater components are also present where freshwater runoff enters the estuary; for example, north of Thesen Island.

Many species spend their entire life cycle in the plankton (holoplanktonic), while others are only temporary residents (meroplanktonic). Examples of the meroplankton include the larvae of many benthic animals. The zooplankton of estuaries are also classified according to their salinity tolerances (Figure 7.29). Stenohaline species are those that tolerate salinity values down to about 28 ppt (seawater salinity = 35 ppt); freshwater associated species penetrate the estuary from the river up to a salinity of about 5 ppt. True estuarine species have a wide salinity tolerance range (euryhaline). Some species in each group overlap with those in adjacent categories and the boundary therefore represents a zone, rather than a line. Typically, the stenohaline group is composed of many species (high species richness), but numbers of individual species are relatively low. The euryhaline group reflects the opposite, with relatively few species and high abundance of individual species. The freshwater group

Figure 7.28 Members of the zooplankton occur in many different forms. Copepods (arrowed) are among the most abundant of the various groups that occur in the Knysna Estuary (Photograph © Christian Sardet).

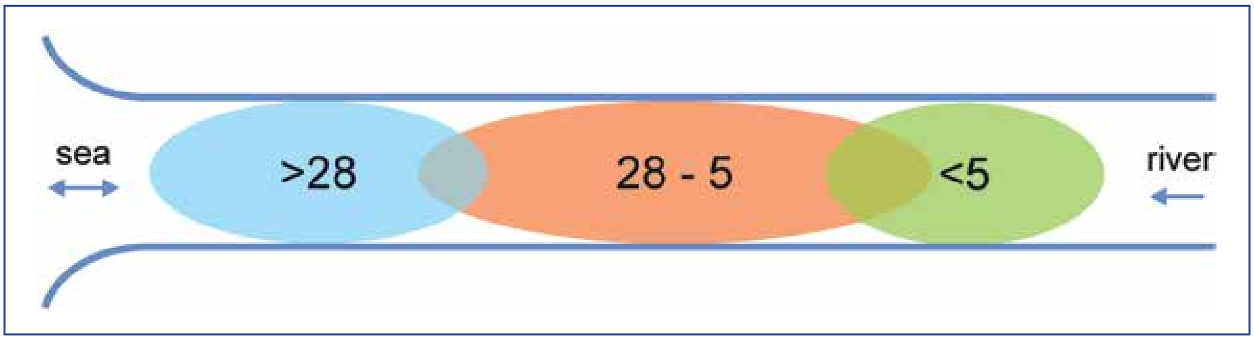

Figure 7.29 Diagramatic representation of the three broad categories of zooplankton in a tidal estuary having a full salinity gradient. Note the overlap between groups, rather than set boundary lines.

characteristically have a species richness as well as numbers of individuals per species ranked between steno- and euryhaline groups.

In most tidal estuaries, larval development of estuarine benthic species such as *Upogebia africana* occurs in the marine nearshore where they benefit from the more stable physico-chemical environment[60]. To optimize for survival and export of *Upogebia* larva from estuaries, behavioural characteristics have also evolved. For example, larvae are released by female prawns under the cover of darkness and at the start of the ebb tide (Figure 7.30). Sunset is a trigger that is easily perceptible, and when coupled to the start of the ebb tide, mass release of larvae by a population will reduce predator build-up since the release period is relatively short and not protracted beyond the ebb tide[60]. When, after their planktonic phase, postlarvae return to the estuarine benthic populations, timing may also be specific (Figure 7.30).

However, the nursery area used by *Upogebia* larvae may be different in the Knysna Estuary where the water body below the railway bridge is strongly influenced by the sea. The tidal prism is large and salinity levels remain close to that of seawater. It is therefore possible that *Upogebia* larval development takes place in the lower section of the estuary itself, rather than in the nearshore. Although the nursery area may be different compared to most tidal estuaries, larval patterns of release and return of post-larvae are unlikely to change from those already described.

In addition to the possible nursery function provided by the lower basin area, the stenohaline zooplankton assemblage found here is also likely to remain resident in the estuary. This contrasts with most other permanently open estuaries where the marine group usually flush to sea on the ebb tide or when river flooding occurs.

In the Knysna Estuary, most floods will lead to a relatively thin veneer of reduced salinity water (forming a halocline) over a large surface area and over the relatively stable, high salinity water body. In the Knysna Estuary, the stenohaline assemblage below the railway bridge includes species such as the copepods *Paracartia longipatella*, *Euterpina cutifrons*, *Oithonanana*, *Paracartia crassirostris*, *Paracalanus parvus*, while other marine species less tolerant of reduced salinity levels occur nearer the mouth. These include *Centropages brachiatus*, *Clausocalanus furcatus* and *Corycaeus* spp. Meroplanktonic forms include gastropod and bivalve larvae (not identified), fish eggs and larvae[56].

On occasions of nearshore upwelling, cold, deep water marine forms temporarily penetrate the lower estuary on a flood tide. The stenohaline community is characterized by high species richness (potential number of species entering the estuary is likely to exceed 100), but each species occurs in relative low abundance compared to euryhaline estuarine forms. Note that like in the zoobenthos, marine-associated planktonic species penetrate the estuary to different degrees, depending on their respective tolerances to prevailing salinity. *Paracartia longipatella* for example, will extend relatively far upstream of the railway bridge and overlap with some of the euryhaline group. Generally, the upstream boundary zone of the stenohaline group is not rigidly fixed and may fluctuate according to the tidal volume passing through The Heads and the magnitude of the river flow volume entering the estuary. This boundary zone will therefore change between spring and neap phases of the tidal cycle and according to the river regime.

Upstream of the railway bridge a typical euryhaline community occurs which includes estuarine copepod specialists such as *Acartiella natalensis* and *Pseudodiaptomus hessei*. Both species favour the 5–20 ppt salinity range where they provide an important source of food for numerous post-larval

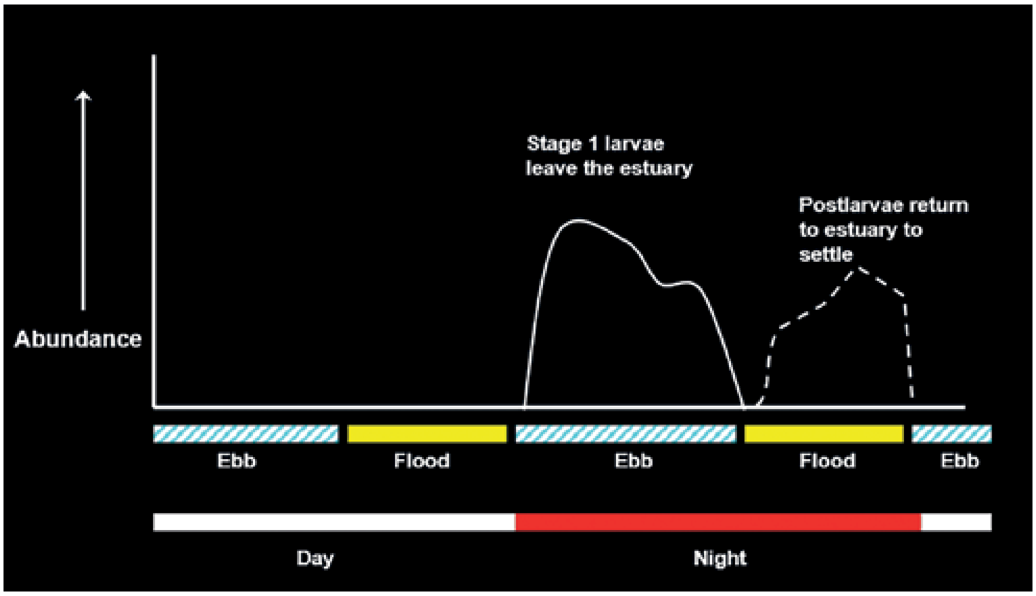

Figure 7.30 The mudprawn *Upogebia africana* is abundant in the Knysna Estuary and is an example of a benthic invertebrate having meroplanktonic larvae. Early-stage *Upogebia* larvae are released into the plankton in the warmer months and at specific times of the diel, tidal and lunar cycle. Data shown above reflects the release of larvae by females in the nearby Swartvlei Estuary where larvae are exported to the nearshore where they metamorphose through several stages before returning to estuarine environments to colonize the benthos.

and juvenile fish species[61]. These two copepod species also respond positively to pulses of freshwater inflow to an estuary when population densities (expressed as the number of individuals per cubic metre of water) can well exceed the combined density of the other estuarine mesozooplankters present[62]. The geographical range of *Acartiella natalensis* also reaches its southern limit at Knysna where it is likely to occur in the plankton only during the hottest summer months. This species undergoes seasonal succession in the plankton[63], unlike in more tropical estuaries where in remains permanently in the plankton[64]. During its non-planktonic phase, dormant eggs of *A. natalensis* remain in bottom sediments[65].

Very few freshwater-associated zooplankters were collected below Charlesford Rapids[56], although a species of *Cyclops* and the amphipod *Paramoera capensis* were present. The latter species is not strictly planktonic and is better described as 'bentho-planktonic', i.e. partly associated with the water and partly with the bottom sediments. Fifteen species of ostracods were also noted[59], with some of these described[66]; others appear to repre-sent freshwater genera. Most ostracod species probably inhabit the benthos, although others may temporarily move into the plankton.

Mysid shrimps were also present in the estuary, but numbers were described as very low. *Mysidopsis similis* and *Gastrosaccus brevifissura* were recorded near Leisure Island[1,56]. *Gastrosaccus brevifissura* is benthoplanktonic and has a strong association with a sandy substratum, although it tolerates a wide salinity range[67]. The third mysid species recorded in the Knysna Estuary *Rhopalophthalmus terranatalis* is strictly planktonic and the largest mysid in South African estuaries (up to 25 mm length[60]). It is a euryhaline species and mostly recorded upstream of the railway bridge[1, 56]. The only other mysid species (*Mesopodopsis africana*) listed for the Knysna Estuary[56] is probably a misidentification and likely to be *M. wooldridgei* previously *Mesopodopsis slabberi*). The latter species is broadly described as planktonic, also found in the marine nearshore, but also penetrating the lower uryhaline zone of temperate estuaries[68]. *Mesopodopsis africana* on the other hand, occurs from Tropical East Africa and reaches its limit of southern distribution in the northern parts of the Eastern Cape Province[64]. The "low abundance" of mysids described for the Knysna Estuary is also debatable, since mysids (and many copepod species) are easily able to avoid small zooplankton nets, particularly those having a fine mesh that easily clogs with detritus and phytoplankton. This again underlines the need for appropriate sampling techniques.

Cumaceans, isopods and amphipods, like mysids, retain their young in a brood pouch on the underside of the body (and form the peracaridan group of crustaceans, see Appendix). Included is the benthopelagic cumacean *Iphinoe truncata* which also has a strong affinity with a sandy substratum. The amphipods *Grandidierella lignorum* and *Melita zeylanica* on the other hand, prefer a muddy substratum. Although these species have specific sediment preferences, all are euryhaline and *G. lignorum* is known to become part of the zooplankton community during periods of elevated river flow through Eastern Cape estuaries.

7.5 The Knysna oyster

Some readers may be amazed that there has been no mention in this chapter of the invertebrate that according to the popular press 'is famously synonymous with Knysna' and for which 'Knysna is the Capital of South Africa, if not of the World'. Beginning in the late 1940s and continuing for many decades thereafter, various species of non-native oyster were farmed commercially in the estuary by The Knysna Oyster Company, and for several years there was a hatchery at Belvidere. From the 1970s the farmed species was the estuarine Pacific oyster, *Crassostrea gigas*. Apart from escapees, however, these oysters were never really part of the Knysna fauna. The Belvidere hatchery failed, and seed oysters were brought in from abroad, reared in Port Elizabeth (as it then was), before being laid out in 'poches' on racks in the lagoonal section of the estuary to fatten up. However the commercial operation was "not profitable socially, environmentally, or financially"[69], and it eventually closed in Knysna in 2014.

Naturalised populations of *C. gigas* totalling some 1 000 individuals were observed in 2001 but numbers appear to have dwindled since then, perhaps to zero[70]. That does not mean that there are no longer 'Knysna oysters' nor indeed no annual festival devoted to them, just that the *C. gigas* consumed are imported from the Eastern Cape, and the Knysna Oyster Company is another iconic Knysna institution now based in Cape Town instead.

7.6 Overview

This chapter has set out to introduce the main invertebrate cast of the ecological drama enacted at Knysna. In many respects it is much as might be expected in a large, open South African estuary or sheltered bay, and there are obvious similarities with Langebaan[71], including occurrence of the rare eelgrass false-limpet *Siphonaria compressa* and seagrass populations of the diminutive cushion star *Parvulastra exigua*. Some elements, however, seem unusual. Such great abundance of the small gastropod *Alaba pinnae* has not been observed in any other South African estuary, for example, and neither have such large densities of '*Assiminea*' *capensis*. But then *Alaba* was not known to be so common in Knysna until the subtidal eelgrass zone was investigated very recently using scuba; and '*Assiminea*' may simply have been missed elsewhere because it is so small and so easily overlooked—tiny gastropods are notoriously difficult to identify from preserved samples. In contrast, they are very easy indeed to identify when alive but all too few zoologists seem to examine their invertebrate material whilst it is still living (no one would think of shooting all the antelope in a National Park to see what they are, but it seems a different matter when they are 'only' invertebrates). Perhaps only when other localities receive the same level and type of attention as has Knysna will it be possible to know how unusual a system it might be. In the future, such comparisons of faunal biodiversity within and across localities are likely to be achieved much more rapidly, using DNA barcoding, once the molecular signatures of individual estuarine species have been established. The process has already begun at Knysna[71].

We know the invertebrate fauna well enough to be sure that it is unlikely that there are any animals larger than a millimetre or so that are completely unknown to us. We may not know their names, but we know that they are there and the broad outlines of their distributional patterns are fairly clear; and we can make a good guess as to who does what. That having been said it is certain that there remain large areas of ignorance. As has been commented above, very little work has been carried out on the plankton, many subtidal regions are yet to be explored, and most importantly we do not know the main processes and pathways that structure and maintain the system's status quo. We are therefore still in a very poor position to estimate how the invertebrate fauna and its ecology will react to global warming, to sealevel rise, and to further stress from eutrophication and other human activities. What will happen when the accumulation of organic matter in the Ashmead Channel is removed, and does it matter how this is achieved? Will marina channels serve as a refuge for the aquatic fauna? What will be the consequences of population growth around the estuary's periphery? How is exploitation of the estuary changing its ecology and what can be done to mitigate this? These are important questions for the next few decades and for the next generation of researchers.

7.7 Endnote

Scientific papers describing aspects of the ecology of Knysna's aquatic invertebrate fauna frequently include a sentence to the effect that it was not possible to identify all animals to named species. Because of lack of systematic studies, only a few of the area's sponges, hydroids, flatworms, ribbon worms, oligochaetes and bryozoans, for example, and not all members of some types of polychaete and gastropod, are known. Usually the larger types of animal can be identified (and their occurrence even noted by their distinctive burrow systems, Figure 7.31), but the smaller ones cannot. For these, there are no monographs available and so the researcher has to state that there were, for example, five or six seemingly different types of such and such an invertebrate present, and leave it as that (see Appendix 1). Mention was made above that two of the most numerous members of the Knysna fauna still do not have genera assigned to them, and several of the commoner species remain named on the basis that they are the same species as is present in Europe whereas zoogeographical considerations suggest they are unlikely to be conspecific. In fact, for many of the types of invertebrate present we only know what and how many species there are because of the activities of one or two dedicated global specialists per group. There is, therefore, much scope for the animals that are poorly known in Knysna, and more generally in South Africa, to be 'adopted' by enthusiastic amateurs — much as Charles Darwin took up the study of barnacles.

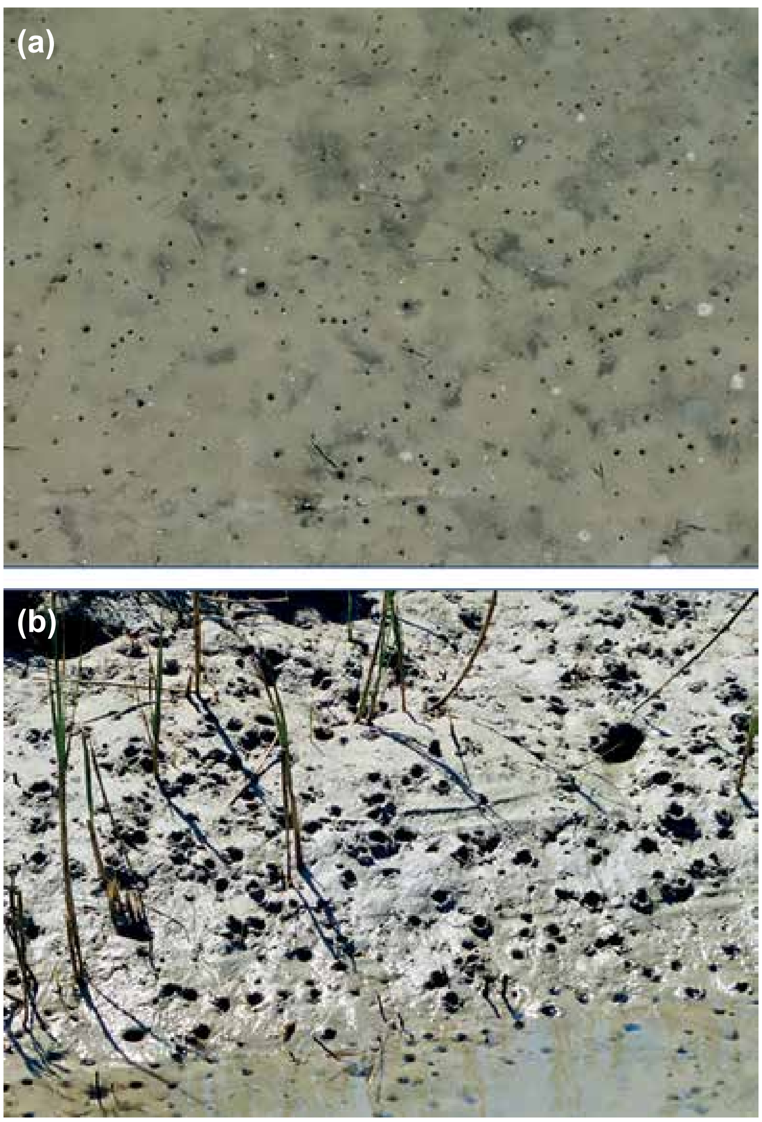

Figure 7.31 Some of the larger Knysna invertebrates such as (a) *Upogebia* and (b) *Parasesarma* are 'ecosystem engineers' and structure their habitat to the benefit or detriment of other species; their effects are often much more obvious than the animals themselves.
(Photographs: © Richard Barnes).

View over the Knysna Lagoon towards the Outeniqua Mountains (Photograph: © Richard Barnes).

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Fish attracted to a baited underwater video camera in an eelgrass bed (Photograph: © Louw Claassens).

Chapter 8 : Fishes of the Knysna Estuary

Alan Whitfield, Louw Claassens & Kyle Smith

8.1 Introduction

Estuaries are one of the most productive aquatic ecosystems, on a per unit area basis, on our planet and society needs to avoid compromising the biodiversity and functionality of such valuable systems. Our actions in terms of preventing habitat degradation, pollution or over-exploitation of the estuarine resources are paramount for a healthy system that remains attractive for the wide variety of fish species that occupy these waters. Altogether 119 fish species have been recorded in the Knysna Estuary (see Appendix 1 for details), the majority of which are marine migrants or marine stragglers. A relatively small proportion of the species list are represented by permanent residents, and one species (African longfin eel *Anguilla mossambica*) uses the estuary as a conduit to and from the river catchment.

Apart from the high primary and secondary productivity of the estuary, the Knysna system has the distinct advantage of being permanently open to the sea, thus allowing fish free access to and from the estuary. This is particularly important to those marine fish species that need to spawn at sea and, if the mouth were to be closed during their breeding season, they would miss out on contributing to the next generation of their species in that particular year.

The Knysna Estuary is located within the warm temperate biogeographic region on the subcontinent. Most abundant fish species located in the estuary have the centre of their distribution located within this zone. Tropical species such as the thornfish *Terapon jarbua* occasionally find their way into the estuary during spring but may be unable to survive the winter water temperatures or the incursion of cold marine upwelled water during summer. However, with climate change already upon us, the increasing numbers of subtropical species such as the spotted grunter *Pomadasys commersonnii* are a sign that a new ecological shift is taking place within the Knysna fish community.

8.2 Fish life cycles in South African estuaries

The overwhelming majority of fish species found in estuaries are of marine origin with very few freshwater fishes able to survive the salinity regimes found in these systems. Some species are able to complete their life cycles within estuaries and are termed residents, but most are classified as marine migrants or estuary-associated marine species (Figure 8.1). Some of these are completely dependent on estuaries as nursery areas and these taxa are termed estuary-dependent species.

Late larvae and early juveniles of many marine fishes migrate actively into estuaries at about 1 cm in length where they remain for varying periods of time before returning to the marine environment, prior to, or after attaining sexual maturity. This type of life cycle has led to estuaries being termed key nursery areas for fishes and is reflected in the very large numbers of small juveniles in the shallow littoral waters of these systems. The reliance of juveniles of migrant marine species on estuarine nursery grounds varies considerably, and ranges from marine stragglers which are seldom found in estuaries, to those species that are dependent on estuaries during the juvenile phase of their life cycle.

Some species such as the white stumpnose *Rhabdosargus globiceps* and elf *Pomatomus saltatrix* appear to use favourable estuarine conditions opportunistically, the juveniles also being abundant in the sea. Other species, like the Cape stumpnose *Rhabdosargus holubi* and white steenbras *Lithognathus lithognathus* are considered to be dependent on estuarine nursery grounds and might even become extinct if these systems were destroyed or became unavailable due to permanent closure of all estuary mouths. Fortunately the Knysna Estuary has no major dam on the river but weirs, freshwater abstraction and alien infestation in the catchment has drastically reduced perennial river flow into the estuary.

The other major group of fishes to occupy the Knysna Estuary comprises mostly small estuarine species that use the estuary, not only as a nursery, but also as a spawning ground. The estuarine roundherring *Gilchristella aestuaria* and Knysna seahorse *Hippocampus capensis* are two examples of this fish guild which spend their entire life cycle within the estuary (Figure 8.2). All these small species are estuarine dependent and therefore their future

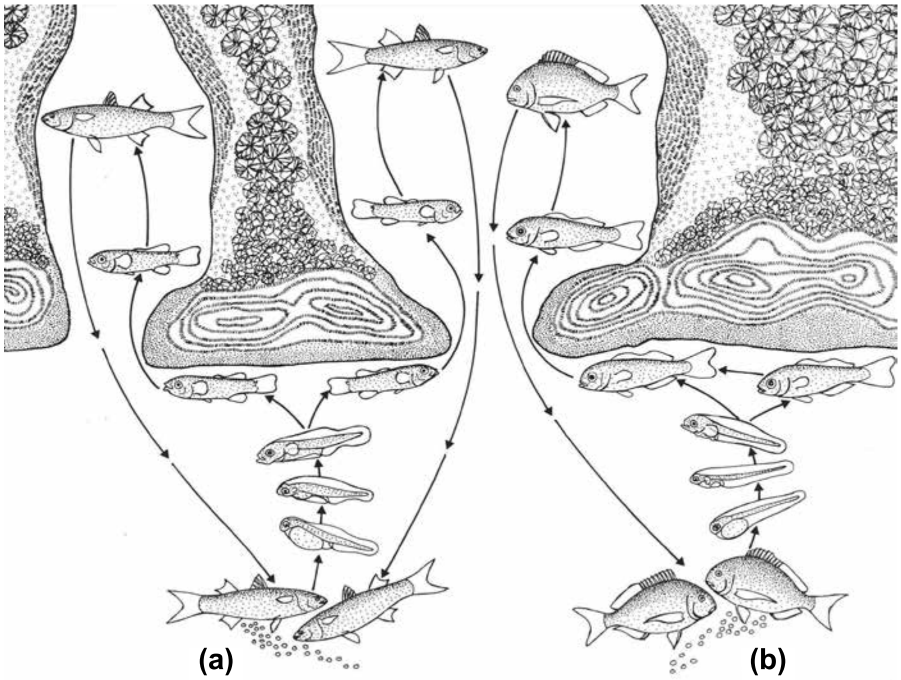


Figure 8.1 Diagrammatic representation of the life cycles of (a) southern mullet (*Chelon richardsonii*) and (b) Cape stumpnose (*Rhabdosargus holubi*) off the southern Cape coast. Both these species spend about 2 years in estuaries as juveniles before migrating back to the sea where they become sexually mature. Breeding only occurs in the marine environment but both species are dependent on healthy estuaries such as Knysna as nursery areas.

survival is closely linked to the health of the estuary.

There are no indigenous freshwater fish species recorded in the Knysna Estuary, mainly due to the inability of the few taxa to survive the salinity fluctuations that characterize this system. This reflects global trend of poor utilisation of estuaries by freshwater fishes when compared to marine species[2]. In addition, the historic catchment isolation of the Knysna River by the Outeniqua Mountains in the north and the sea in the south has meant that few freshwater fish species have managed to colonize this system, and only a few regional endemics such as Cape kurper *Sandelia capensis* and Cape galaxias *Galaxias zebratus* have made the Knysna River their home. Added to this biogeographic isolation, are low pH waters with poor nutrient levels, and limited suspended particulate organic matter for the aquatic food web. Although dissolved organic matter is present in the Knysna River in the form of humates that give the water its dark colour, this material only precipitates out of suspension when the freshwater mixes with seawater in the estuary. Nevertheless, the Knysna River can boast of at least one freshwater species, one that is unique to the area, namely the forest redfin that has still to be formally described as a new species[3].

8.3 Fish recruitment into the Knysna Estuary

Seasonal spring and summer increases in juvenile fish abundance in the Knysna Estuary has been documented by Whitfield & Kok[4] and relates to the recruitment of early juveniles from the sea into the estuary and the utilization of shallow littoral habitats as nursery areas. The high abundance of fish in the estuary has been partially attributed to the strong marine influence associated with the deep, permanently open mouth, which also makes it a more stable and predictable nursery area compared to nearby open/closed estuaries such as Goukamma or Swartvlei. Indeed, ad hoc artificial winter breaching of the Swartvlei mouth occurred during the 1960s and 1970s, and led to the premature closure of the system and loss of the 'head' of water needed for the spring/summer opening. This type of mouth manipulation results in reduced availability of estuarine nursery areas for marine fishes along the southern Cape coast.

Comparisons between the recruitment of juvenile fishes into the Knysna and Swartvlei estuaries indicate that higher densities of most species were recorded in the former system, linked to the greater

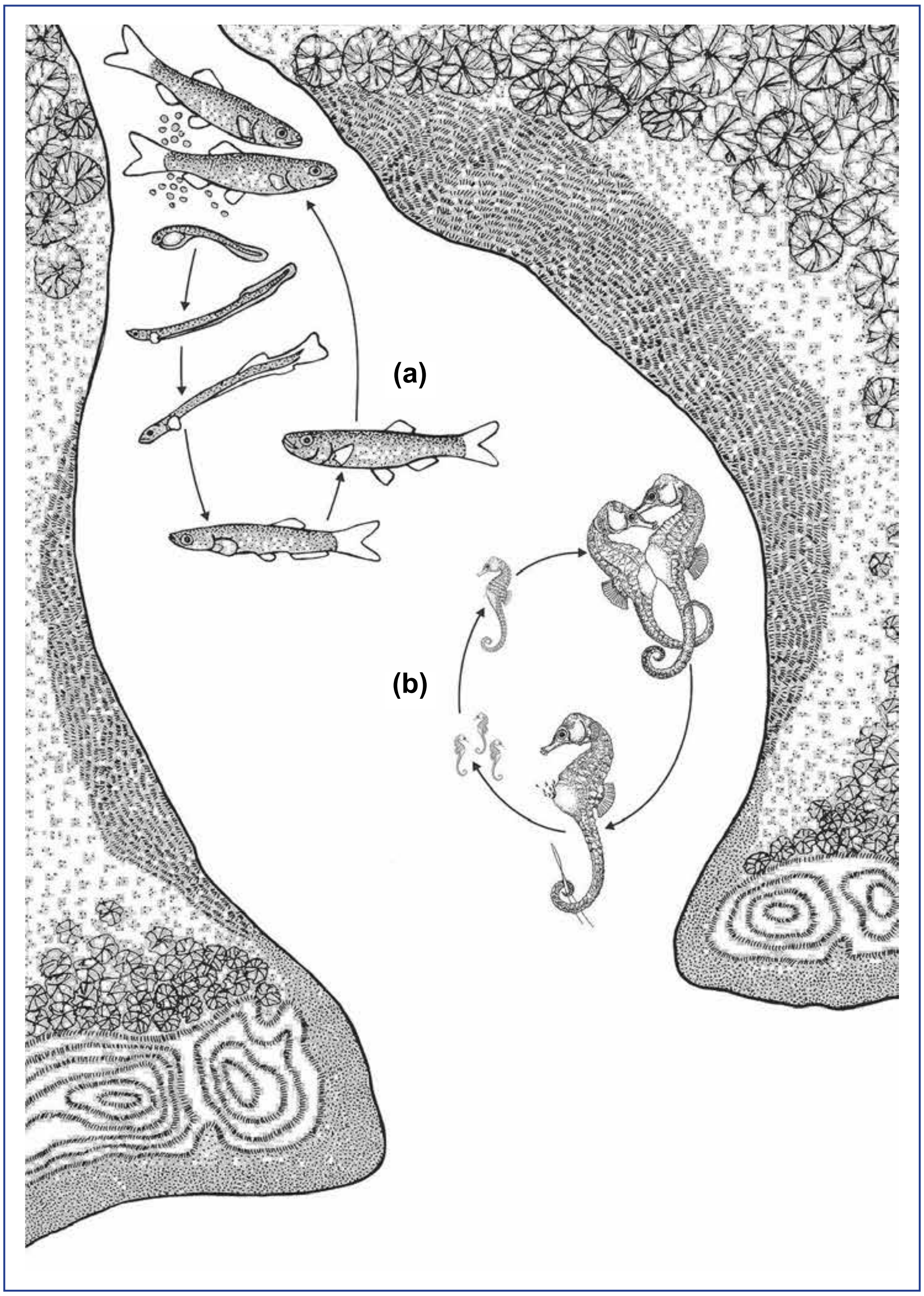


Figure 8.2 Diagrammatic representation of the life cycles of (a) the estuarine roundherring (*Gilchristella aestuaria*) and (b) the Knysna seahorse (*Hippocampus capensis*) in the Knysna Estuary.
Both these species spend their entire life cycle within the estuary, with *G. aestuaria* spawning in the upper reaches open water areas and *H. capensis* males releasing live young from their brood pouch into shallow sheltered habitats.

estuarine-marine connectivity of the former system. However, in a regional context both Knysna and Swartvlei are large, generally unpolluted systems, which serve as important nursery areas for many species of fish. On this basis alone, these contrasting estuarine systems should be allocated the highest possible conservation status.

Fish abundance patterns in estuaries have been shown to be directly linked to the seasonal variations in recruitment of marine fishes into these systems. In the southern Cape the peak recruitment of fishes into estuaries occurs mainly during the summer months (Figure 8.3) when primary and secondary production is at a maximum. Growth of these juveniles is rapid, with some species increasing their length by more than 1 cm per month in their first year.

Most early marine fish larvae are transparent in the sea, with very little pigment and the only discernable structure being the eye. An example of the major changes that can take place between the early larval stages in the nearshore marine environment, the later stages in the surf zone, and the early juvenile stages in the estuary are shown for the blackhand sole *Solea turbynei*, a small sole species that is abundant in the Knysna Estuary. Of particular interest is the migration of the left eye as this fish changes from an early larva 2.8 mm body length, a larva 3.0 mm body length, a late larva 4-5 mm body length, and finally a juvenile 22 mm body length with both eyes now firmly situated on the right-hand side of the head (Figure 8.4). During the larval life stages the fish was moving in the water column of the sea and surf zone but, when it reaches the early juvenile stage in the estuary, it will now live on the bottom for the rest of its life.

The question is often asked — how do small marine fish, only a few millimetres in length, manage to find an estuary nursery area such as Knysna? Although the embryo and very early larval stages are unable to swim and merely drift passively in the ocean currents, once the larvae develop fins they become active swimmers and can travel several kilometres in a day. Using their highly developed sense of smell, they follow olfactory chemical cues in the water towards the coast, initially being attracted to the surf zone, and then travelling along the coast within the surf zone until they 'hit' an estuary. Some larvae follow the olfactory concentration gradient directly into the estuary and may avoid the surf zone altogether. At this stage we have no knowledge of what the olfactory cue is for these fishes — however there is some evidence to suggest that dissolved chemical compounds in river and/or estuarine waters are responsible for creating the gradient for these postlarvae to follow. If it is indeed a catchment derived substance, then river flow into estuaries is not only important for creating salinity gradients within an estuary, it is also important for attracting recruiting fish and invertebrate larvae towards and into these systems.

Some fish postlarvae enter the estuary on the flood tide, letting the water carry them far into the system before moving into the shallows so that they are not carried out of the estuary on the ebb tide. Shoals of early juveniles can also be seen making their way against the ebb tide, keeping to the shallows where the water current is slow or absent altogether. If the shoals are chased into deeper waters, they are sufficiently strong swimmers to maintain, or even continue their movement in an upstream direction.

The few fish species that do breed within the Knysna Estuary have the opposite problem—they need to retain their eggs and larvae within the estuary. To do this, some species such as the Cape silverside *Atherina breviceps* attach their eggs to submerged plants (Figure 8.5) whereas others such as the speckled goby *Psammogobius knysnaensis* attach their eggs on the underside of submerged stones or large shells. There are also some species such as the Knysna seahorse *H. capensis* and super klipfish *Clinus superciliosus* that carry their fertilised eggs and embryos until they can give 'birth' to miniature replicas of themselves that have a better chance of not being washed out to sea. In the case of the super klipfish it is the female that gives birth to the young in the normal manner but for the Knysna seahorse it is the male that carries the developing young in his brood pouch and then releases them into their nursery habitat when they are ready for the next stage in their development.

Some estuarine resident species such as the stuarine roundherring *Gilchristella aestuaria* have neither sticky eggs to attach to submerged objects or the ability to give live birth — in this instance the free-floating eggs are released into the water column in the upper reaches of the estuary during spawning (Figure 8.2) and the hope is that the river will not come down in flood and wash them out to sea before they hatch. As a partial safeguard against such events the estuarine roundherring spawns at different times during the spring and summer, thus ensuring that at least some batches of eggs will be able to develop normally and not be washed out to sea.

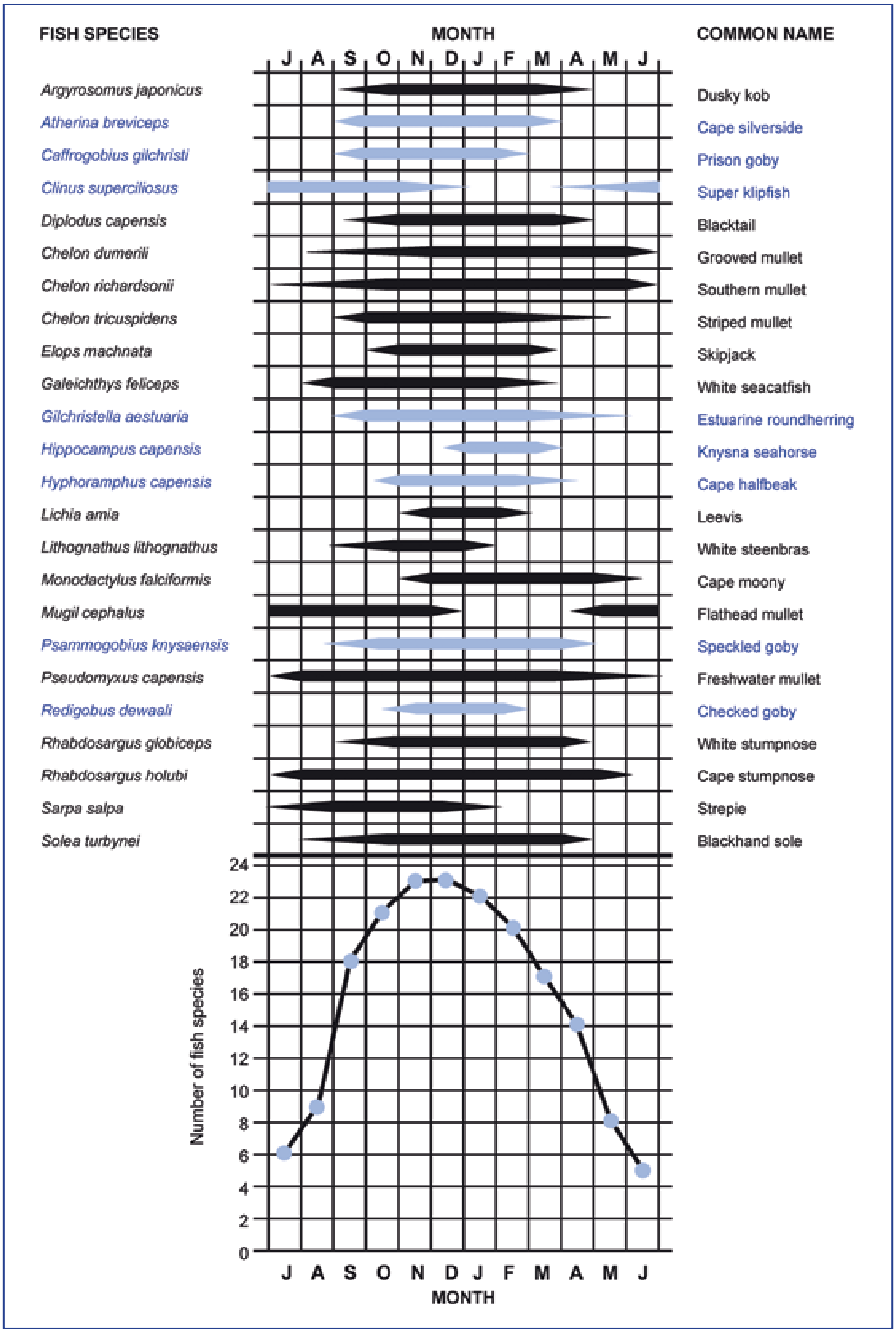


Figure 8.3 (a) Diagrammatic representation, indicated by the horizontal bars, of the early juvenile recruitment periods of selected marine migrant (in black) and estuarine resident (in blue) fish species from the Knysna Estuary. (b) The graph at the bottom of the figure is a summation of all the species data relating to the annual recruitment cycle of the above fish taxa in the estuary, and illustrates that most early juvenile cohorts are present in the system mainly during spring and summer.

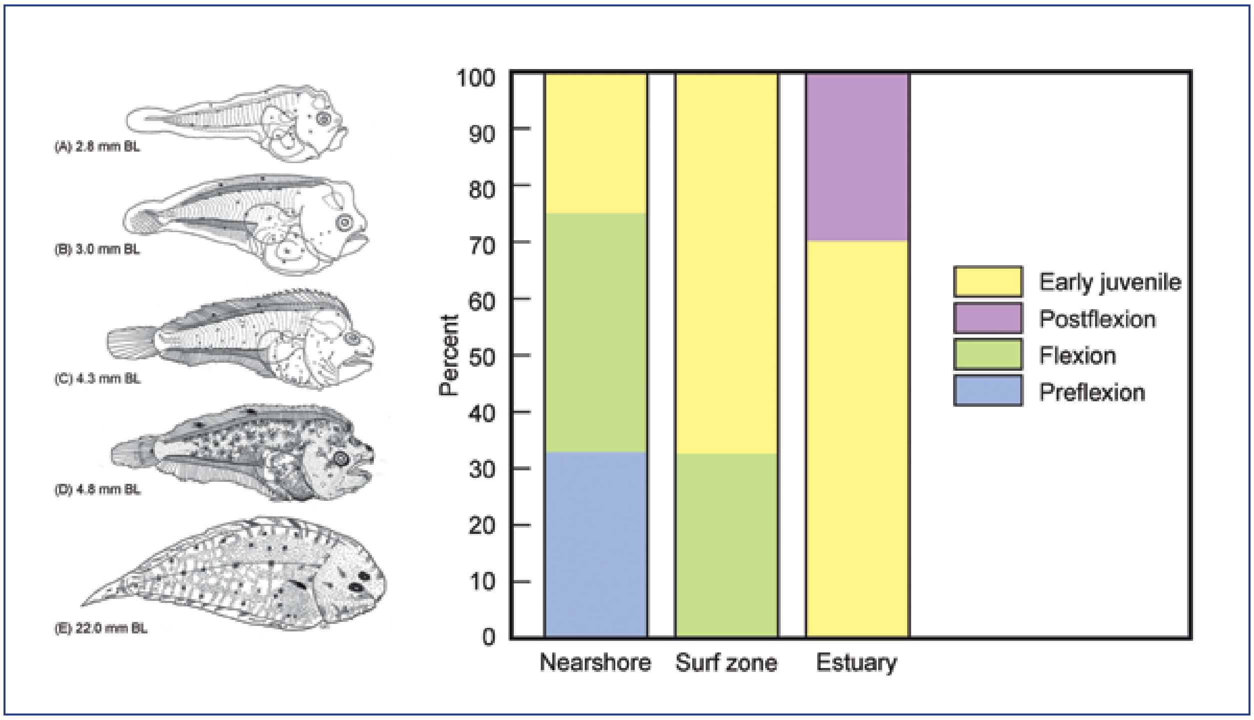


Figure 8.4 Graph showing the changes in body shape and eye position in the blackhand sole *Solea turbynei* as it grows and moves from the nearshore marine zone (preflexion and flexion larval stages, 2-3 mm body length), into the surf zone (mostly postflexion larval stages, 4-5 mm body length), and finally into the estuary as an early juvenile (modified from Strydom et al.[5]).

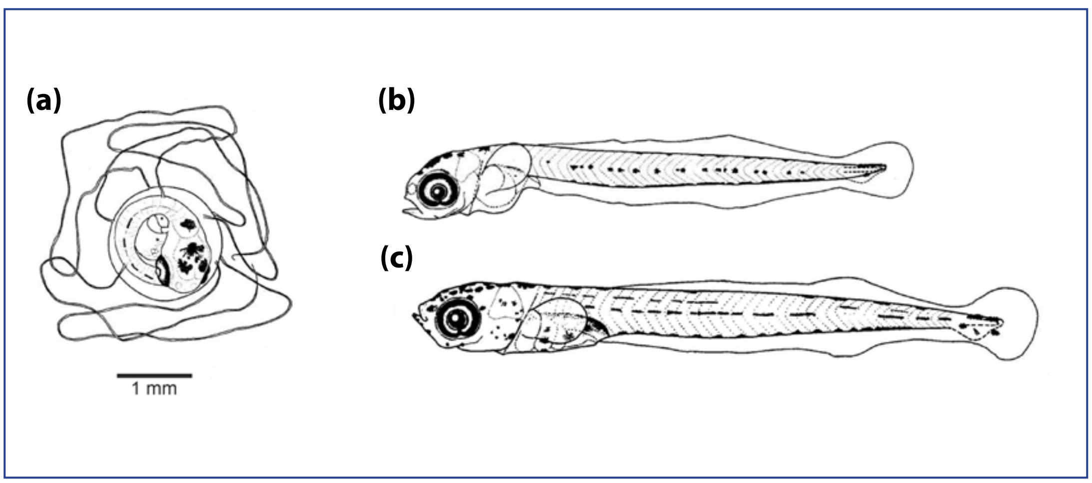


Figure 8.5 (a) Late egg stage of the Cape silverside *Atherina breviceps*. Note the thin chorionic filaments that are used to attach the fertilised egg onto the leaves of submerged plants. Early development of larva of *A. breviceps* at (b) 5 mm body length and (c) 7 mm body length is also shown (after Neira et al.[6]) .

8.4 Fish nursery areas in the Knysna Estuary

Estuaries are ideal nursery areas for fishes for three main reasons; firstly they provide highly productive environments with an abundance and variety of suitable food items, secondly they offer extensive shallow sheltered areas for small fishes, devoid of strong water currents or heavy wave action (Figure 8.6), and thirdly the littoral zone offers protection for these juvenile fish from large piscivorous species that patrol the estuary channel hunting for small fish that may stray into deeper water[7]. Most observers of nature in the Knysna Estuary would have witnessed small fish leaping out of the water towards the shore as they attempted to flee from an attacking predator advancing from deeper water[7].

Eelgrass (*Z. capensis*) contributes to habitat complexity which provides shelter to newly-settled fish larvae and juveniles when compared to other habitat types. Indeed, a recent review of global vegetated nurseries for fishes showed that eelgrass or seagrass habitats in estuaries are very important in terms of providing both food and shelter for small ishes[8]. As they grow, many fish species will move rom one habitat type to another, thus indicating that conservation of fish habitats must include the complete range used by various species as they grow to maturity.

Invertebrate prey densities are often orders of magnitude higher inside seagrass beds compared with adjacent unvegetated areas but a detailed study on the Knysna Estuary macrobenthos (larger invertebrates) has shown that, in the absence of burrowing activities by sandprawn (*Kraussillichirus kraussi*), overall invertebrate numbers in bare sediment areas was often higher than in nearby seagrass beds[9]. As far as fish species are concerned, most studies have found a greater diversity, abundance and biomass of juveniles in seagrass areas compared with neighbouring bare sediment areas, possibly linked to the protection these plants provide for small fishes trying to evade large predators. Thus the nursery function of this habitat type, particularly for estuary-associated marine fish species, needs to be emphasized.

Eelgrass occurs in 62 of the approximately 290 South African estuaries in the region, mainly in the lower and middle reaches of these systems. A total of at least 100 fish species from 44 families are associated with eelgrass beds in estuaries on the subcontinent, with seabreams in particular being attracted to this habitat type[10]. The eelgrass beds in the Knysna system cover the largest area of any South African estuary, occupying 66 ha of the intertidal zone and 355 ha of the subtidal zone. In particular, there are extensive eelgrass beds around the Ashmead Channel, where they are up to 200 m wide, as well as north of the railway bridge. In fact, the Knysna eelgrass beds account for almost half of all the seagrass area in South African estuaries.

Submerged aquatic plants such as eelgrass have many valuable functions, including carbon sequestration, reducing the impact of wave action on shorelines, sediment stabilization by binding the sands and muds with their roots, detrital production and export to the sea and the rest of the estuary, increasing vital dissolved oxygen concentrations of estuarine waters, promoting nutrient recycling between the sediments and overlaying water column, and the provision of an optimal habitat for growth, survival and reproduction of a diverse range of invertebrates and fishes.

Eelgrass beds and the small invertebrates that this habitat supports are of very high conservation importance, with the invertebrates living on the eelgrass leaves, as well as in or on the sediment within these beds (see Chapter 7 for details). Eelgrass is, however, under increased pressure from various human pressures such as bait extraction, nutrient pollution and damage caused by outboard motors, e.g. it has been estimated that the total area of Knysna Estuary eelgrass has been reduced by 26% in the last 54 years[11].

Eelgrass meadows also play an important role in the juvenile stages of economically and recreationally important species such as Cape stumpnose and white steenbras. A recent study[12] tested the hypothesis that mullet are dominant in the unvegetated shallow areas of the Knysna Estuary whereas seabream species predominate within eelgrass beds located in the same zone. Results indicated that most mullet were better represented at unvegetated sites when compared to the seabreams but that both fish families were very abundant in sparse eelgrass beds (Table 8.1). This may be because patchy eelgrass incorporates both bare sediment and vegetated areas, thus fulfilling a suitable habitat role for both mullet and seabream species (Figure 8.7). The main fish taxa responsible for the separation of fish assemblages in unvegetated sites versus vegetated areas were the southern mullet *Chelon richardsonii* and grooved mullet *Chelon dumerili* in the bare areas, and Cape stumpnose *Rhabdosargus holubi* and strepie *Sarpa salpa* in the vegetated areas[12].

Historical fish data sets from the Knysna Estuary have shown that there are differences in fish species composition across the different habitats, the different reaches of the estuary, as well as changes in seasonal abundance of each species. The Cape stumpnose is one of the most common species in

Figure 8.6 Shallow littoral areas around the Knysna Estuary provide ideal feeding and refuge areas for juvenile marine fish only 10 mm in in length. The upper picture (a) shows a school of small mugilids (mullet) in a sandy littoral area and the lower picture (b) shows a school of sparids (seabreams) in an eelgrass bed (Photographs: © Alan Whitfield).

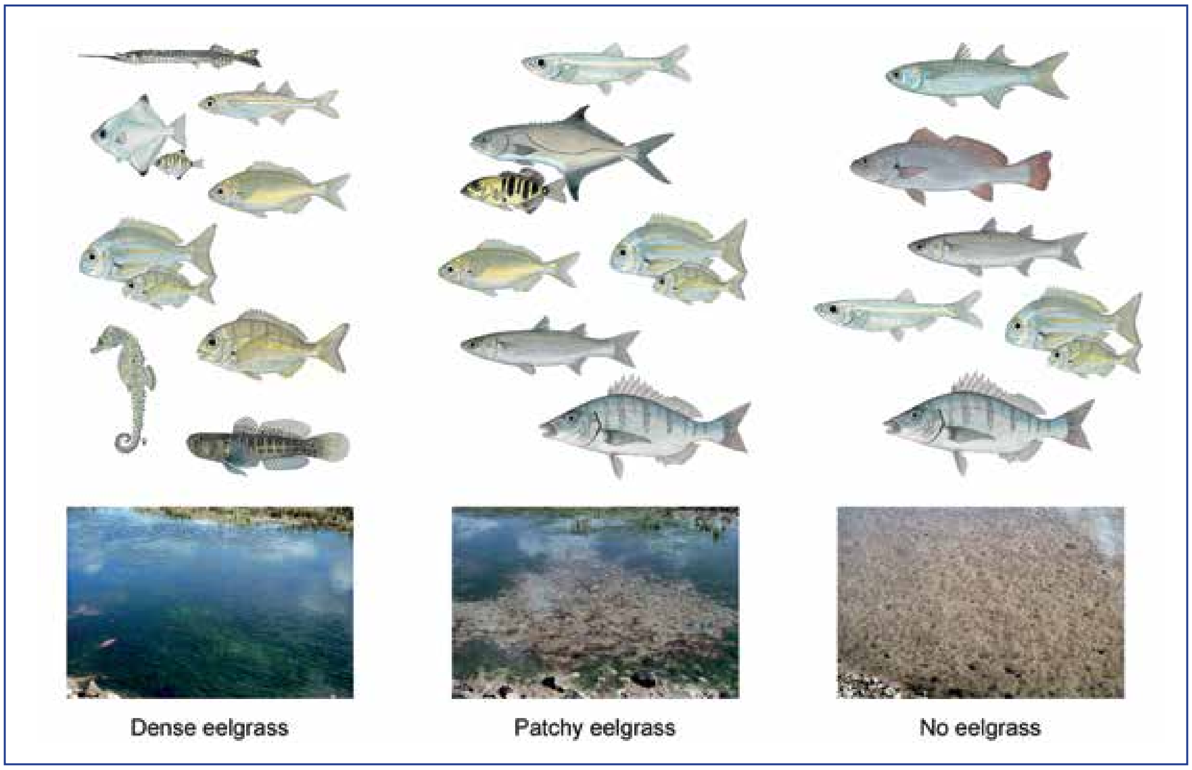


Figure 8.7 Diagrammatic representation of dominant fish species associated with different densities of eelgrass (*Zostera capensis*) in the Knysna Estuary. Note the overlap between the major species that occur in the different habitats but also the preferences of certain taxa for particular habitats (see text for more details).

the estuary, occurring across all habitat types and thus reinforcing the adaptable nature of this fish to different parts of the estuary (Table 8.1). Most individuals are less than 150 mm total length, thus indicating that they are juveniles. However, once they become subadults they leave the estuary, never to return. At the same time their sharp cutting incisor teeth that are used to crop plant material in the estuary change into molariform grinding teeth as adults. This new set of dentition is vital for the crushing of molluscs and other marine reef invertebrates that become part of the new diet of adult Cape stumpnose in the coastal waters of the southern Cape.

8.5 Fish food webs in the Knysna Estuary

Knowledge of the structure and functioning of food webs is essential for the proper understanding and management of estuarine ecosystems. Indeed, it could be argued that the successful conservation of fishes in the Knysna Estuary can only be achieved by a sound understanding of the links between primary producers, through microbial and microfaunal intermediaries, to invertebrate prey, the various intermediate predatory fish groups associated with different parts of the estuarine food web, and finally to the large piscivorous fishes at the top of the food chain[13].

The primary producers in the Knysna Estuary comprise three main components. The single cell microalgae that occur in the water column as phytoplankton, and on the sediments of the estuary as microphytobenthos (e.g. diatoms), are invisible to the eye but are important energy sources for consumers and give the water its greenish colour. Diatoms, which sometimes give pale sediments a brown tinge, or under extremely high densities actually create a distinct surface film on intertidal sand or mud flats, are a favoured food item of the various mullet species in the estuary. These fish detritivores are actually 'telescoping' the food chain by feeding directly on microalgae and detrital food resources within the estuary (Figure 8.8). In contrast the phytoplankton is not directly consumed by fishes but it is the primary food of microscopic invertebrates such as copepods which are preyed upon by small planktivorous fishes such as the Cape silverside and estuarine roundherring (Figure 8.8).

Table 8.1 Catch per unit effort (= number of fish per 10 seine net hauls) of dominant sparid (seabreams) and mugilid (mullets) fish species in bare sediment, sparse and dense eelgrass (*Z. capensis*) areas in the Knysna Estuary (modified from Pollard et al.[12]).

Species	Bare sediment	Sparse eelgrass	Dense eelgrass
Sparidae: Cape stumpnose (*Rhabdosargus holubi*)	13	103	50
Sparidae: Strepie (*Sarpa salpa*)	11	67	33
Mugilidae: Southern mullet (*Chelon richardsonii*)	96	13	54
Mugilidae: Grooved mullet (*Chelon dumerili*)	84	24	59

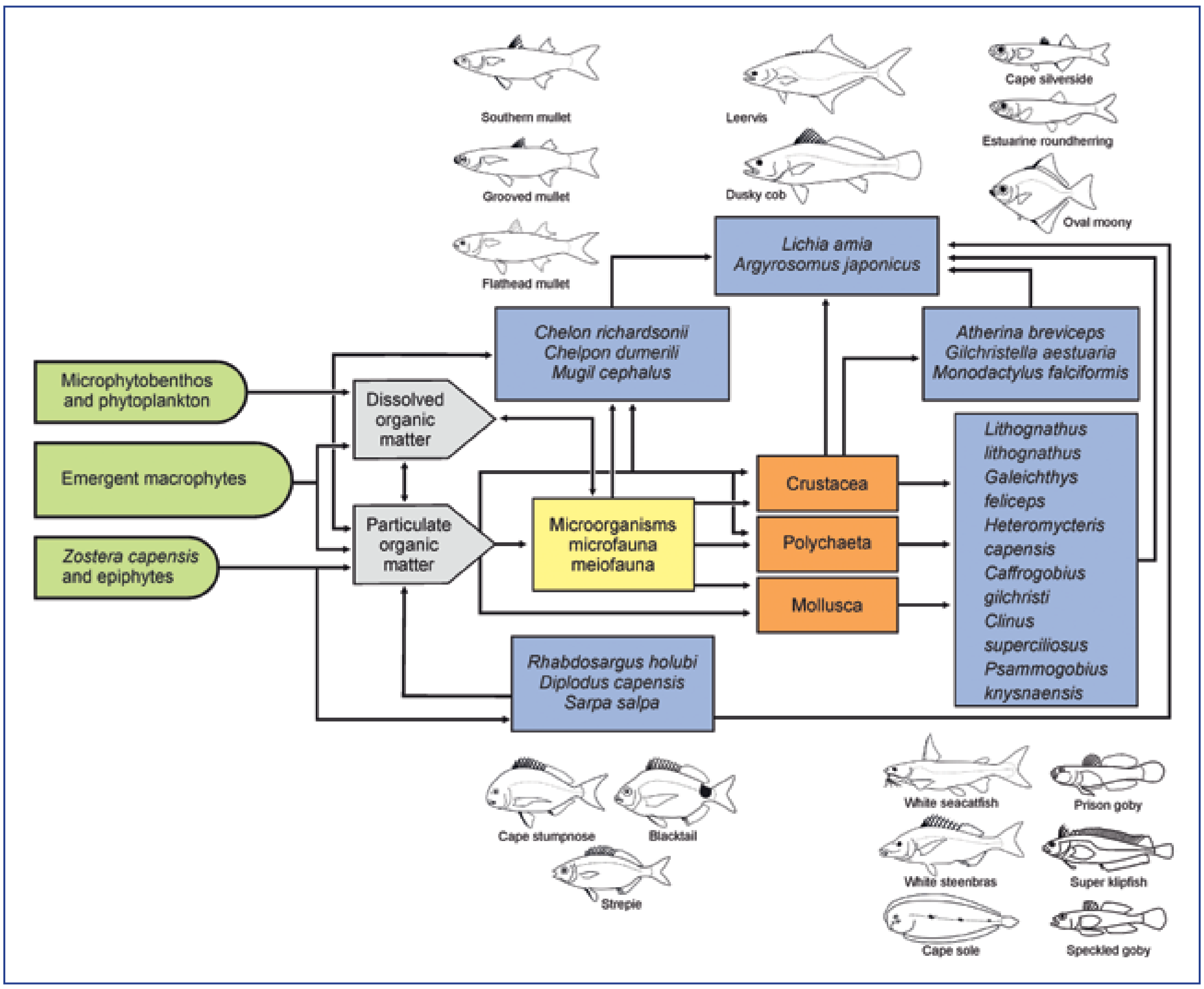


Figure 8.8 Major energy pathways through the Knysna Estuary food web. Some of the important fish species involved in the food web are both listed and shown in diagrammatic outlines.
The arrows generally go from food to consumer but also show some important 'loops' when it comes to particulate organic matter (detritus), a major driver that underpins energy flow through estuarine ecosystems.

The second major primary producer in the Knysna Estuary includes the extensive eelgrass beds together with the epiphytes (microalgae) that grow on the leaves of these plants. The sparids such as Cape stumpnose, strepie, blacktail *Diplodus capensis* and zebra *Diplodus hottentotus* consume the eelgass leaves but only digest the microalgae (especially the diatoms) that are on the plant blades. Faeces of these fishes then return the 'cleaned' leaves back to the estuary as macrodetitus and particulate organic matter. This material provides an important food source for the invertebrate microfauna, meiofauna and macrofauna such crabs, snails, bivalves, amphipods, isopods and polychaete worms (Figure 8.8). These invertebrates are, in turn, consumed by the zoobenthivorous fish component of the estuary, including white steenbras, sea barbel, Cape sole, prison goby, super klipfish and speckled sandgoby (Figure 8.8).

The third primary producer habitat within the estuary is the intertidal and supratidal salt marsh plants. Much of the carbon photosynthesized by these plants enters the estuary as detritus that is consumed by the large numbers of crabs living in association with the salt marsh plants. These crabs and other invertebrates are then consumed by wading birds such as the sacred ibis *Threskiornis aethiopicus*. However, some of the salt marsh detritus also finds its way into the salt marsh creeks where it then becomes part of the subtidal food web, including the zooplankton and zoobenthos, which are in turn preyed upon by zooplanktivorous and zoobenthivorous fishes such as Cape silverside and white steenbras respectively[14].

8.6 Habitat complexity and fish associations

Part of the reason why the Knysna Estuary provides a home for such a wide variety of fishes (see Appendix 1 for details) is linked to the variety of intertidal, subtidal and channel habitats present within the system. Intertidal salt marshes are particularly important as refuge areas for small fish at high tide, with the plant stems of cord grass *Spartina maritima* offering ideal protection from large predatory fish that may enter these areas during spring high tide. Similarly, the intertidal and subtidal eelgrass beds offer small fish protection from predation, particularly bottom dwelling species such as the super klipfish and prison goby *Caffrogobius gilchristi*. Subtidal macroalgal species such as *Codium tenue* offer both shelter and potential holdfast sites for the Knysna seahorse *Hippocampus capensis*. The Knysna Estuary is also well endowed with rocky intertidal and subtidal areas in the lower reaches and these provide an ideal habitat for reef associated fish species such as the kappie blenny *Omobranchus woodi* and steentjie *Spondyliosoma emarginatum*. The sandy areas in the estuary channel are a favoured habitat of species such as sand steenbras *Lithognathus mormyrus* and bartail flathead *Platycephalus indicus*. Muddy subtidal areas are preferred by species such as spotted grunter and blackhand sole, whereas intertidal sandy areas have large populations of speckled sandgoby and Cape sole *Heteromycteris capensis*. Pelagic waters are occupied by zooplanktivorous fishes such as the Cape silverside *Atherina breviceps* and estuarine roundherring *Gilchristella aestuaria*, together with their major predators such as the dusky kob *Argyrosomus japonicus* and skipjack *Elops machnata*. Occupying the surface waters of the estuary, especially during nocturnal hours, are the two halfbeaks *Hyporhamphus capensis* and *Hemiramphus far*. Although the various mullet species such as flathead mullet *Mugil cephalus* and southern mullet forage on the sediments at the bottom or sides of the estuary during the day, they swim in shoals at the water surface at night, presumably to avoid large nocturnal mid-water predators in the channel.

The range in water depth within the estuary also provides a diversity of habitat types for various fish species. For example, the checked goby *Redigobius dewaali* is usually restricted to intertidal areas, often taking refuge in Knysna mudcrab *Scylla serrata* burrow pools at low tide. Other fish species such as the sand snake eel *Ophisurus serpens* prefer subtidal or channel sandy areas in which to burrow, with only its head exposed. The deep mouth of the Knysna Estuary allows typical marine fishes to occupy the lower part of the system where little or no dilution of the seawater occurs, e.g. records of karanteen *Crenidens crenidens* and Fransmadam *Boopsoidea inornata* in the lower reaches of the estuary may be linked to the strong marine connection. In particular, most sharks and rays cannot tolerate typical fluctuating salinities but the seawater conditions result in species such as the spotted ragged-tooth shark *Carcharius taurus* and blue stingray *Dasyatis chrysonota* being able to penetrate the estuary. Larvae of small pelagic shoaling species such as the pilchard *Sardinops ocellatus* and anchovy *Engraulis capensis* are frequently washed into and out of the estuary with the tides, but neither species is a resident within the system.

An important aspect of the Knysna Estuary is the refuge status this system provides when there is a major upwelling of cold water into the adjacent coastal zone, causing marine sea temperatures to decline by up to 10°C within 24 hours. Reef and other marine fish species attempting to escape the upwelled water often enter the Knysna Estuary where water temperatures are much warmer. These fish, such as the baardman *Umbrina robinsoni* and gnomefish *Scombrops boops*, seldom enter estuaries under normal circumstances but have been recorded in the Knysna system during such events. Adult white musselcracker *Sparodon durbanensis* also take up residence in the Knysna Estuary during upwelling events and are unfortunately targeted by anglers during this vulnerable period.

8.7 White steenbras and Knysna seahorse case studies

White steenbras *(Lithognathus lithognathus)*

The geographic range of this species (Figure 8.9) extends from the Orange Estuary mouth in the west to KwaZulu-Natal in the east and it is therefore a South African endemic, i.e. occurs in our coastal waters and nowhere else in the world. Juveniles are abundant in some of the larger warm-temperate estuaries on the Western and Eastern Cape coasts but they are very rare in subtropical systems along the east coast. Post-estuarine juveniles larger than about 14 cm in length are semi-resident in the surf zone, with the adults extending into coastal waters up to 25 m deep[15].

The Knysna estuarine population of *L. lithognathus* is sexually immature, with no signs of reproductive development which usually occurs at sea. This species is a rudimentary hermaphrodite and, although some mature fish have approximately equal ovarian and testicular development, individuals function only as males or females[16]. Out of a total of 425 mature *L. lithognathus* examined, 172 were males, 233 females and 20 hermaphrodites[15]. Most white steenbras are mature by 54 cm standard length, with late winter spawning occurring in coastal waters[17]. In contrast, spotted grunter *Pomadasys commersonnii* have actually been recorded spawning within the mouth region of the Knysna Estuary[18].

Egg and larval development of white steenbras occurs at sea, with late larvae less than 15 mm standard length and juveniles (less than 50 mm total length) entering estuaries mainly between September and November[15]. In the Knysna Estuary small juveniles, less than 40 mm total length, were

Figure 8.9 The white steenbras, *Lithognathus lithognathus*, is an endemic South African sparid that has the centre of its coastal distribution in the vicinity of the Knysna Estuary (Photograph: © Alan Whitfield). Inset shows the sandprawn *Kraussillichirus kraussi* which is a major prey for large juvenile and adult white steenbras (Photograph: © George Branch).

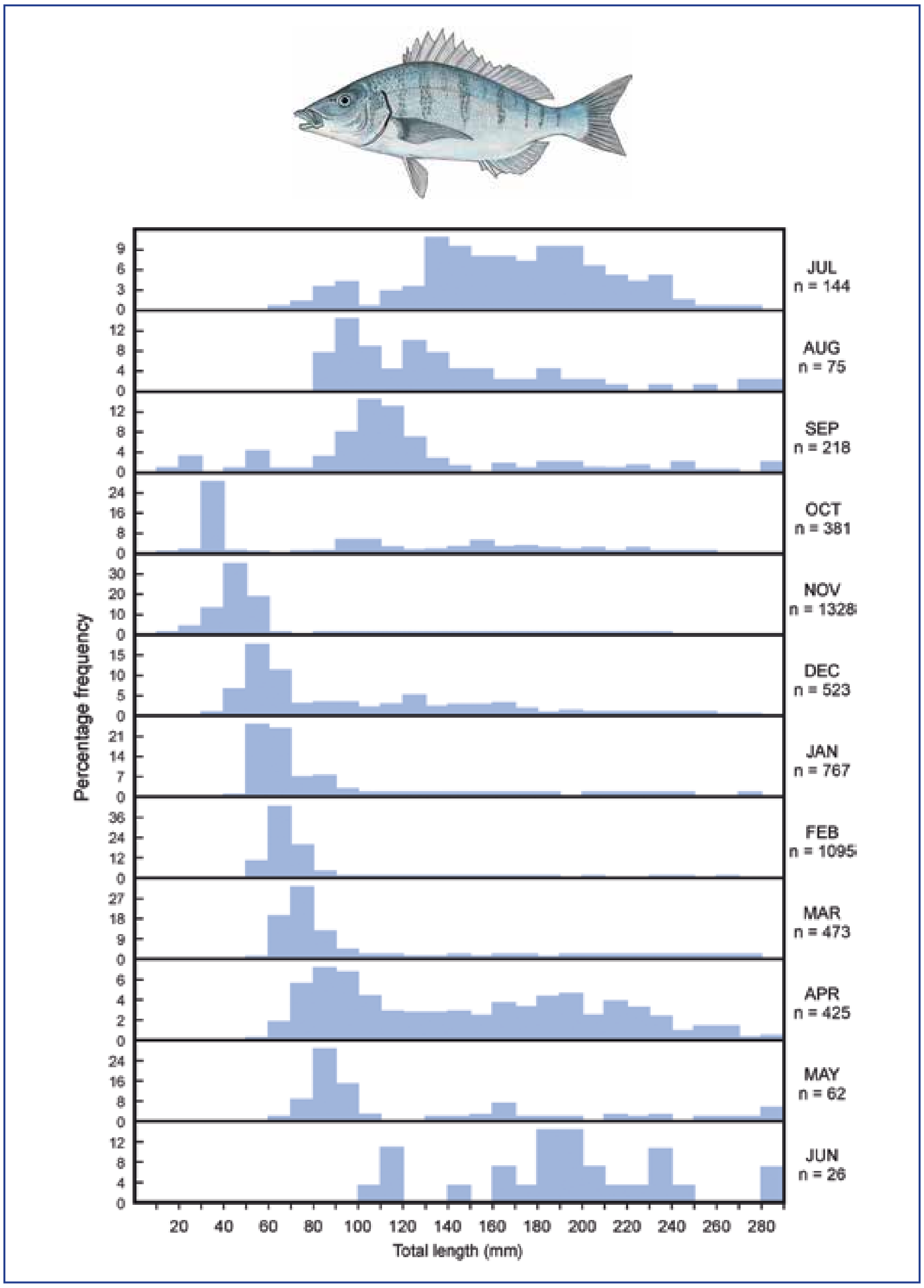


Figure 8.10 Percentage length frequency distribution per month of juvenile white steenbras *Lithognathus lithognathus* in the Knysna Estuary (n = number of fish in the sample). After Whitfield & Kok[4].

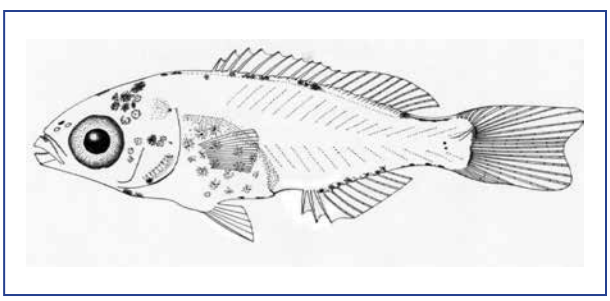


Figure 8.11 A drawing of a late larval white steenbras *Lithognathus lithognathus* (12 mm standard length) that has not developed scales or the pigmentation associated with later growth stages. This sized fish would still be feeding on zooplankton and not on zoobenthos that it preys on in later life.

first recorded recruiting from the sea in September (Figure 8.10) and grew rapidly, attaining a modal size of 80 mm total length by the end of summer (March). This converts to a summer growth rate of more than 5 mm per month.

The largest numbers of these juveniles occurred in the middle and upper reaches of the estuary[4] where they occupy both eelgrass and salt marsh creek habitats[12,14]. This species tends to avoid the more muddy and rocky areas in the extreme upper reaches of estuaries and is particularly attracted to sandy areas where burrowing invertebrates are common. The larval stages of white steenbras feed on plankton within the nearshore marine environment. Early juveniles (Figure 8.11) remain predominantly zooplankton feeders when they first enter estuaries and prey mainly on copepods and amphipods at this life stage[19,20]. Larger individuals in estuaries have a more diverse diet, with amphipods, anomurans, brachyurans, isopods, polychaetes and insect larvae being important prey taxa[15,21]. A study by Schlacher & Wooldridge[22] in the Gamtoos Estuary has shown that male amphipods of *Grandidierella lignorum* are consumed by white steenbras in significantly higher numbers than females, probably due to behavioural differences between the amphipod sexes.

The white steenbras sometimes enters extremely shallow areas, where its tail can often be seen protruding out of the water as it forages for invertebrates on or in the sediment. Prawns are mostly extracted from their burrows using the pumping action of the powerful gill chamber which acts like a 'bellows'. When pursuing sandprawns *Kraussillichirus kraussi*, almost the entire front half of the head may be thrust into the sediment, with sand billowing out of the large excavation created by the pumping action of the opercular 'bellows'. A similar foraging method is used by the spotted grunter but competition for sandprawns is reduced by the grunter preying predominantly on mudprawns *Upogebia africana*.

Indications are that the white steenbras is highly resident, each individual showing strong site fidelity to a particular area in an estuary[23]. The bigger the estuary, the greater is the home range covered by the fish[24], so white steenbras in the Knysna Estuary will range more widely than those individuals in a smaller estuary. There are movements onto or away from foraging areas according to the tide and time of day or night[25] but, as a rule, each individual juvenile fish does not move long distances whilst using estuarine nursery areas. There are also strong indications that larger juveniles of this species prefer more sandy areas in the lower reaches of estuaries and may stay in these systems for up to four years[24]. Once the subadult life stage is reached, the fish then depart their natal estuary and become primarily marine, travelling long distances within their natural distributional range[17].

This species has been recorded in salinities ranging from almost fresh to 90 ppt (more than twice the salt concentration of seawater) and is associated with both clear and turbid waters. White steenbras can survive in freshwater for up to a week[16] and were recorded dying in the closed Seekoei Estuary when salinities increased above 90 ppt. Prolonged near freshwater conditions can also result in mortalities of this species[26], as do dissolved oxygen concentrations less than 1 mg l^{-1}[27]. Although ectoparasitic leeches and parasitic copepods have been recorded on white steenbras[16], the fluctuating physico-chemical conditions in estuaries probably assist in keeping these parasite infestations under control.

The white steenbras has been heavily exploited by recreational anglers for almost a century[28] and by subsistence fishers in more recent decades[29]. There were also periods in the 1900s when large seine net hauls of reproductively active adults were made in the surf zone of False Bay, thus placing the breeding success of this species under considerable threat. Fortunately that fishing pressure has now come to an end due to government legislation regarding the use of seine nets in this bay, but estuarine degradation continues to remain a threat to the nursery areas of this species[30].

Studies have shown that virtually all white steenbras retained by anglers are less than the 60 cm legal size limit for this species[31]. Overall, it has been estimated by scientists that the current spawner stock biomass of white steenbras is less than 5% of pristine levels, i.e. more than 95% of the adult population has been removed and the remaining stock is struggling to recover. Hence it is not surprising that this fishery species is now classified on the International Union for the Conservation of Nature (IUCN) Red List as endangered.

Knysna seahorse *(Hippocampus capensis)*

Seahorses, pipefish, pipehorses and seadragons all belong to the family Syngnathidae and are found in shallow, coastal environments across the globe. The words 'syn' and 'gnathus', Greek for together and jaws respectively, describe the tube-like mouthparts that are inherent to all syngnathids. Most of these species occur in the sea and the Knysna seahorse is the only one that occurs exclusively in estuaries. The Knysna seahorse (Figure 8.12) is South Africa's only endemic seahorse species and is found in three estuaries along the south coast of South

Figure 8.12 The Knysna seahorse *Hippocampus capensis* in a *Caulerpa filiformis* seaweed bed. Note the tail of the seahorse curled around one of the seaweed leaves for anchoring (Photograph: © Mike Gratwicke).

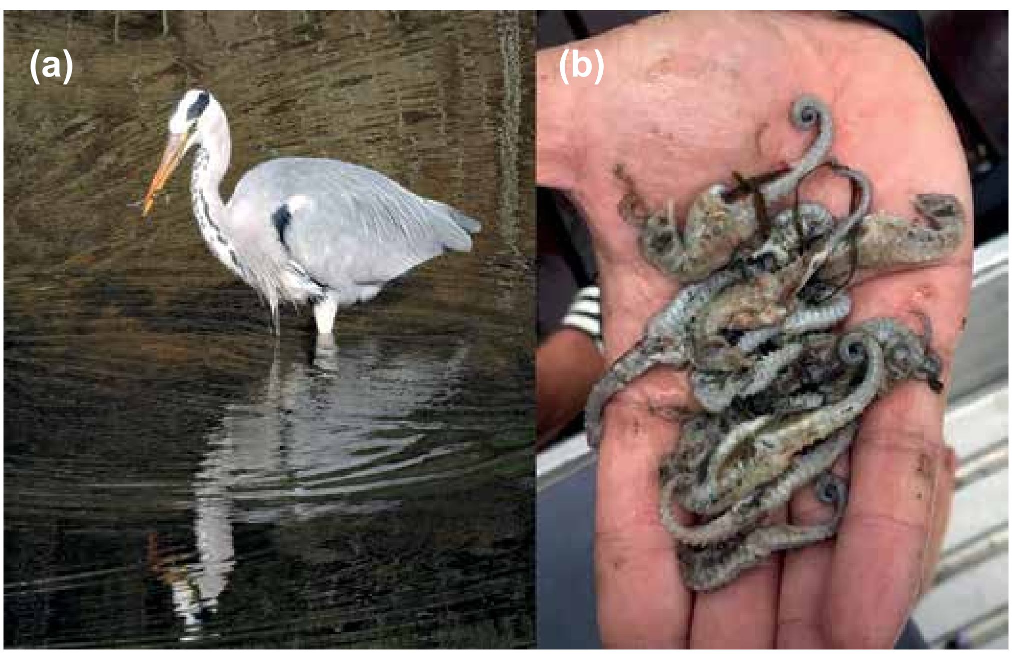


Figure 8.13 Examples of predation on *Hippocampus capensis*: (a) by a grey heron *Ardea cinerea* and (b) *H. capensis* from the stomach contents of a spotted grunter (*Pomadasys commersonnii*) caught in the Keurbooms Estuary.

Figure 8.14 *Hippocampus capensis* holding onto the wire of a Reno mattress structure in the Thesen Island Marina (Photograph: © David Harasti).

Africa[32]. Anecdotal records suggest that *H. capensis* was found in other estuaries close to Knysna including the Klein Brak, Breede, Duiwenshoks and Goukou[33,34]. However, various surveys conducted in the early 2000s concluded that the Knysna seahorse currently only occurs in the Keurbooms, Knysna and Swartvlei estuaries.

Hippocampus capensis was the first seahorse in the world to be listed as Endangered on the IUCN Red List in 2004[32]. This classification was owing to this species limited range, small population size and habitat vulnerability. The genetic age of the Knysna seahorse is estimated to be between 46 000 and 186 000 years old[35]. Oceanic conditions during this time were much colder than today and it is unlikely that tropical or subtropical species such as *Hippocampus kuda*, which gave rise to *H. capensis*, could survive this far south. This narrows down the founder event to the Eemian interglacial period, 27 000 – 122 000 years ago, a short warmer phase within the Pleistocene[35].

This founder event is believed to have taken place within the Knysna Estuary owing to the high haplotypic diversity found in this population[35]. The large size, permanently open mouth and three distinct hydrographical regimes (bay, lagoon and estuary) within the Knysna Estuary would have presented an optimal transitional environment between the marine and estuarine environment. The Knysna seahorse is perfectly adapted to estuarine conditions with a salinity tolerance range of 1 to 59 ppt[36]. The extant Knysna seahorse populations found in the Keurbooms and Swartvlei estuaries could be explained by a historic vicariance event or dispersal of juvenile seahorses through ocean currents and related recruitment events[35,37].

The Knysna seahorse is usually brown green in colour but can also be found in bright yellow if associated with sponges of the same colour. This species depends on crypsis and slow movements to hide from predators, which includes birds such as herons and cormorants, as well as fish such as grunters (Figure 8.13).

Hippocampus capensis is born at 0.1 cm in size and reaches maturity at 4 cm[38], with smallest free swimming individual being 8.4 mm in length. Knysna seahorses show rapid initial growth for the first 200 days and can grow larger than 10 cm, with the biggest seahorse recorded being a female at 11.4 cm[38]. Seahorse sizes vary across different habitat types, and significantly larger seahorses were found in artificial Reno mattress (wire boxes filled with stones) habitat in the Thesen Island Marina. Size differences between males and females also vary, but generally, males are larger than females and have longer tails[33].

The Knysna seahorse breeds during the austral summer and breeding activity is highest from October to January[40]. Morning greetings, whereby

Figure 8.15 A female Knysna seahorse tagged with red Visible Implant Fluorescent Elastomer (VIFE) tags (Photograph: © David Harasti).

the male and female clasp their tails and sway sideways and vertically, have been confirmed for this species both in the laboratory[41] and in the estuary[42]. These morning greetings help to confirm the pair bond between seahorses and synchronises the timing for the next mating event.

Once the male gives birth, the female will transfer another set of mature eggs into his brood pouch. Knysna seahorses thus mate multiple times during the breeding season. In an ex situ study[38], it was found that a male seahorse gives birth to approximately 39 juveniles every 34 days during a four-month breeding period. Seahorses generally disperse as juveniles floating in the water column. Once juveniles reach a certain size, they will settle in suitable benthic habitats such as seagrass, macroalgae or even artificial structures (see below for details).

Information on sex ratios for *H. capensis* vary. In 2000, a transect survey indicated male bias, but equal using a focal grid method[33]. In 2001, Lockyear et al.[34] also recorded a 1:1 sex ratio from transect surveys. During surveys between 2014 and 2017, the sex ratio varied across habitats and seasons and changed from being equal to female biased[40,43]. In *Codium tenue* macroalgal habitats, the sex ratio for Knysna seahorses remained equal over an 18-month period[44].

Seahorses depend on specific habitats that provide refuge from predators, enough prey to feed on, and a holdfast (structures used by seahorses to curl their tails around). Within the Knysna Estuary, *H. capensis* is found within a range of different habitat types, which includes seagrass (*Z. capensis*, *Halophila ovalis*, *Ruppia cirrhosa*), macroalgae (*C. tenue*, *Caulerpa filiformis*, *Asparagopsis taxiformis*) and artificial structures such as Reno mattresses[33,34,43].

H. capensis is threatened by habitat loss and alteration[45], and a lot of research has focused on habitat use by this species. Bell et al.[33] found that *H. capensis* was more frequently found in less dense vegetation (< 20 % cover), whilst Teske et al.[46] concluded that seahorses prefer higher density vegetation (>75 % cover). Subsequent research found that *H. capensis* can adapt to some extent of habitat change and seahorses were also found using the invasive algae *Asparagopsis taxiformis* as a home.

Reno mattresses in the Thesen Island Marina were documented to be significantly more likely to be used by *H. capensis* when compared to *Z. capensis*[47]. One reason could be the high complexity provided by the Reno mattress structure as well as high prey densities[48].The wire of the Reno mattress also acts as a permanent holdfast for seahorses and was found to be used as a holdfast significantly more often compared to other available holdfasts within this habitat (Figure 8.14). The Thesen Island Marina has added an additional 25 ha of subtidal habitat to the Knysna Estuary[43], thus benefitting the Knysna seahorses in this system.

In addition to the Reno mattress habitat within the Thesen Island Marina, dense beds of *Codium tenue* were found to be an important habitat to *H. capensis*[44]. *Codium tenue* is a free-floating macroalga and is found in high densities in the Thesen Island Marina where it accumulates in dead-end channels and inlets.

An initial population assessment of *H. capensis* conducted in 2000 found an average density of 0.008 seahorses per m^2 [33]. A subsequent survey conducted in 2001 recorded a slightly higher average density of 0.01 seahorses per m^2 [34]. Both these assessments used visual underwater surveys along a transect to record seahorse densities and were conducted as once-off surveys. These surveys provided a good baseline understanding of the population status of *H. capensis* but were limited in terms of capturing finer resolution temporal and spatial variability. For example, monthly surveys across different types of habitats conducted between 2014 and 2017 found high variability in seahorse densities across different habitat types, but also within the same habitat type[40,43]. Average seahorse densities recorded in the same seagrass habitat (*Z. capensis*) at two different locations ranged from 0.01 to 0.06 seahorses per m^2. Subtidal habitat in the Knysna Estuary was mapped in 2019 and provided a first estimate of the extent of habitat available to *H. capensis*[49].

High densities of *H. capensis* within the Reno mattress habitat in Thesen Island Marina provided an opportunity to focus research on the behaviour and life-history of *H. capensis*. The behaviour of *H. capensis* was investigated using GoPro cameras and this research compared seahorse behaviour throughout the day (morning, midday and afternoon) as well as across periods with varying human activity (holiday season and non-holiday season). Seahorses were much more active during the morning compared to midday or late afternoon and spent >80% of the active period hunting. In addition, a decrease in seahorse feeding during the holiday season was linked to an increase in boat noise[41].

The latest research on *H. capensis* used Visible Implant Fluorescent Elastomer (VIFE) tags to determine the population size, growth and movement patterns of this species (Figure 8.15). VIFE tags (1-2 mm) are injected under the skin of the seahorse and each seahorse is given three tags which provides a unique three number code for each individual seahorse. This allows for the long-term monitoring of individual seahorses. In February 2018, 78 adult Knysna seahorses were tagged within a 50 m^2 area of Reno mattress and monitored on a monthly basis for 13 months. Eighty percent of tagged seahorses were successfully resighted, and one individual was sighted 17 times over 388 days. The population size for this area was estimated to be 132 in February 2018, which decreased to 72 in February 2019. High site fidelity was observed and, on average, *H. capensis* was found to move a mere 5 m over the 13-month period[39].

Habitat loss and alteration is the major threat to *H. capensis*[32]. Eutrophication in particular has been identified as a threat to *H. capensis* in the Knysna Estuary[45]. The excessive increase of nutrients in the estuary, mostly from land-based sources such as wastewater effluent, can cause nuisance algal blooms (e.g. *Ulva lactuca*) which displaces seagrass habitat[50,51]. Seagrass and macroalgal beds can also be damaged by boats and bait digging[45].

Impacts of anthropogenic noise on seahorse behaviour have been studied for certain seahorse species. The decrease in activity and feeding of *H. capensis* found during a December holiday season was linked to an increase in the number of boats present in the estuary and the noise generated by these boats[41]. In addition, the marked decrease in the number of seahorses monitored on Reno mattress habitat in Thesen Islands Marina[39] could be owing to maintenance work that was conducted on a jetty adjacent to the site. Such localised activities could have a significant impact on seahorse populations, especially considering their high site fidelity.

All syngnathids in South Africa are protected under the National Environmental Management Biodiversity Act of 2004. According to this act, members of the family Syngnathidae are not allowed to be captured, collected or disturbed in any way. Not only are seahorses protected in South Africa, but the habitats and estuaries in which *H. capensis* are found are also protected through various laws and regulations. All three estuaries in which *H. capensis* is found are protected areas—the Knysna and Swartvlei estuaries are part of the Garden Route National Park managed by SANParks and sections of the Keurbooms Estuary are part of the Keurbooms River Nature Reserve managed by CapeNature. Estuaries are protected under the National Environmental Management: Integrated Coastal Management Act of 2008, which regulates development within the estuaries amongst other things. In addition, effluent discharge into estuaries need to comply to specific standards under the ational Water Act of 1998. The Knysna seahorse and its habitats are thus well protected legally, although compliance to and implementation of the various Acts are limited[45].

Poaching of *H. capensis* for use in the aquarium trade or for traditional Chinese medicine is not considered to be a major threat. The trade of all seahorses is regulated under Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) of which South Africa is a signatory. All captive breeding of this species is heavily regulated and permitted in only two aquariums (Two Oceans Aquarium in Cape Town, uShaka Aquarium in Durban) and at the Garden Route National Park in Knysna.

The Knysna Estuary has the greatest potential to ensure the longer-term survival of *H. capensis* owing to the relatively large population found in this system and subdued impacts from freshwater floods[52,53]. The protection of subtidal habitat in the Knysna Estuary should thus be a priority for the future survival of the Knysna seahorse. Areas with particularly high densities of seahorses, such as Reno mattress habitats in Thesen Island Marina, should also be protected. In addition, focus should be placed on ongoing education of the public on the importance of the Knysna seahorses as an iconic species for the region.

8.8 Recreational and subsistence fisheries in the Knysna Estuary

Introduction

Recreational and subsistence fishing play major roles in the lives of many people and, although there are many similarities in techniques and equipment used, the motivations for participation are generally very different between the two groups. Subsistence, as the name implies, is undertaken by fishers who are poor and who personally harvest marine resources as a source of food or to sell in order to meet basic food security needs. Furthermore, they operate on or near to the estuary shore, live in close proximity to the resource, consume or sell the resources locally, and use low-technology gear (often as part of a long-standing community-based or cultural practice)[54]. A survey in 2000 estimated that in South Africa there were about 30 000 subsistence fishers and about 28 000 households that depended on harvesting near-shore marine resources[55].

On the other hand, recreational fishing is a popular activity undertaken by many diverse participants who demonstrate a wide range of motivations revolving around leisure rather than profit or the provision of food. They have varied interests and experience and may not sell or trade part or all their catch. Individual variation in fishing behaviour, including where people choose to fish, species targeted and catch retention is shaped by a wide range of social, economic, ecological and personal factors. Globally it is estimated that within developed countries 1 in 10 people or a minimum of 200 million people fish recreationally[56]. Within South Africa, estimates of total marine and estuarine recreational fishers have ranged from 365 000 in the early 1990s up to an estimated 544 000 in 2017. Regardless of the actual numbers, participation in recreational fisheries is recognised to be increasing on a global scale. With the large number of participants, the recreational fishery has been shown to have high economic value due to the associated tourism, tackle and boat building businesses.

Both recreational and subsistence fishers use hook and line (handlines and/or rod and reel) to target a wide range of species with considerable overlap in areas fished and species targeted. Fishing pressure in estuaries is high due to the proximity of urban developments, general ease of access, all year round fishability, and as an indirect impact of the beach driving ban which shifted coastal fishing pressure onto estuaries. In general, larger systems and estuaries closer to urban nodes experience higher pressures than smaller more remote systems.

Although there is growing scientific evidence

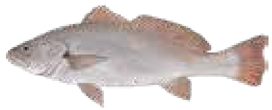
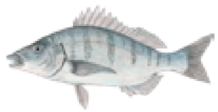
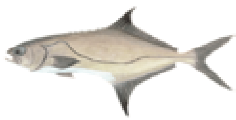
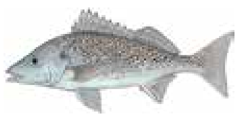
Species	Regulations	Movement	Stock Status	SBR	ICUN category	Max. age
 Dusky kob (*Argyrosomus japonicus*)	Min. size: 60 cm; Bag limit: 1	Migratory	Collapsed	1.1-4.5%		42
 White steenbras (*Lithognathus lithognathus*)	Min. size: 60 cm; Bag limit: 1	Migratory	Collapsed	6%		25-30
 Leervis/Garrick (*Lichia amia*)	Min. size: 70 cm; Bag limit: 2	Migratory	Collapsed	14%	Not assessed	10
 Spotted grunter (*Pomadasys commersonnii*)	Min. size: 40 cm; Bag limit: 5	Resident	Over-exploited	35%	Not assessed	15-19

Figure 8.16 Current regulations governing the minimum retained fish size and bag limit, species movement behaviour, current stock status, percentage remaining spawner biomass, IUCN category and estimated maximum age in years of four targeted estuary-associated marine fish species. IUCN category = International Union for Conservation of Nature red list categories; SBR = Spawner Biomass per Recruit, provides a reference of how many large adult breeding fish are left compared to historic levels.

highlighting the impacts of recreational fishing on fish populations and the environment[58] it is often difficult for a lone angler or group of friends to comprehend or understand the impacts of their actions. However, it is a matter of scale and when you multiply the number of fish a single angler catches in a day by the millions of anglers globally, you have a significant number of fish harvested. In particular, when you consider the long history of recreational fishing and hence the removal of large numbers of fish over consecutive years.

Within South Africa many of our linefish species have been overfished and populations of key species have collapsed, with over-exploitation recognized as the single biggest threat to estuarine-associated fishes[30]. Fishery assessments indicate that at least one popular species (spotted grunter) is over-exploited whilst the populations of a further three popular species (white steenbras, leervis and dusky kob) have collapsed (Figure 8.16). Unfortunately, a large portion of estuarine fishing effort targets these vulnerable, over-exploited species[31]. Impacts on fish populations is not only cause for concern ecologically but their collapse has social and economic implications with the total value of estuarine and estuary-dependent fisheries in South Africa estimated at more than R1.25 billion per annum[59].

Knysna line fisheries

Participation

Interviews (Figure 8.17) indicate that most fishers in Knysna Estuary are local (~79%), either from Knysna or the surrounding communities, whilst ~6% came from within the Garden Route and a further ~14% are national visitors. In the early 2000s it was estimated that Knysna Estuary supported 30 full-time and a further 200 part-time subsistence fishers[29]. Approximately 29% of anglers indicated that they were fishing for subsistence purposes in 2008, which corresponded to 32% of respondents having no income or an income below R1 000 per month. With the high level of unemployment in the Knysna area it's not surprising that there is a major subsistence fishery operating on the estuary.

Ongoing monitoring by SANParks has shown how large-scale perturbations can influence fishery

Figure 8.17 SANParks survey clerk interviewing a local fisherman on Knysna Estuary to obtain catch and effort data (Photograph: © Kyle Smith).

Table 8.2 Target rates (%) and species catch composition (%) for Knysna Estuary over a two-year period (adapted from Smith & Kruger[61]). Any fish species indicates anglers who were not targeting specific species. Other includes a number of different species targeted at very low frequencies.

Target Species	**Knysna**			
	2008 - 2009		2009 – 2010	
	Targeted (%)	Numerical catch composition (%)	Targeted (%)	Numerical catch composition (%)
Any fish species	46		46	
Cape stumpnose	6	43	7	33
Spotted grunter	17	4	16	8
White steenbras	10	12	12	12
Leervis	5	2	6	3
Strepie	5	18	4	16
Other	11	21	9	287

participation. In the aftermath of the 2008 global recession, the proportion of subsistence and supplementary fishers increased from 29% up to 52%, which essentially shifted the fishery from being primarily recreational to one dominated by fishers reliant on the resources as a source of nutrition or income. During this period the total number of subsistence and supplementary fishers was estimated to have increased from around 230 up to around 500. Movement of individuals into and out of subsistence fisheries adds to the complexity of their management and, although the number of fulltime subsistence fishers can be more stable and easier to estimate, the number of part-time subsistence or supplementary fishers is far more difficult to obtain due to the continual influx and exit of individuals.

Fishing effort

Fishing effort in Knysna follows seasonal trends with an increase in fishing effort occurring over school holidays, with particular emphasis over the summer (December and January) and autumn (April) periods. Over a six year monitoring period, total annual fishing effort fluctuated between 17 700 and 25 189 angler outings. Although relatively few South African estuarine line fisheries have been formally assessed, the only system which has been shown to have more fishing pressure on an annual basis is Durban harbour with an estimated total of 64 015 angler outings occurring during 2000[60]. The Knysna Estuary is clearly an important and popular system for recreational and subsistence fishers.

The proportion of boat versus shore fishers is relatively constant across years with most anglers (73%) fishing from the shoreline. The remaining fishers use some form of boating platform including rowing boats, motorboats or kayaks. Fishing effort occurs heterogeneously throughout the estuary with certain areas showing consistently higher fishing effort. Ease of access and proximity to home are two important considerations taken by shore-based fishermen and in this regard the Ashmead Channel, Thesen Jetty, the railway bridge and adjacent intertidal mudbanks are popular fishing areas. Boat based fishermen are more mobile and generally fish multiple spots on any given fishing trip.

Figure 8.18 A subsistence fishers mixed catch comprising sand steenbras, white steenbras, blacktail, olive grunter and white stumpnose (Photograph: © Kyle Smith).

Figure 8.19 An undersized white steenbras caught by an angler in the Knysna Estuary and illegally retained. A fin clip is about to be removed from the fish for genetic analysis (Photograph: © Kyle Smith).

Catch

Most anglers (45%) are not targeting specific species and would be happy to catch anything (Table 8.2). Of those species actively targeted, spotted grunter (17%) is the most popular followed by white steenbras (10%), Cape stumpnose (6%), strepie (5.5%), dusky kob (5%) and leervis (5%). There are however, differences in target species and catch composition between recreational and subsistence fishers. Most subsistence fishers indicate they are not targeting specific species and are happy to catch "whatever is biting". Their catches are dominated by smaller bodied species including Cape stumpnose, strepie, sand steenbras and juvenile blacktail and white steenbras (Figure 8.18). In particular, the subsistence fishers found on Thesen Jetty and the railway bridge catch higher numbers of strepie, whilst those fishing Ashmead Channel catch a higher proportion of Cape stumpnose. Fishing on the western bank south of Lake Brenton is productive for sand steenbras during summer.

Recreational anglers target a wide range of species with white steenbras, spotted grunter, leervis, dusky kob and at certain times elf being important target species. During upwelling events when sea water temperatures drop rapidly, white musselcracker are actively targeted as they 'escape' the cold water by moving into the estuary. Although primarily targeted by boat anglers in the lower portions of the estuary, white musselcracker have been caught as far up as the N2 bridge. Overall recreational catches have been dominated by spotted grunter, Cape stumpnose, white steenbras and leervis.

Retention rates for all species is high for both recreational anglers and subsistence fishers with recreational anglers keeping around 74% of the catch and subsistence anglers 91%[61]. There is a more pronounced difference in the retention rate of white steenbras between the groups than for other species, with more white steenbras being kept by subsistence fishers (97%) than recreational anglers (63%). Of concern is that quite a high proportion of retained fish for both subsistence (53%) and recreational anglers (29%) has been below species specific minimum legal size limits[61].

Case study : the white steenbras *Lithognathus lithognathus*

White steenbras are targeted by both recreational and subsistence fishers, including those fishing with setlines[29]. Currently white steenbras is a no sale recreational species with a minimum size limit of 60 cm (total length) and a daily bag limit of one. The species was decommercialised in 2001 due to its population decline. Under the small scale fisheries policy smallscale commercial fishers are permitted to catch and sell white steenbras but are limited by the size and daily bag limit. Individuals of this species mature at around 65 cm and age 6 years, with the maximum recorded age being between 25 and 30 years and a maximum size of 137 cm.

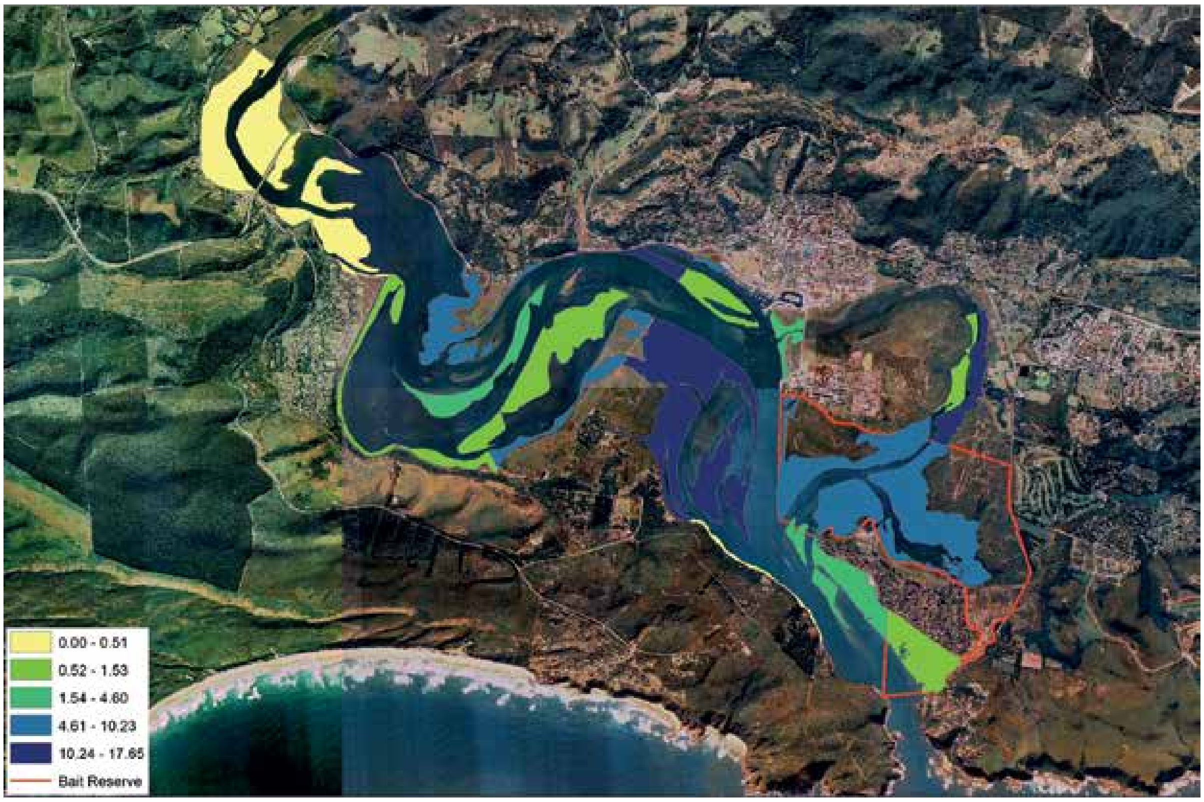


Figure 8.20 Spatial patterns in total observed invertebrate harvesting within the Knysna Estuary during 2019. Data is represented in each section as the proportion of total observed annual baiting effort.

Table 8.3 Estimated annual harvest of select invertebrates for bait usage within the Knysna Estuary (data from Smith[68]).

Bait	08/09	09/10	11/12	12/13	13/14
Mudprawn	1 041 373	883 508	723 746	624 501	578 408
Sandprawn	16 855	25 303	39 107	20 409	29 763
Cracker shrimp	2 221	5 418	13 286	3 230	6 037
Moonshine	9 224	6 498	18 952	14 994	13 745
Bloodworm	8 805	6 676	7 399	5 048	8 368
Polychaete	2 636	2 840	2 522	2 347	3 743
Pencil bait	513	102	6 138	1 038	1 708

Research conducted on the Sundays Estuary highlighted a high level of non-compliance amongst recreational and subsistence fishers with a high proportion of retained fish being undersized[31]. Similarly, during ongoing fishery monitoring conducted on Knysna Estuary, annual undersized retention rates of white steenbras have varied between 44 and 100% (Figure 8.19). The retention of undersized fish contributes to over-exploitation by removing individuals before they have an opportunity to breed and replace themselves. This is known as growth overfishing and, while fastgrowing and short-lived species can to some degree withstand juvenile fishing, long-lived and late-maturing species such as white steenbras show dramatic reductions in catch and abundances under such fishing conditions.

It is a conservation and fishery management concern that we are consistently, across systems, showing high retention rates of undersized white steenbras. This undermines fishery and conservation management and ultimately limits the success of population rebuilding initiatives, with direct negative consequences for all fishers.

8.9 Bait harvesting

The exploitation of invertebrate species used as bait by recreational and subsistence fishers take place in virtually all estuaries along the South African coast and is particularly prevalent in those estuaries within or close to densely populated areas, or systems that are popular for holiday makers/visitors. Although bait collection and fishing go hand in hand, and the possible impact of bait harvesting has been raised as early as 1967, only a limited number of studies in South Africa have specifically addressed bait fisheries.

The primary direct impact of bait harvesting is the reduction in density of target species, although the size structure of a target population may also be altered by the preferential extraction of larger individuals. Although some studies have indicated that the number of bait organisms harvested only represent a small proportion of the total population[62] the indirect impacts of bait collecting, mainly related to the disturbance of sediment associated with harvesting, can be far greater than direct impacts. High-intensity collecting with tools such as suction pumps has been shown to have negative long-term (>18 months) effects on the densities of prawns, bacteria and microflora in the sediment, and on the biomass and species richness of meio- and macrofauna[63,64].

Importantly sediment disturbance, which includes trampling, may lead to higher prawn mortality than through direct extraction and may result in as much as an additional 25% reduction in prawn densities[64]. Similarly, for the Swartkops Estuary[65] it was estimated that mortality of mudprawn populations increased by 18% through disturbance, compared to an 18% loss through consumption by bird and fish predators, and only about 2% removed by bait collectors.

Overview of Knysna Estuary bait fisheries

Amount harvested

The amount of mudprawn harvested by recreational and subsistence users in the Knysna Estuary was first quantified by Cretchley[66], with individual recreational fishers removing ± 59 prawns per day, and subsistence fishers ± 102 (double the legal quota) prawns per day. Subsistence fishers comprised 77% of collectors and accounted for 85% of prawns removed[62]. Overall, they estimated that 2.85 million mudprawn were harvested annually within the Knysna Estuary, which represented about 0.9% of the entire standing stock.

More recently, Napier et al.[29] estimated that subsistence fishers removed less than 600 000 mudprawns per year or less than 0.3% of standing stock. Similar to Cretchley[66], Simon et al.[67] showed subsistence fishers collected more mudprawns more frequently than recreational fishers. Over a 6-year monitoring period SANParks[68] estimated that between 578 000 and 1 041 000 mudprawn were harvested annually from the Knysna Estuary by recreational and subsistence fishers combined, with an average harvest of 71 mudprawns per fisher per outing. These include intertidal areas falling within the bait reserve, Loerie Park, Costa Sarda, to intertidal areas south east of the railway bridge (Table 8.3).

Spatial distribution in harvesting

Various sites within the estuary have been monitored for bait harvesting effort. Hodgson et al.[62] showed that there was no significant difference in baiting effort between most of the six sites that they monitored, with only Thesen Island and Ashmead being significantly different (increased activity at Thesen Island and lower activity at Ashmead). More recently, Simon et al.[67] found that subsistence harvesters preferred the mudbanks around Thesen Island whilst recreational fishers utilised the intertidal area around Leisure Island. In contrast to this, Napier et al.[29] indicated that the railway bridge and Ashmead were preferred harvesting sites for mudprawn by subsistence harvesters.

Both Hodgson et al.[62] and Simon et al.[67] restricted their monitoring to 6 sites and hence patterns in baiting effort are not representative of the entire system. Annual monitoring of the local fisheries undertaken by SANParks included counts of bait harvesters observed throughout the Knysna Estuary from the White Bridge down to The Heads. Results indicate annual fluctuations in harvesting pressure on intertidal areas, but observations of bait harvesters were consistently higher in some areas (Figure 8.20). These include the intertidal areas falling within the bait reserve, including Loerie Park, Costa Sarda and the intertidal areas opposite Thesen Island, and up towards the Railway Bridge. Importantly this work indicates that bait harvesting pressure, and hence direct and indirect pressures on harvest species and habitats, occurs throughout the estuary.

Perceived changes and regulations

A large percentage (71%) of subsistence users interviewed by Cretchley[66] felt that the daily allowable quota for mudprawn was insufficient, while most recreational anglers interviewed felt that the number was more than enough. Similarly, Simon et al.[67] showed that subsistence fishers desired the daily bag limit for mudprawn to be increased to 100. Furthermore, subsistence fishers were more likely to see the bait regulations as restrictions preventing them from making a profit rather than as a means to sustainably manage species populations. Suggestions varied between subsistence and recreational fishers regarding proposed improvements in bait management and conservation. Subsistence fishers preferred a rotational no baiting zone whilst recreational fishers recommended improving policing and enforcing bait regulations[67].

Smith[68] found an increase in law enforcement was a desired outcome by anglers but that importantly there was also a call for increased knowledge, awareness and education initiatives targeting bait harvesters. Furthermore, it is apparent that there are differences between the needs of subsistence and recreational fishers and this suggests that different management approaches or strategies accommodating both groups may be warranted[67].

Bait value

Napier et al.[29] estimated that bait collectors on Knysna Estuary collectively earned between R66 000 to R88 000 from the sale of prawns alone, although their income increased if they collected more expensive species to order for regular customers. Furthermore, the intrinsic value of prawn (to catch fish for personal consumption) added an additional R99 000 to R132 000. Overall the subsistence fishery was valued between R0.7 and R1.1 million per annum, with individual full-time fishers earning at least R11 000 – R17 000 per annum from the estuary. These estimates suggest that a small-scale commercial bait fishery is already in existence and has potential if properly managed. However, experience with subsistence bait fisheries in other South African estuaries (e.g. Swartkops) suggests that commercialising bait harvesting will have to be managed very carefully to prevent uncontrolled collecting and unintended consequences[67].

8.10 Knysna fishery challenges

The primary mandate of protected areas is the conservation of biodiversity both for its intrinsic value and for the conservation-related benefits for people. With natural resources being important for socio-economic well-being, sustainable resource use is increasingly becoming an important aspect of protected area anagement.

The Knysna Estuary has been shown to be an important system for recreational and subsistence fishers. Although management of fisheries in South Africa, including permitting systems and the setting of species specific regulations (daily bag limits and size restrictions) is a national competency falling under the Department of Forestry, Fisheries and Environment (DFFE), SANParks is the designated management authority and is involved in fishery management through research, monitoring and law enforcement activities.

A major issue within recreational fisheries is the high rate of non-compliance to regulations[69]. Contraventions to linefish regulations have been documented back at least 20 years in South Africa when roughly 32% of recreational coastal shore fishers admitted to illicit angling behaviour[70]. A generally poor regulatory knowledge base combined with poor compliance has since also been shown in a number of recreationally dominated estuarine fisheries in South Africa[31] including Knysna[61]. Although there is evidence to suggest that the level of enforcement influences compliance, individual behaviour is often shaped by what people around them consider to be appropriate or desirable. Ideally we would like to work towards a situation where voluntary compliance with regulations increases and fishermen self-regulate. A situation potentially achieved through manipulation of social norms—the perceptions of what is common behaviour, approval or opinion about a particular behaviour, and the perceived social pressure to engage or not engage in certain behaviour.

Large scale disruptions, including the economic crisis during 2010 and the COVID-19 pandemic, have been shown to influence local fisheries[71]. In particular, associated unemployment and poverty levels are a major driver in motivating people to fish, for either household consumption or to sell their catch to supplement any income, placing increasing pressure on the estuary. It would be expected that the necessity for food would dictate that a subsistence type fisher would be more likely to keep undersized fish and have a general overall higher retention rate than recreational anglers.

South African National Parks (SANParks), has a resource use policy that adopts a complex sytems view and outlines principles for sustainable resource use, including the implementation of an adaptive management approach to determining sustainable use levels[72]. The challenge in Knysna is to facilitate equitable and legal access to fishery resources, enhancing social relevance (through impacting positively human well-being), and in so doing build a vested interest in conservation while maintaining ecological integrity and economic viability.

8.11 Catch and release angling

Of particular importance is the growth in catch and release fishing behaviour by some recreational anglers. Although only a minority of fishers practise catch and release angling, it is on the increase and young participants in the fishery are often leading the way (Figure 8.21). However, if catch and release angling is to be a valuable tool for conserving fisheries resources it needs to be done correctly, thereby ensuring a high survival rate of released fish (Box 8.1).

8.12 Future of fishes in the Knysna Estuary

The high diversity of fish species in the Knysna Estuary is due to a number of estuarine characteristics including the large size of the system and the diversity of habitats from rocky areas, open water, sandy and muddy substrates, through to extensive eelgrass beds and intertidal saltmarshes. The geographical location of the estuary is within the

Figure 8.21 A young fisherman about to release a dusky kob *Argyrosomus japonicus* that he caught in the Knysna Estuary in December 2020. This type of angler behaviour is providing hope for the future of overexploited fish species in the estuary (Photograph: © Leslie Ter Morshuizen).

BOX 8.1 : TIPS TO IMPROVE SURVIVAL OF RELEASED FISH.

If practicing catch and release angling there are a few steps that should be followed to help improve the survival rate of your released fish. Understanding what gear to use and how to handle fish in a conservation friendly manner will help in this regard.

• Use the proper weight-class tackle; land your catch quickly, and when possible, leave the fish in the water while you release it. Fish that struggle intensely for a long time accumulate excessive amounts of lactic acid in their muscles and blood and are usually exhausted and stressed. This leads to physiological imbalance, muscle failure, or death.

• Choose your hooks carefully. Barbless and circle hooks are known to reduce injury and mortality of released fish. Barbless hooks are easily removed and reduce tissue damage whilst circle hooks reduce deep hooking mortality. For deep hooked situations it is better to cut the leader and leave the hook embedded than to try and remove it. Steel and bronze hooks are less toxic and are rejected or 'dissolved' sooner than are stainless steel and cadmium-plated or nickel-plated hooks.

• Always handle the fish with wet hands and keep your fingers away from the eyes and gills. Hold the fish horizontally and don't drop it onto a hard surface.

• Do not use a gaff and try to keep the fish in the water whilst releasing it. If you do remove the fish from the water keep the time to a minimum.

• Release your fish gently head first into the water, to help push water through the mouth and over the gills. Revive exhausted fish by placing the fish in the water, facing the current if possible, with one hand underneath the belly and the other hand holding the bottom lip or tail. At the first sign of it trying to swim away let it go.

middle of a number of endemic species distributions whilst tropical and subtropical species may find their way into the estuary when the warm Agulhas Current lies close inshore. A prominent feature of the Knysna Estuary and key in promoting the diverse fish community is the deep, wide and permanently open mouth, enabling recruitment of larva and juveniles and the unrestricted movement of adults both into and out of the system. Furthermore, the prominent marine influence in the lower sections drives the high occurrence of marine stragglers not normally associated with smaller estuarine systems.

As can be seen from Appendix 1, the Knysna Estuary is an exceptional system when it comes to fish species richness. With more than 100 bony fishes and 13 species of sharks and rays recorded in the estuary, the ichthyofaunal richness of this system is unmatched by any temperate or subtropical estuary on the subcontinent. Clearly the maintenance of this rich biodiversity and the high primary (plants) and secondary (invertebrates) productivity needs to be maintained for the future of the fishes in the Knysna Estuary to be assured. The increased sedimentation rate within the Knysna Estuary over the past century or more, primarily due to road and rail infrastructure impinging on the natural flood lain, catchment degradation leading to increased iltation, as well as diverse riparian developments round the lagoon reducing intertidal and subtidal habitats, are all cause for concern. Reduced water depths and loss of parts of the intertidal zone lead to reduced habitat diversity for fishes and ultimately a decrease in the numbers and size ranges of fishes that can be supported by the estuary.

Although declared a protected environment and incorporated within the Garden Route National Park, the Knysna Estuary is also a system under pressure from multiple threats and pressures. The land area is largely developed, particularly on the northern and eastern shores with as much as 80% of the estuarine shoreline being modified under hardened structures[45] and 490 ha of the estuarine functional zone covered by development. Direct and indirect pressures from development include habitat modification and various types of pollution which can impact the nursery function of the system. For example sewerage and waste water from inadequate treatment plants and storm water drains are both a human health issue, with elevated levels of

E. coli above unsafe human levels, but are also an ecological issue with nutrient levels influencing algal growth and other water quality parameters.

Knysna Estuary is important as a place for recreation and in securing and improving livelihoods. Many of these activities rely on a healthy system but by their actions may also impact the system. The question remains, how do we enable multiple benefits whilst minimising impacts, thereby promoting sustainability? Recreational and subsistence fishing are important social and economic activities but noncompliance to fishery regulations undermines conservation efforts with over-exploitation a serious threat to fish populations. Promoting catch and release and increasing voluntary compliance will be key in promoting sustainable local fisheries, whilst the creation of strategically placed closed areas for bait and fishing would be highly beneficial.

Estuaries are vulnerable to climate change impacts, with drivers of change in the system being terrestrial, freshwater or marine in origin. In addition to direct impacts on most ecological processes, climate change is considered a multiplier of pressures on biodiversity, both exacerbating the effects of those pressures as well as altering their frequency, intensity and timing. Changes in rainfall and freshwater input will influence salinity regimes, the river estuarine interface and associated fish communities. Intertidal salt marshes will need to keep pace with climate change in terms of sediment accretion as the heavily developed shoreline prevents migration. Rising nearshore and land temperatures will result in niche changes and shifts in fish species distribution, with both temperate and subtropical species showing shifts in distribution that will influence the composition of fishes in the Knysna Estuary. Increased upwelling events along the Garden Route coastline may also increase the use and importance of estuaries such as Knysna as thermal refuge areas.

As we continue to understand more about the system from both an ecological and a social perspective we can continue to improve our management, providing adequate protection and sustaining ecosystem functioning whilst enabling access to the important ecosystem services from which society derives so much value. Ongoing research and monitoring will be pivotal to improving knowledge and supporting evidence based decision making.

From the previous sections in this chapter, it is apparent that there are three main legs that support the Knysna Estuary fish 'stool'. The first leg are the habitats occupied by the fish species at different stages of their life cycle. Of particular importance in this regard are the eelgrass beds which are vital nursery areas for a number of fish species that are of recreational and subsistence fishery value. Unfortunately, the intertidal eelgrass is under increasing pressure from bait harvesting activities and has been considerably reduced in extent, density and overall primary productivity. On top of this physical damage done to intertidal eelgrass beds, there is also the deteriorating water quality, caused mainly by the inputs of nutrient rich water from the wastewater treatment plant which results in the proliferation of pest macroalgae that smothers intertidal and subtidal eelgrass.

The status of the second leg is related to what has been happening to the first leg, namely the progressive decline in invertebrate prey resources brought about by intensive bait harvesting and associated smothering and trampling of invertebrates living in or on the mud surface. There is an abundance of evidence that previously common invertebrates such as bloodworm have declined dramatically over the past few decades due to overexploitation during bait harvesting.

The third leg of the stool is the actual exploitation of key fish species by both recreational anglers and subsistence fishers. This targeted fishing has the impact of 'fishing down the food chain'—that is the removal of top predators from the fish population which impacts negatively on the natural functioning of the ecosystem. In this regard there is strong evidence that targeted fish species such as white steenbras, dusky kob, leervis and spotted grunter are already heavily harvested and, in some cases, less than 5% of the potential spawning population remain. Compounding this overexploitation is the fact that undersized fish of these species are generally not returned alive to the estuary and this places additional pressures on the ability of breeding populations of these fish to recover.

Having identified that the stability and growth of certain fish populations in the estuary is compromised by the above scenarios, what needs to be done to ensure recovery of overexploited species? Clearly there needs to be some protection provided to eelgrass habitats, intertidal invertebrate populations and fish populations so that the human impacts on these components can be reduced. The creation of more closed areas to both bait harvesting and fishing would go a long way towards providing a 'subsidy' to those areas that are the focus of heavy levels of exploitation. Adherence to bait regulations, fish size and bag limits are also of prime importance, so the policing of existing fishery legislation needs to be rigorously enforced. If these main issues are actively addressed, the future of fishes in the Knysna Estuary will be assured and angling catch rates would increase (Figure 8.22).

Figure 8.22 A lone recreational angler enjoying the solitude and evening ambience of the Knysna Lagoon (Photograph: © Kathy Kay).

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An African fish eagle in full flight (Photograph: © Dreamstime.com).

Chapter 9 : Waterbirds of the Knysna Estuary

David Allan, Ian Russell, Jane Turpie, Lorna Watt & Pat Nurse

9.1 Introduction

Knysna Estuary is the largest estuary, and the only estuarine bay, in the 'Warm Temperate' coastal biogeographical zone of South Africa (roughly Cape Point to the Mbashe Estuary)[1]. Covering a total area of 1 366 ha, it falls within the top 10% of estuaries in the country in terms of size. It rates as the most important of all South African estuaries in terms of its overall conservation value[2,3,4] taking estuary size, type, rarity and biodiversity (plants, invertebrates, fish and birds) into account. The estuary is ranked 13th out of 258 estuaries in the country in terms of its importance for avifauna[4,5].

An early assessment[6] ranked Knysna Estuary as the second most important site for Palearctic migratory waders in the southern and eastern Cape, although numbers were considered lower than expected given its size and extent of apparently suitable habitat. Subsequent observers have similarly noted that although the numbers of waterbirds is high, their density is typically lower than at many other permanently open estuaries[1,7]. The likely main cause of the relatively low waterbird density has been attributed to human disturbance, e.g. from boaters, fishermen, bait collectors, holidaymakers and other human presence on the estuary[1,7,8]. It has been suggested that a further cause is the possible unavailability of invertebrate prey due to dense eelgrass *Zostera capensis* and sea lettuce *Ulva lactuca* cover in some areas. Claims that relatively low densities of some waterbirds species, specifically invertebrate feeders such as migratory waders, is due to a relatively low biomass of benthic invertebrates seems unfounded as the zoobenthos of the Knysna Estuary is rich and abundant (see Chapter 7 and references therein). The estuary water column, however, has been described as a "nutrient poor (oligotrophic) system largely due to the large volumes of nutrient poor marine waters that pass through The Heads twice daily. Associated with the oligotrophic status of the system is high water clarity"[9]. The estuary nevertheless, by virtue of its size, apparently supports the greatest number of waterbirds of all the estuarine systems in the warm temperate biogeographical zone[7].

The aim of this chapter is to provide a review and update of the status of the waterbirds of Knysna Estuary based on an examination of past knowledge and, especially, on information from waterbird counts. Particular attention is paid to the species richness, abundance, seasonality, spatial distribution, population trends, breeding and conservation status of these birds.

9.2 Information sources

Early accounts of the waterbirds of Knysna Estuary go back to the mid-1900s, although compared to several other large estuarine systems in South Africa, such as Langebaan Lagoon and St Lucia, the avifauna of Knysna Estuary has been relatively poorly studied.

There is a very early account that includes counts or estimates of the numbers of many waterbird species compiled during the period March-August 1944[10]. The first comprehensive count of the waterbirds was made during January 1979[6,11] (with an earlier partial count[12]). The first comprehensive list of waterbirds in the estuary was compiled in the mid-1980s drawn from several sources and includes the maximum number of individuals counted[13]. One report covers the waterbirds around Thesen Island prior to its development as a marina[8].

The most extensive count information on the waterbirds comes from the Coordinated Waterbird Counts (CWAC) project[14]. These counts were conducted at low tide biannually in summer (usually January) and winter (usually July). The first count was made in January 1993 and the latest count considered here is from January 2022, i.e. a period spanning 30 years. No counts were made in the winter of 2020 and both the summer and winter of 2021, due to the lockdowns associated with the global Covid 19 pandemic. Most of the information presented in this chapter is based on these counts, which comprise 29 summer and 27 winter surveys.

A detailed analysis of information from the first 12 CWAC counts spanning the six years 1993-1998 has been presented[7]. The most recent review of the estuary's waterbirds[1] was based on information from earlier sources, the CWAC counts up to 2008 and a further single comprehensive count made in February 2008.

Information presented here on rare and vagrant waterbirds (Appendix 1) come from a wide variety of sources, including bird-club newsletters.

Table 9.1 Summary of details of the 72 waterbird species counted during 56 biannual Coordinated Waterbird Counts Project (CWAC 2022) counts over the period January 1993 to January 2022. Details shown are migratory status[20] (Mig. = Palearctic/Nearctic nonbreeding migrant, Res. = Resident), main diet[20] (H = herbivore, O = omnivore, I = invertebrate feeder, P = piscivore, A = amphibians, M = mammals), weight[20], percentage of counts during which each species was recorded, summer, winter and overall average, maximum (Max.) number of each species recorded, and breeding (Br.) status (C = confirmed breeding, S = suspected breeding).

Common name	Mig. status	Diet	Wgt (g)	% of counts	Summer avg.	Winter avg.	Overall avg.	Max.	Br.
Spur-winged goose	Res.	H	4 300	13%	3	1	1.70	45	
Egyptian goose	Res.	H	2 125	100%	314	121	221.05	604	C
South African shelduck	Res.	H	1 400	20%	1	1	0.55	5	
Blue-billed teal	Res.	H	246	5%	0	0	0.18	6	
Cape shoveler	Res.	H	629	98%	70	53	61.95	216	C
Yellow-billed duck	Res.	H	900	96%	86	82	84.45	490	C
Mallard	Res.	H	1 100	21%	0	0	0.25	2	
Cape teal	Res.	H	400	98%	22	33	27.41	97	
Red-billed teal	Res.	H	649	27%	2	1	1.46	19	
Southern pochard	Res.	H	775	2%	0	0	0.02	1	
African rail	Res.	I-R	165	7%	0	0	0.16	4	
Common moorhen	Res.	I-R	260	88%	6	9	7.54	29	C
Red-knobbed coot	Res.	I-R	730	96%	6	5	5.95	16	C
Black crake	Res.	I-R	90	16%	0	1	0.41	4	C
Little grebe	Res.	P	178	66%	2	13	7.20	40	
Great crested grebe	Res.	P	620	7%	0	0	0.11	5	
Greater flamingo	Res.	I-R	2 750	4%	0	0	0.05	3	
Water thick-knee	Res.	I-R	303	21%	1	1	0.66	7	
African oystercatcher	Res.	I-R	698	100%	60	70	65.20	148	C
Black-winged stilt	Res.	I-R	165	100%	54	101	76.73	184	C
Pied avocet	Res.	I-R	343	88%	20	41	30.21	103	C
Blacksmith lapwing	Res.	I-R	165	100%	61	73	67.11	139	C
Grey plover	Mig.	I-M	250	95%	271	37	158.34	666	
Common ringed plover	Mig.	I-M	51	55%	37	1	19.73	140	
Kittlitz’s plover	Res.	I-R	36	98%	24	43	33.34	101	C
Three-banded plover	Res.	I-R	34	73%	2	12	7.07	61	
White-fronted plover	Res.	I-R	35	48%	2	4	3.20	17	
Greater sand plover	Mig.	I-M	86	2%	0	0	0.02	1	
Eurasian whimbrel	Mig.	I-M	490	100%	271	45	161.96	554	
Eurasian curlew	Mig.	I-M	735	39%	2	0	1.20	8	
Bar-tailed godwit	Mig.	I-M	255	4%	0	0	0.04	1	
Ruddy turnstone	Mig.	I-M	100	5%	0	0	0.11	4	
Ruff	Mig.	I-M	135	13%	2	0	0.82	15	
Curlew sandpiper	Mig.	I-M	69	71%	1 329	10	693.54	3 205	
African snipe	Res.	I-R	115	13%	1	0	0.32	4	S
Little stint	Mig.	I-M	28	16%	2	0	0.98	18	

Pectoral sandpiper	Mig.	I-M	60	2%	0	0	0.02	1	
Common sandpiper	Mig.	I-M	55	46%	3	0	1.71	13	
Marsh sandpiper	Mig.	I-M	70	41%	19	1	9.98	116	
Wood sandpiper	Mig.	I-M	60	13%	2	0	1.09	50	
Common greenshank	Mig.	I-M	185	100%	396	84	245.57	780	
Grey-headed gull		Gull	280	5%	0	0	0.09	2	
Kelp gull		Gull	970	100%	331	411	369.82	639	C
Caspian tern		P	690	50%	1	1	1.30	6	C
Swift tern		P	390	45%	35	4	20.30	727	
Sandwich tern	Mig.	P	210	43%	11	0	5.45	34	
Common tern	Mig.	P	125	77%	103	13	59.70	207	
Black stork	Res.	P	3000	2%	0	0	0.02	1	
Cape gannet	Res.	P	2675	2%	0	0	0.09	5	
African darter	Res.	P	1500	80%	1	8	4.38	21	C
Reed cormorant	Res.	P	555	100%	196	291	241.86	506	C
Cape cormorant	Res.	P	1200	96%	104	367	230.64	1052	C
White-breasted cormorant	Res.	P	3038	100%	17	38	27.13	119	C
African sacred ibis	Res.	I-R	1525	100%	150	224	185.68	526	C
Hadeda ibis	Res.	I-R	1350	95%	33	38	35.48	98	C
Glossy ibis	Res.	I-R	634	5%	0	0	0.16	5	
African spoonbill	Res.	P	1600	82%	5	35	19.48	134	C
Black-crowned night heron	Res.	P	630	5%	0	1	0.25	8	
Western cattle egret	Res.	I-R	375	79%	30	18	24.29	191	C
Grey heron	Res.	P	1500	100%	67	65	65.91	138	C
Black-headed heron	Res.	M	1525	91%	5	4	4.61	26	C
Purple heron	Res.	P	870	5%	0	0	0.05	1	
Yellow-billed egret	Res.	P	415	2%	0	0	0.02	1	
Little egret	Res.	P	522	100%	81	173	125.63	343	C
Hamerkop	Res.	A	503	9%	0	0	0.09	1	
Western osprey	Mig.	P	1475	95%	2	1	1.95	4	
African fish eagle	Res.	P	2700	93%	2	3	2.14	5	C
Half-collared kingfisher	Res.	P	40	9%	0	0	0.14	4	C
Malachite kingfisher	Res.	P	17	34%	0	1	0.61	8	
Giant kingfisher	Res.	P	365	55%	1	2	1.14	6	
Pied kingfisher	Res.	P	85	100%	15	23	19.23	42	S
Cape wagtail	Res.	I-R	21	95%	32	46	38.82	117	S

Figure 9.1 The rather specialised Cape teal (a male shown here in the Ashmead Channel area) is one of the more common Anatidae on the estuary (Photograph: © David Allan).

Figure 9.2 The black-winged stilt is the most abundant of the resident Charadriformes waders at Knysna Estuary (Photograph: © David Allan).

A particularly valuable source of such records in recent times is the internet-based South African Rare Bird News (SARBN; see: http://groups.google.co.za/group/sa-rarebirdnews).

9.3 Species richness and diversity

Ninety-three species of waterbirds have been recorded from Knysna Estuary (Appendix 1). These come from 13 orders and 25 families of waterbirds[15]. Thirty of these species were either not recorded on CWAC counts or were recorded on <5% of these counts and can be considered rare vagrants to Knysna Estuary, i.e. the community of waterbirds typical of the estuary comprises some 63 species.

9.4 Key waterbird groups

The waterbird community is numerically dominated by ducks and geese (Anatidae), oystercatchers (Haematopodidae), stilts and avocets (Recurvirostridae), plovers and lapwings (Charadriidae), scolopacid waders (Scolopacidae), gulls and terns (Laridae), cormorants (Phalacrocoracidae), ibises and spoonbills (Threskiornithidae) and herons and egrets (Ardeidae). The smaller waterbirds are represented by the kingfishers (Alcedinidae) and wagtails (Motacillidae) (Table 9.1).

Among the Anatidae, Egyptian goose is the most abundant, followed by yellow-billed duck, Cape shoveler and Cape teal (Figure 9.1). Other waterfowl are much less common. African black duck surprisingly has never been recorded during CWAC counts and is not mentioned in any of the other sources examined for this review but this species is present on dams adjacent to the Knysna River and a female with ducklings was seen at Woodbourne Pan in 2021 (L. Watt personal observation).

Of the Palearctic migratory charadriiform waders, curlew sandpiper is the most abundant, as is typical at many South African estuaries[16], followed by common greenshank, Eurasian whimbrel, grey plover, common ringed plover and marsh sandpiper. The most abundant resident charadriiform wader is black-winged stilt (Figure 9.2), followed by blacksmith lapwing, African oystercatcher, Kittlitz's plover and pied avocet.

Figure 9.3 The piscivorous and invertebrate-feeding little egret is the most abundant of the Ardeidae, with a maximum of 343 having been recorded on a single count. Individuals like this bird photographed in the Ashmead area likely benefit from the clear-water conditions in the estuary and abundance of small juvenile fish and shrimps in the shallows (Photograph: © David Allan).

Kelp gull is the second-most abundant waterbird after curlew sandpiper. A relatively unusual feature of the aquatic avifauna is the essential absence of a small gull species, with grey-headed gull being rare and the estuary is outside the normal range of the endemic Hartlaub's gull *Larus hartlaubi*.

The migratory common tern is the most abundant of the terns, followed by the resident swift tern. These terns, however, perhaps especially the swift tern, often use estuaries primarily as roosting sites rather than feeding areas, commuting regularly between such roosts and their open-ocean fishing grounds[24].

Of the two widespread cormorant species in South Africa, the reed cormorant is some ten times more abundant than the larger white-breasted cormorant, which may reflect the size of the available fish prey and/or water depth. The average number of the marine-associated Cape cormorant is similar to that of the reed cormorant. This extensive use of the estuary by marine cormorants is unusual[1].

Among the ibises and spoonbills, African sacred ibis is the most abundant, followed by hadeda ibis and African spoonbill. The particularly high abundance of African sacred ibis seems somewhat unusual in a natural estuary like Knysna and is perhaps linked to the dense human settlement of the surrounding area, with attendant rubbish dumps and other scavenging opportunities. Little egret (Figure 9.3) is the most abundant of the Ardeidae, followed by grey heron and western cattle egret. The hadeda ibis, western cattle egret and black-headed heron typically feed largely in dryland rather than aquatic habitats and their inclusion here as 'waterbirds' is perhaps questionable, although these species often nest and roost in or close to wetlands. All members of the Threskiornithidae and Ardeidae, however, are traditionally included in studies of waterbird communities, and this approach has been followed here.

Of the smaller waterbirds, the most abundant are Cape wagtail and pied kingfisher. Although the Cape wagtail is the only passerine counted, there are several other passerine species that could be classed as waterbirds, e.g. white-throated swallow and lesser swamp warbler. The pied kingfisher (Figure 9.4), the only kingfisher that hunts primarily by hovering rather than from perches, is typically by far the most abundant kingfisher in open wetlands like Knysna Estuary. Its abundance is further facilitated by its largely non-territorial feeding, and cooperative and sometimes semi-colonial nesting, habits[20].

Figure 9.4. The hovering ability of the pied kingfisher frees it from the reliance on perches for hunting that constrains other kingfisher species, allowing it to exploit the entire open estuary area and thus to occur at much higher densities than other members of this family (Photograph: © David Allan).

Figure 9.5 This kelp gull scavenging a dead fish on the shores of Leisure Isle is one of, if not the most, generalist of the waterbirds at the estuary in terms of diet, taking invertebrates, fish and offal (Photograph: © David Allan).

Other kingfisher species are limited by the paucity of sheltered perches from which to hunt, especially in the lower and middle reaches of Knysna Estuary, and are typically territorial birds occurring in isolated and well-spaced pairs.

9.5 Dietary guilds

Birds vary greatly in their preferred food and can be categorised into broad feeding guilds based on the dominant components of their diets. In waterbirds this includes herbivores feeding predominantly on plant matter and associated fauna, invertebrate feeders taking mostly benthic invertebrates, piscivores preying mostly on fish, and generalists like gulls which exploit a wide range of food sources (Figure 9.5).

Herbivores are represented largely by the waterfowl, many of which also consume small invertebrates associated with the submerged aquatic plant leaves. In the Knysna Estuary this guild is dominated by Egyptian goose, which often forages predominantly in terrestrial habitats and roosts in estuaries but which also feeds on intertidal mudflats. Other waterfowl tend to feed mostly on submerged macrophytes, typically brackish associated species such as fennel-leaved pondweed *Stuckenia pectinata*. Although there is little of this aquatic plant within the estuary proper, there is some freshwater wetland habitat in the estuary floodplain near Thesen Island, and particularly at Woodbourne wetlands, which is extensively utilised by several duck and other herbivorous species.

Invertebrate-feeding waders are generally opportunistic foragers on macroinvertebrate fauna, with their diets typically dominated by mud prawns (*Upogebia africana*), crabs (e.g. *Hymenosoma* spp.), polychaetes (e.g. *Ceratonereis* spp.) and amphipods[1]. Invertebrate feeders can be subdivided into those that are migratory and occur on Knysna Estuary predominantly in the austral summer, and those that are resident throughout the year. The large numbers of invertebrate feeders, particularly in summer, feed extensively on the broad intertidal mudflats of the estuary which support a high diversity though, in places, low density of certain large

Figure 9.6 This reed cormorant has caught a clinid (klipvis) in the Ashmead Channel. This small cormorant is about ten times more abundant than the larger white-breasted cormorant in the estuary and its abundance is particularly noticeable and increasing (Photograph: © David Allan).

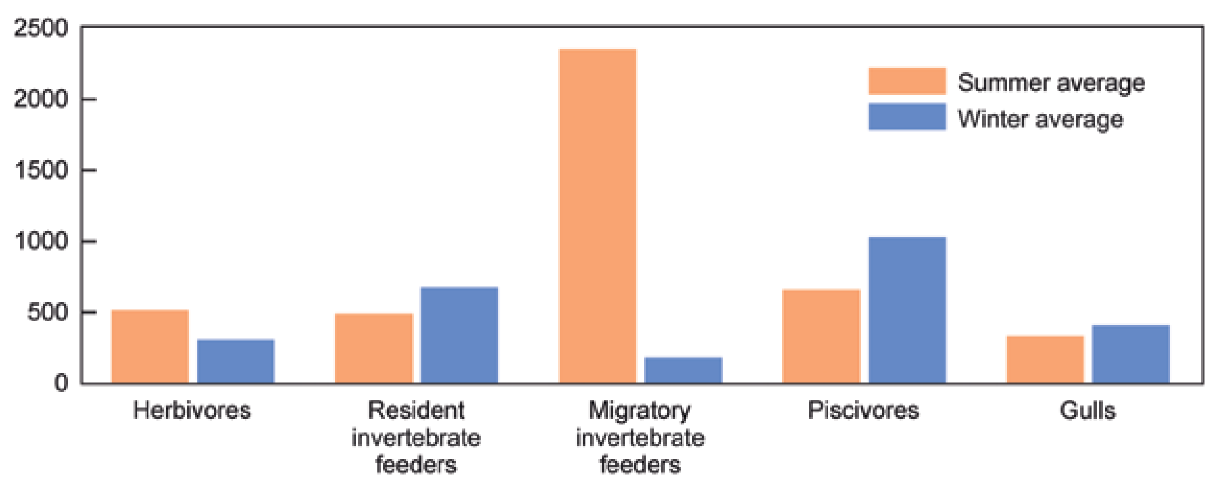

Figure 9.7 The seasonality of abundance of the major avian dietary guilds present at Knysna Estuary drawn from CWAC counts.

Figure 9.8 Eurasian whimbrel is the largest of the common Palearctic migratory waders visiting the estuary in summer (Photograph: © David Allan).

invertebrate species that are targeted for bait collection[17]. Invertebrate diversity may have increased in some areas due to increased muddiness of the system as a result of the deposition of fine eroded sediments[18] thus creating enhanced feeding opportunities for this guild.

The piscivores include terns, cormorants, spoonbill, herons and egrets, osprey, fish eagle and kingfishers. Some of these species also take a variety of other prey (e.g. swimming prawns) but in Knysna Estuary would probably concentrate on fish. Reed cormorants (Figure 9.6) probably feed mainly on estuarine round-herring and gobies, and grey heron on mullet and Cape stumpnose[1]. The larger cormorants and egrets in the lower estuary probably rely on gobies and the juveniles of certain marine fish species using the estuary as a nursery area. Kingfishers likely feed mostly on estuarine round-herring and Cape silverside, and African fish eagles on various mullet species and spotted grunter (based on Turpie and Russell personal observations).

9.6 Seasonality

The average number of waterbirds is typically higher in summer (4 338 birds) than in winter (2 530 birds). This is mainly due to the large numbers of Palearctic migratory waders present during the summer.

Relative to dietary guilds, invertebrate feeders numerically dominate in summer (Figure 9.7). Higher summer abundance is overwhelming due to the seasonally increased abundance of Palearctic migratory waders, mainly grey and common ringed plovers, Eurasian whimbrel (Figure 9.8), curlew and marsh sandpipers, and common greenshank, although the ongoing decrease in some of these species is progressively reversing this domination. By contrast the resident invertebrate feeders (mainly African oystercatcher, black-winged stilt, pied avocet, blacksmith lapwing, Kittlitz's and three-banded plovers, African sacred and hadeda ibises, and Cape wagtail) are typically more abundant in winter (Table 9.2).

The piscivorous guild shows a marked increase in winter and is the numerically dominant guild during this season. Most of the members of this guild (little grebe, reed, Cape and white-breasted cormorants, African spoonbill, little egret and pied kingfisher) follow this pattern (Table 9.2). Exceptions are the terns, including the migratory Sandwich and common terns, as well as the resident swift tern. Many of these piscivores feed elsewhere during the summer breeding season or are coastal species that

Table 9.2 Waterbird species which are significantly more abundant in summer in the Knysna Estuary, significantly more abundant in winter, those which are aseasonal in abundance, and those with insufficient sample sizes for meaningful statistical analysis, based on CWAC counts.

Significantly more abundant in winter	**Aseasonal in abundance**
Pied avocet	Yellow-billed duck
Black-winged stilt	Cape teal
Kittlitz's plover	African oystercatcher
Three-banded plover	Blacksmith lapwing
Kelp gull	Hadeda ibis
African darter	Western cattle egret
Reed cormorant	Grey heron
Cape cormorant	Cape wagtail
White-breasted cormorant	
African sacred ibis	**Insufficient sample sizes**
African spoonbill	Spur-winged goose
Little egret	Red-billed teal
Pied kingfisher	Southern pochard
	Common moorhen
Significantly more abundant in summer	Red-knobbed coot
Egyptian goose	Little grebe
Cape shoveler	Great crested grebe
Grey plover	Greater flamingo
Common ringed plover	Ruff
Eurasian whimbrel	Little stint
Curlew sandpiper	Wood sandpiper
Marsh sandpiper	Glossy ibis
Common greenshank	Purple heron
Common tern	

seek more sheltered feeding areas such as estuaries during winter[1]. Domination by invertebrate feeders (mainly waders) in summer and by piscivores in winter is typical of large South African open estuaries[16].

Gulls, essentially kelp gull, are generalist feeders, taking both fish and invertebrates, and also scavenge on a wide variety of food resources, and are therefore considered separately here. Kelp gull also shows a higher abundance in winter (Table 9.2), as with resident invertebrate feeders and piscivores.

The herbivorous guild, consisting largely of Anatidae (although many of this family are omnivorous), is the only resident waterbird guild to show a lower abundance in winter, although this pattern is only strongly evident in the Egyptian goose and less so in most other key members, specifically Cape shoveler and yellow-billed duck (Table 9.2). Egyptian geese show summer and winter average counts of 314 and 121 birds respectively (Table 9.1). As largely a winter breeder, it is thus likely that the estuary is used at least partially as a non-breeding moult refuge, although breeding is recorded regularly during counts and the first such record is dated January 2000.

Seasonal variability in avian seasonal biomass reveals a quite different pattern of relative importance of each dietary guild. The relatively small-bodied invertebrate-feeding migratory Palearctic waders, which are (or were) overwhelmingly dominant in numerical terms in summer, are replaced by the larger-bodied herbivores (Anatidae), mainly Egyptian goose, and by piscivores in terms of biomass, with the resident invertebrate feeders and

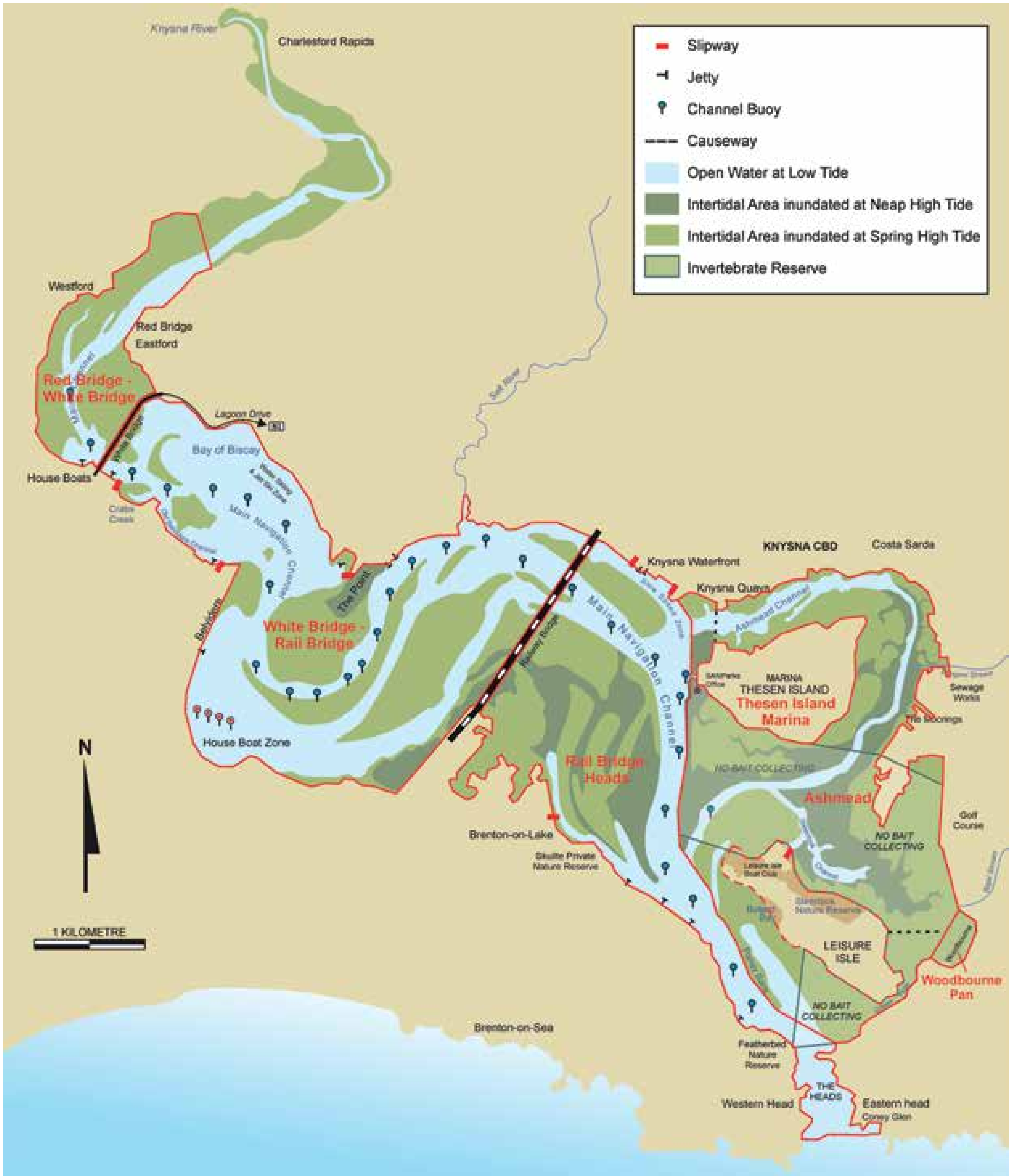

Figure 9.9 Map of Knysna Estuary showing the six sections for which waterbird count data were collected separately (Red Bridge-White Bridge, White Bridge-Rail Bridge, Rail Bridge-The Heads, Ashmead, Thesen Island and Woodbourne Pan).

kelp gull having summer biomasses not far behind (and in recent years ahead of) that of the Palearctic waders. Piscivores are the dominant guild in winter in terms of both numbers and biomass, thus indicating the ready availability of fish prey during all seasons of the year. Total average avian biomass remains fairly similar between summer (2 343 kg) and winter (2 254 kg).

9.7 Spatial distribution

The counts have been compiled keeping the information separate for different areas of the estuary. This allows an examination of how waterbird species are distributed across the wetland. Waterbird counts were undertaken separately in six sections (Figure 9.9), though some of this information, notably counts undertaken from the summer of 1999 to the winter of 2006, and the winter counts of 2009 and 2015, have been lost due to destruction wrought by the widespread Knysna wildfires of June 2017. Thus the most recent and comprehensive dataset also including spatial use of the estuary by waterbirds covers the period summer 2007 to summer 2022, and comprises 15 summer and 11 winter counts.

Review of historical information on waterbird spatial distribution

Descriptions of these six sections and their use by individual waterbird species as presented below are largely based on existing information[1,7]. It should be noted though that circumstances may have changed since these publications were compiled.

Red Bridge – White Bridge:

This uppermost section of the estuary is characterised by low-lying marshes and a narrow intertidal in the upper areas, and elevated marshes, *Spartina* dominated saltmarshes and creeks, and intertidal mudflats in the lower area. Waders present in this area are typically resident species[1]. Cormorants roost in less disturbed areas[1].

White Bridge – Rail Bridge:

Characterised by extensive mudflats with dense *Zostera* and *Spartina* saltmarshes, bisected by several channels, with the uppermost areas also containing more elevated, drier saltmarsh habitat and some sandy shoreline. During the winter the shallow areas of this section are important for piscivorous birds (cormorants, grey heron and common tern) but during the summer months most cormorants were recorded below the Rail Bridge[7]. The uppermost areas attract loafing waterfowl[1].

Rail Bridge – The Heads:

The upper area has extensive mudflats, dense *Zostera* beds and *Spartina* saltmarshes. The saltmarshes in this area and in the immediately adjacent part of White Bridge-Rail Bridge are important high-tide roosts for waterbirds[1,7]. Saltmarsh is largely shunned by feeding waterbirds but the higher-lying saltmarshes provide important breeding habitat for species such as African oystercatcher and Kittlitz's plover[1,7]. Creeks in the saltmarshes are sometimes frequented by egrets, but most piscivores are found on the main channels throughout the estuary (Figure 9.10)[1]. The intertidal areas on the Brenton side of this section are (or at least were) important for over-wintering grey plovers and curlew sandpipers[7]. The uppermost reaches of this section, with some small exposed mudflats, abut the town and are hence subject to particularly heavy human disturbance. Bait collecting in this area disturbs many waterbird species but attracts large numbers of kelp gulls.

The western shoreline along the lower reaches of Rail Bridge-The Heads section comprises narrow, mostly rocky, intertidal along the shoreline between just south of Brenton-on-Lake and The Heads. The lowermost reaches at The Heads is a marine-dominated habitat with deep water, rocky shores, tall cliffs and offshore stacks, including Coney Glen offshore stack off Eastern Head. These rocky shorelines support relatively few feeding waterbirds.

Thesen Island:

This section originally comprised terrestrial habitat, similar to Leisure Isle, and was hence excluded from the early counts but was extensively transformed into a commercial and residential aquatic marina development from 2000 onwards and considered as a separate section in counts from that period onwards.

Ashmead:

This area contains the highest diversity of habitats. The extensive upper areas north of Leisure Isle are characterised by extensive mudflats, dense *Zostera* beds, *Spartina* saltmarshes, other low-lying marshes and adjacent terrestrial habitats. This section also has, at times, abundant floating macroalgae, the sea lettuce *U. lactuca*, due to the nutrient inputs from influent streams and the waste-water treatment works. The intertidal regions of this area are important for over-wintering Eurasian whimbrels and common greenshanks[7]. Part of the Ashmead Channel around Thesen Island is extremely shallow

Figure 9.10 A small flock of little egrets hunting in a major channel on an outgoing tide with Knysna town as a backdrop (Photograph: © David Allan).

and thus naturally protected from excessive boat disturbance, although the Ashmead section generally can be subject to high levels of human disturbance, especially when visitor numbers to Knysna are at a summer peak. This area supports large numbers of waterfowl and waders, and has historically been utilized by a substantial proportion of the African oystercatcher population (Figure 9.11)[1]. The intertidal areas south/south-east of Leisure Isle comprise large sandflats.This area supports low numbers and diversity of waterbirds due to its sandy nature[1]. It has apparently shifted from muddy to sandy since the 1950s, probably due to the ingress of marine sands and reduced flushing of these sands to the sea by floods[1,18,19].

The majority of marine invertebrate-feeding waders, i.e. African oystercatcher, grey and common ringed plovers, Eurasian whimbrel, curlew sandpiper and common greenshank, occur on the intertidal mudflats of lower White Bridge-Rail Bridge and upper Rail Bridge-The Heads south of the main channel, and Ashmead north of Leisure Isle[7]. Kelp gulls and common terns also favour these sections[7]. It has been claimed[1] that Ashmead north of Leisure Isle is the preferred area for most waterbird groups (although see below where Rail Bridge-The Heads is shown to support the highest total numbers of waterbirds) with upper Rail Bridge-The Heads also supporting high numbers of waders and terns.

Woodbourne Pan:

This small wetland is an atypical habitat in the estuary[1,7]. The elevated road embankment along the western edge of this section supports only a narrow piped connection between the pan and the estuary proper. The embankment serves to partially impound inflowing freshwater from Hornlee Stream forming permanent freshwater marsh in places. It also impedes the inflow of tidal water from the estuary resulting in a tidal delay in the pan providing valuable habitat for some waders when other parts of the estuary are already inundated. This pan is particularly important for waterfowl (Anatidae), Rallidae and other resident and migratory waders, i.e. pied avocet (Figure 9.12), three-banded plover, ruff and common and marsh sandpipers[7]. Black-winged stilts concentrate at Woodbourne Pan in summer but move to Ashmead during winter[7].

Information on current spatial distribution of waterbirds

The mean number of waterbirds supported by each of these sections calculated from both summer and winter surveys conducted during 2007-2022 is: Red Bridge-White Bridge – 111 (1.7% of the total number of waterbirds in the estuary), White Bridge-Rail Bridge – 1 225 (18.7%), Rail Bridge-The Heads – 2 339 (35.7%), Ashmead – 1 875 (28.6%), Thesen Island marina – 567 (8.7%) and Woodbourne Pan – 431 (6.6%). The three sections White Bridge-Rail Bridge, Rail Bridge-The Heads and Ashmead therefore support some 83% of the waterbirds on the wetland (and cover about 87% of the total area of the estuary).

More waterbirds were recorded in summer compared with winter in all six sections. This

Figure 9.11 African oystercatchers typically forage at low tide alone or in pairs but roost in flocks at high tide in salt-marsh habitat such as here at Ashmead, with Leisure Isle in the background (Photograph: © David Allan).

Figure 9.12 A small flock of pied avocets roosting at high tide at Woodbourne Pan, a favourite locality for the species (Photograph: © David Allan).

difference is most pronounced for Rail Bridge-The Heads due to the large number of migratory waders and Egyptian geese using this section in summer. However, the average number of migratory waders in this section declined from more than 1 600 in the 1993-1998 summer period to only about 600 in the 2007-2022 summer period (Figure 9.13). Rail Bridge-The Heads also supported the highest overall number of waterbirds in summer and winter, followed by Ashmead and White Bridge-Rail Bridge, with the remaining three smaller regions, the highly modified Thesen Island marina, Woodbourne Pan and, especially, Red Bridge-White Bridge, supporting far fewer birds.

Rail Bridge-The Heads, Ashmead and White Bridge-Rail Bridge are important for invertebrate-feeding migratory waders in summer and for piscivores (mainly common tern, reed and Cape cormorants, African spoonbill, grey heron and little egret) in both seasons but particularly in winter (Figure 9.13). Resident invertebrate feeders (mainly African oystercatcher, black-winged stilt, blacksmith lapwing, African sacred ibis and Cape wagtail) are most abundant in Ashmead in both summer and winter. Kelp gulls are largely restricted to White Bridge-Rail Bridge, Rail Bridge-The Heads and Ashmead in both summer and winter with only negligible numbers in the other three sections throughout the year.

As alluded to above, there is also an earlier series of counts compiled keeping the information separate for different areas of the estuary covering the period summer 1993 to winter 1998, i.e. six summer and six winter counts[7]. This information (raw data obtained from Dr A.P. Martin) is useful for comparison with the similar information from 2007-2022 in order to search for changes in the distribution patterns of waterbirds across the estuary. This earlier information was gathered dividing the wetland into only five sections as opposed to the six sections of the 2007-2022 counts. The relevant difference in this regard was that Thesen Island was essentially excluded from the early counts because at that time it was a terrestrial island (similar to Leisure Isle) and had not yet been developed as a marina.

As with the later survey period, more waterbirds were recorded in summer in all five sections except for Red Bridge-White Bridge. Rail Bridge-The Heads, Ashmead and White Bridge-Rail Bridge at that time also supported the majority of the waterbirds. These sections however showed higher proportions of waterbirds in the summer than the winter compared with the later period, i.e. greater seasonality. These differences in these three sections are largely due to the reduction in recent years in the numbers of migratory waders, especially curlew sandpiper, visiting in summer, particularly evident in the Rail Bridge-The Heads section, as well as an increase in the number of waterbirds present in winter at least in Rail Bridge-The Heads and Ashmead.

Invertebrate-feeding migratory waders showed a greater dominance in summer at Rail Bridge-The Heads, White Bridge-Rail Bridge and Ashmead during the earlier period (Figure 9.13). As with the later period, these three sections were also important for piscivores in both seasons but particularly in winter and the earlier information also suggest an importance of Red Bridge-White Bridge during winter for piscivores (reed and Cape cormorants) that is not as apparent in the later period, despite no reduction in the numbers of these species on the estuary as a whole. Resident invertebrate feeders (mainly African oystercatcher, black-winged stilt, blacksmith lapwing, Kittlitz's plover and African sacred ibis) were again most abundant in Ashmead during the earlier period in both summer and winter, particularly the latter. Herbivores (largely Anatidae) were largely restricted to Woodbourne Pan during in the earlier period but were far more abundant and widespread in the estuary in the later period. This difference is attributable to the enormous increase in Egyptian geese throughout the estuary in recent years. During the earlier period kelp gulls show the same essential restriction to White Bridge-Rail Bridge, Rail Bridge-The Heads and Ashmead in summer and winter as found in the later period.

The six sections covered during the 2007-2022 counts vary greatly in size: Red-Bridge-White Bridge – 140 ha, White Bridge-Rail Bridge – 663 ha, Rail Bridge-The Heads – 427 ha, Ashmead – 568 ha (excluding the terrestrial 74 ha habitat of the densely settled Leisure Isle), Thesen Island marina – 89 ha and Woodbourne Pan – 15 ha. Woodbourne Island has by far the highest density of waterbirds, followed by the highly modified Thesen Island marina. The intermediate-sized and uppermost Red Bridge-White Bridge section has both the lowest overall numbers of waterbirds (Figure 9.13) and the lowest waterbird density in the estuary. Of the remaining three and largest sections, Rail Bridge- The Heads shows both the highest numbers (Figure 9.13) and density of waterbirds in both summer and winter, followed by Ashmead.

High densities at Woodbourne Pan come mainly from herbivores (Anatidae, mainly Egyptian goose, Cape shoveler, yellow-billed duck and Cape teal) and resident (mainly black-winged stilt, pied avocet and three-banded plover) and migratory (mainly

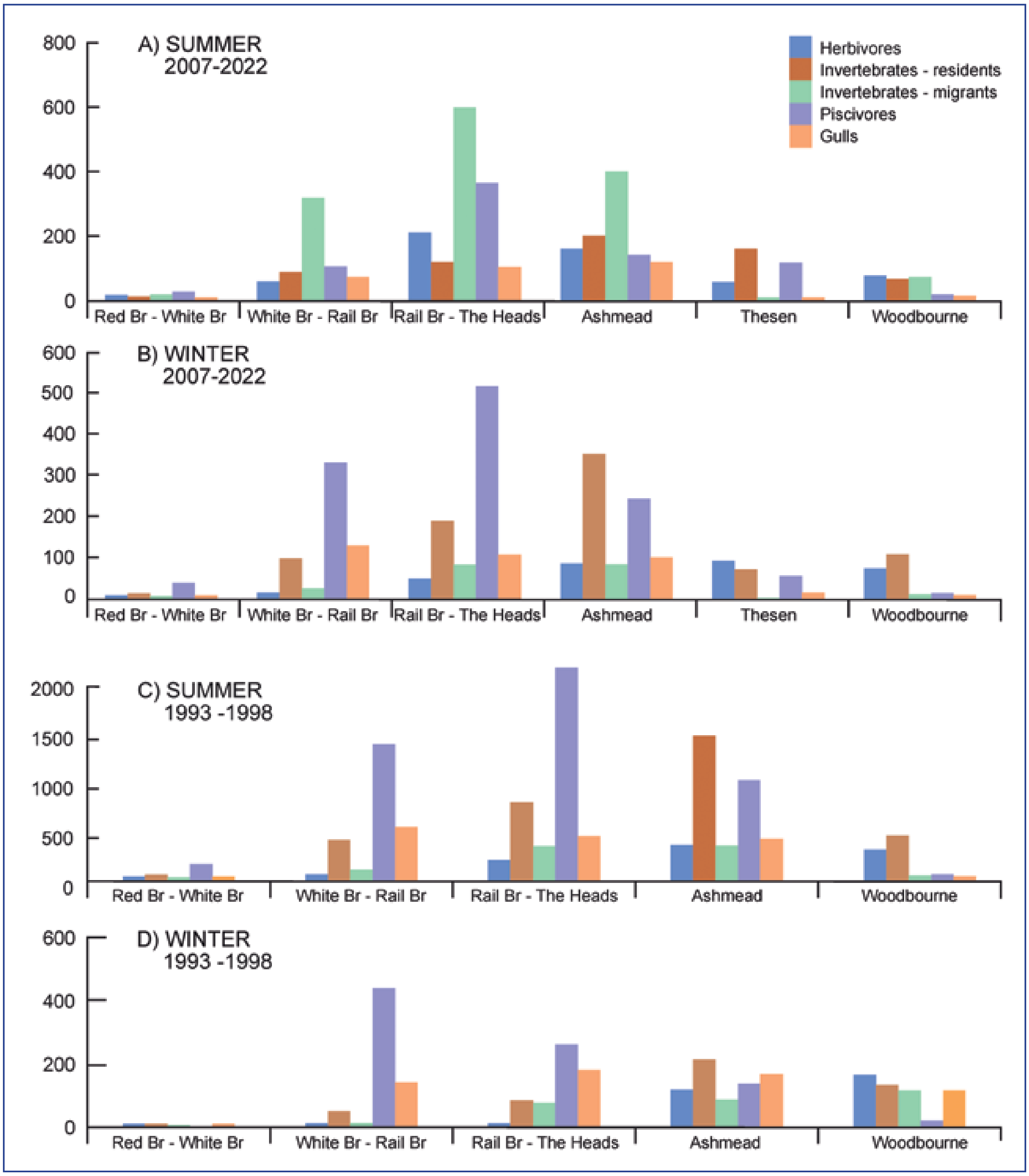

Figure 9.13 The mean number of waterbirds counted in different sections of Knysna Estuary during the summer and winter CWAC counts with the information for the five primary dietary guilds shown separately; a) information from the six sections counted during the period 2007-2022 and b) from the five sections counted during 1993-1998.

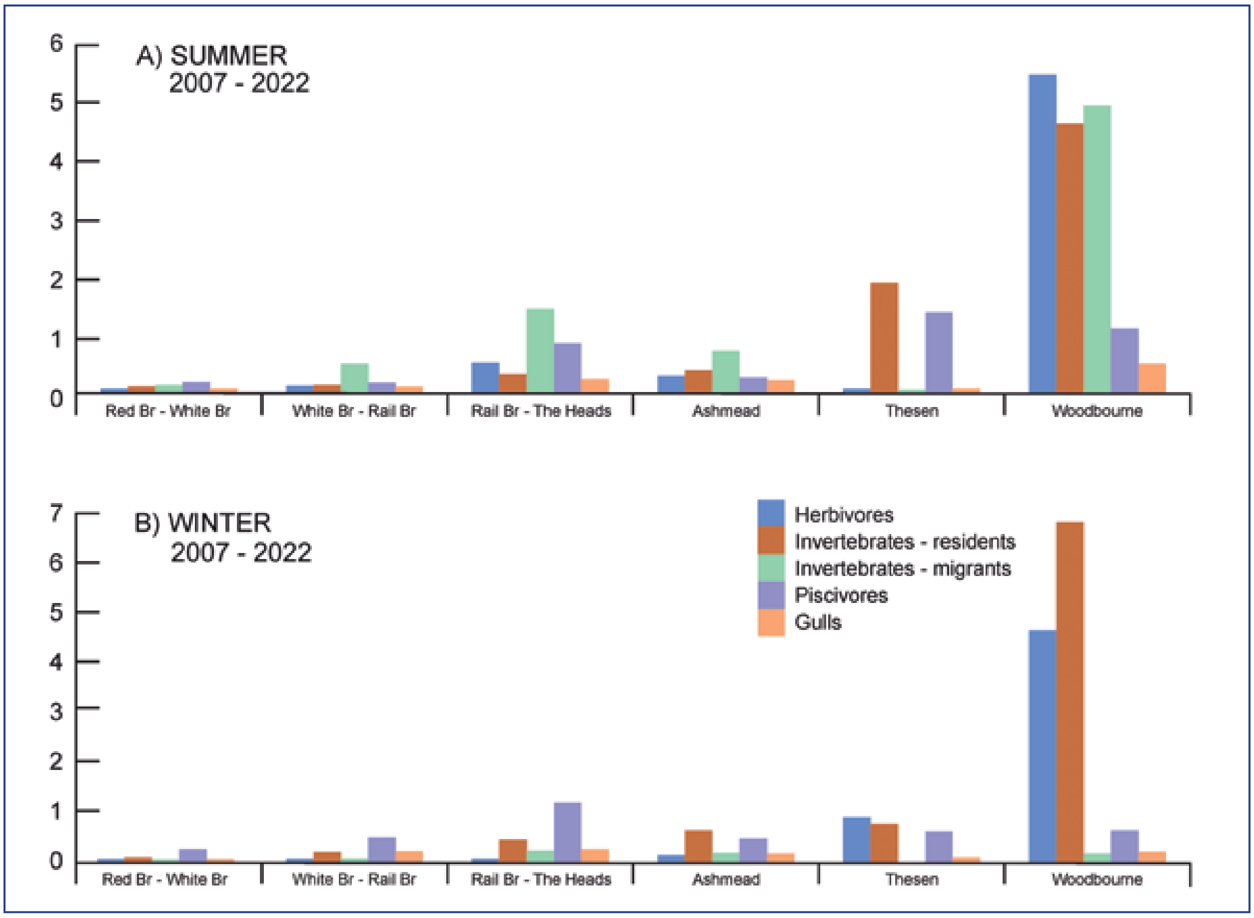

Figure 9.14 The mean waterbird density (birds/ha) in the six sections covered during the 2007-2022 CWAC counts during summer (a) and winter (b) presented separately for each of the five primary dietary guilds.

curlew sandpiper and common greenshank) invertebrate feeders in the summer but only the first two groups in winter when the migratory waders have departed (Figure 9.14). The relatively high densities of waterbirds at Thesen Island marina come mainly from herbivores (Anatidae, mainly Egyptian goose and yellow-billed duck), resident invertebrate feeders (mainly common moorhen, blacksmith lapwing, African sacred and hadeda ibises, western cattle egret and Cape wagtail) and piscivores (mainly reed and Cape cormorants, grey heron and little egret). The highest densities of migratory waders outside Woodbourne Pan are, in descending order, at Rail Bridge-The Heads, Ashmead and White Bridge-Rail Bridge.

In conclusion, overall waterbirds are distributed fairly evenly across the Knysna wetland, which means that the largest sections (White Bridge-Rail Bridge, Rail Bridge-The Heads and Ashmead) support the highest numbers of birds. The small Woodbourne Pan and, to a lesser extent, the large Rail Bridge-The Heads sections though support disproportionately high densities of birds, and the Red Bridge-White Bridge and White-Bridge-Rail Bridge sections disproportionately low densities.

Particular waterbird species and groups show preferences for particular sections and with a few relatively minor exceptions these associations appear not to have changed substantially over time. There has also been relatively little change in the overall distribution of waterbirds comparing the periods 1993-1998 and 2007-2002, although the Ashmead-Thesen Island marina area appears to support an increased proportion of waterbirds during the latter period likely related to the transformation of Thesen Island from a terrestrial habitat to an aquatic marina. The dramatic decrease in summer migratory waders, especially in the Rail Bridge-The Heads section, should be noted and is of major concern.

9.8 Population trends

The 30 years of regular biannual CWAC counts provide particularly detailed insights into long-term population trends (Table 9.3). Eighteen species show significant increases in either summer, winter or both seasons, 11 species show decreasing trends, and 14 show no significant trends. The results for every species are not discussed here in detail and only the most striking and substantial changes are highlighted.

Waterfowl

Egyptian goose has increased significantly over the 30-year period (Figure 9.15). It is now among the top six most numerous waterbird species on Knysna Estuary (Table 9.1). The lowest number recorded, four birds, was during the first year of the counts, in the winter of 1993. Numbers increased initially rather slowly until 1999 after which a more rapid increase became evident. A notable increase occurred in the Thesen Island area when large expanses of planted lawns were established there during the start of the marina development in 2000 (L. Watt personal observations). There is a suggestion that numbers have stabilized since about 2006. The highest number counted was 604 birds (Table 9.1) in the summer of 2009. Early pre-1980 surveys make no mention of Egyptian goose on the estuary[6,10].

The increase in Egyptian geese in Knysna Estuary mirrors a broader and equally dramatic expansion across South Africa[20] and hence likely does not reflect any increase in the suitability of the estuary for this species but rather the ability of this adaptable bird to exploit anthropogenic landscapes, especially those that provide foraging opportunities, e.g. crop fields, cultivated pastures and lawns, etc. (Figure 9.16).

By contrast, the two next-most abundant waterfowl species, Cape shoveler and yellow-billed duck (Figure 9.17) both show significant decreases since 1990 (Figure 9.15). These two ducks both outnumbered Egyptian goose until about 2003. Their decreases could be at least partially due to aggression and competition from the increased numbers of Egyptian goose.

Migratory Palearctic waders

Five Palearctic migrants, grey plover, marsh and curlew sandpipers, little stint and ruff, have all undergone significant decreases in abundance on Knysna Estuary (Table 9.3, Figure 9.18). By contrast, four migratory waders, common ringed plover, Eurasian whimbrel, wood sandpiper and common greenshank, show no significant population trend.

The catastrophic decrease in curlew sandpiper (Figure 9.19) is particularly striking. Up until 2008 this species was present in summer in numbers frequently exceeding 1 000 birds, with a maximum of 3 205 recorded in 1998. However numbers in seven summer counts after 2015 did not exceed 400 birds and dropped further with only three birds counted in the summer of 2019. This species was

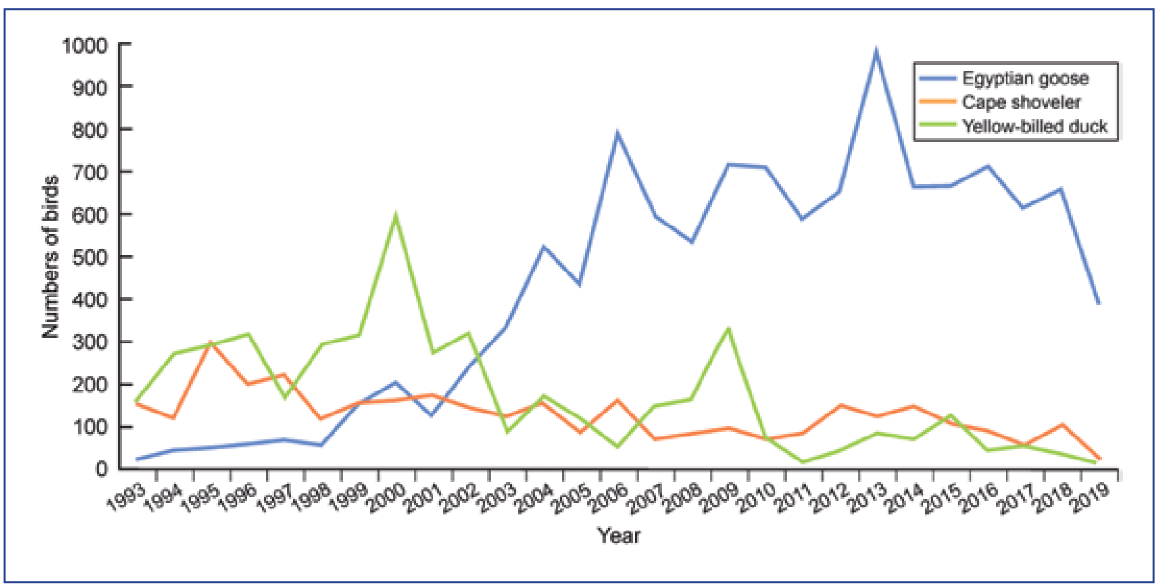

Figure 9.15 Long-term population trends for Egyptian goose, Cape shoveler and yellow-billed duck at Knysna estuary based on CWAC counts. Entries for each calendar year represent the sum of the annual summer and winter count for each year.

Figure 9.16 Egyptian goose is a relatively recent colonizer of the estuary where it is now one of the most abundant waterbird species. It likely forages widely in habitats surrounding the estuary but will also feed in the intertidal zone. Breeding is widespread as with this confiding pair at Thesen Island (Photograph: © David Allan).

Figure 9.17 Yellow-billed duck (shown here) and Cape shoveler were once the most abundant waterfowl on the estuary but they have been supplanted in recent years by Egyptian goose and both have decreased significantly (Photograph: © David Allan).

Table 9.3 Population trends for Knysna estuary waterbird species based on CWAC counts, including the season (summer/winter) for which the trend is apparent.

Significant increase	Grey plover (summer & winter)
Egyptian goose (summer & winter)	Kittlitz's plover (winter)
Red-billed teal (winter)	Marsh sandpiper (summer & winter)
Common moorhen (summer & winter)	Curlew sandpiper (summer & winter)
Little grebe (summer)	Little stint (summer)
Greater flamingo (winter)	Ruff (summer)
African oystercatcher (summer & winter)	Kelp gull (winter)
Blacksmith lapwing (winter)	Common tern (winter)
Three-banded plover (winter)	
African darter (summer)	**No significant trend**
Reed cormorant (summer)	Spur-winged goose
Cape cormorant (summer)	Cape teal
African sacred ibis (summer & winter)	Southern pochard
Hadeda ibis (summer & winter)	Great crested grebe
African spoonbill (summer & winter)	Black-winged stilt
Western cattle egret (summer & winter)	Pied avocet
Grey heron (summer)	Common ringed plover
Little egret (summer)	Eurasian whimbrel
Cape wagtail (summer & winter)	Wood sandpiper
	Common greenshank
Significant decrease	White-breasted cormorant
Cape shoveler (summer)	Purple heron
Yellow-billed duck (summer & winter)	Glossy ibis
Red-knobbed coot (summer & winter)	Pied kingfisher

once far and away the most abundant waterbird during summer counts and is now amongst the rarest.

Similar to the situation with Egyptian goose, the radical change in the abundance of curlew sandpiper in Knysna Estuary does not seem to be directly associated with any obvious shifts in the estuarine ecosystem itself. A dramatic decrease in this sandpiper has also been noted at other coastal waterbodies where this also appears unrelated to local habitat loss or degradation, e.g. Langebaan Lagoon[21], the Western Cape coastal region generally[22], the adjacent Wilderness Lakes (Russell in prep.) and Durban Bay[23,24]. As a long-distance non-breeding migrant the cause of the decreases in regional, and likely global, abundance of this species may primarily lie on the distant breeding grounds and/or on its migratory routes, and could be linked to climate change (affecting breeding habitats in the northern tundras) and plastic pollution (especially mesoplastics such as nurdles that wash up on shorelines, resembling fish eggs).

The number of little stints (37 birds) and common sandpipers (28) counted in January 1979[6] exceeds the highest numbers ever recorded in subsequent CWAC counts, 18 and 13 respectively (Table 9.1). This discrepancy accords with the overall decrease in many migratory waders at both Knysna Estuary and in South Africa generally.

Perception of the historical status of Eurasian curlew at Knysna Estuary, and indeed in southern Africa generally, is potentially controversial. This species was reported as common at Knysna Estuary

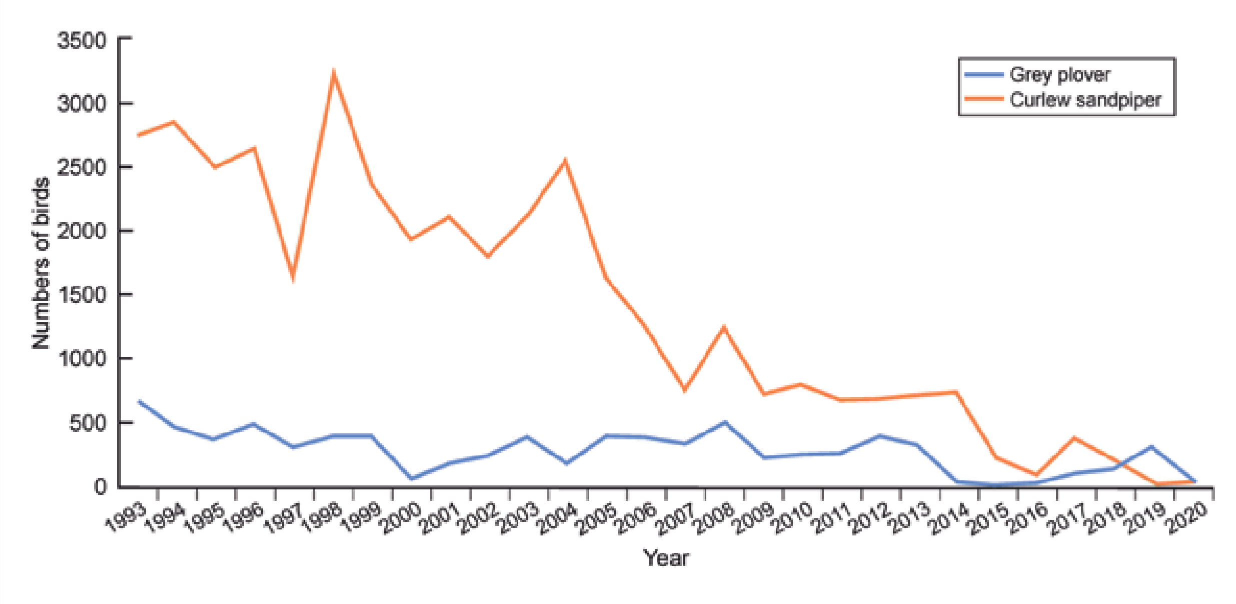

Figure 9.18 Long-term population trends for grey plover and curlew sandpiper at Knysna estuary based on CWAC counts. Entries for each calendar year represent only the summer count of each year.

Figure 9.19 Curlew sandpiper, a Palearctic migratory wader, was once far-and-away the most abundant waterbird on the estuary in summer. It has undergone a catastrophic regional decrease in recent years though and is now increasingly uncommon on the estuary (Photograph: © David Allan).

and at several other large estuaries along the south coast in 1934 - 35, including the Bot and Klein estuaries, and at the Keurbooms Estuary (Plettenberg Bay)[25]. By contrast, this source stated Eurasian whimbrel as much less common and restricted only to the Keurbooms. Sneyd-Taylor[26] reported Eurasian curlew as abundant at Knysna Estuary, with "130 to 150 individuals being counted at a time" in April to early May 1944. He also mentions numerous other records of the species at inland and coastal wetlands in the region. No mention though is made of Eurasian whimbrel, despite providing detailed discussion of all other Palearctic waders encountered. Records such as these have contributed to the conclusion that the Eurasian curlew was historically far more common in southern Africa than the Eurasian whimbrel but that this position reversed by about the middle of the last century[20,27]. This perception as to the ubiquity of the Eurasian curlew in the region dates back to at least Stark & Sclater[28] who stated that the Eurasian whimbrel is "much less plentiful" than the Eurasian curlew in South Africa.

Smithies[10] however discussing Eurasian curlew at Knysna estuary remarked that "Several people stated that there were plenty to be seen; the writer could never find them, and the parties of 'curlew' ... always turned out to be whimbrel", although he did note up to 13 feeding with Eurasian whimbrels towards the end of his observation period. He stated that Eurasian whimbrel was more abundant on the estuary and occurred in flocks of up to 34 birds (all his observations were made in winter). This was during the period May-August 1994, which overlaps with the observations of Sneyd-Taylor at Knysna Estuary as discussed above! It is hard not to suspect that the Eurasian whimbrel at Knysna Estuary (and elsewhere in southern Africa) may have been widely misidentified for the Eurasian curlew by many early observers, perhaps especially those from the United Kingdom where the latter species is the more common and widespread (and hence expected) species. The Eurasian curlew however breeds further south than the Eurasian whimbrel in Eurasia and therefore could have been more prone to disturbance and habitat loss on its nesting grounds.

Figure 9.20 Kittlitz's plover is the only resident Charadriformes wader showing a significant decrease (Photograph: © David Allan).

Resident Charadriformes waders

Resident Charadriformes waders have generally fared better at Knysna Estuary than migratory Palearctic waders (Table 9.3). African oystercatcher, blacksmith lapwing and three-banded plover have increased significantly since the early 1990s. Black-winged stilt and the largely nomadic pied avocet, however, show no change in abundance. Kittlitz's plover (Figure 9.20) is the only fairly common resident wader to show a significant decrease, which manifests during winter counts when the species is most common (Table 9.2). A small population of white-fronted plovers at Thesen Island was largely displaced by the marina development (Lorna Watt personal observations).

African oystercatcher has increased throughout its South Africa range in recent years, linked to the proliferation of an alien mussel and possibly also due to increased protection of its coastal habitat[29]. Blacksmith lapwing (Figure 9.21), like Egyptian goose, has increased substantially in South Africa linked to its exploitation of anthropogenic habitats and its proliferation at the estuary is likely linked to increasingly suitable conditions in surrounding areas rather than in the estuary itself. Smithies[10] 1944 account makes no mention of blacksmith lapwing on the estuary. The number of African oystercatcher (13 birds) and blacksmith lapwing (18) counted in January 1979[6] are lower than the lowest number recorded in all subsequent CWAC counts (28 and 21 respectively).

Large wading birds

The three most common members of the Threskiornithidae (ibises and spoonbills), African sacred and hadeda ibises, and African spoonbill, have all increased significantly (Table 9.3). The same applies to the three most common members of the Ardeidae (herons and egrets), grey heron and little and western cattle egrets, although the increase in the first two applies only to summer counts. It is likely that larger numbers of western cattle egrets roost on the estuary than are counted during the CWAC counts, as they typically fly upstream to

Figure 9.21 Blacksmith lapwing, like Egyptian goose and African sacred ibis, is a relatively recent colonizer of the estuary and likely makes extensive use of anthropogenic habitats surrounding the wetland (Photograph: © David Allan).

forage in farmland in the early morning before the counts are initiated (L. Watt personal observations).

The increase in African sacred ibis (Figure 9.22) is particularly marked and similar in scale to that of the Egyptian goose. Both ibis species have increased in South Africa, particularly in the Western Cape in recent times, benefiting from anthropogenic factors such as agriculture, irrigation and scavenging opportunities[20]. The increase in western cattle egret seems to date only from about 2010 onwards.

It is interesting to note that Smithies[10] 1944 account reported 1-4 yellow-billed storks on the estuary during March-April 1946. The only subsequent record is of a single bird in November 2020 (SARBN 9 Nov, 2020). Even more interesting is that Smithies makes no mention of either African sacred or hadeda ibises at Knysna Estuary, despite noting their presence elsewhere during his travels in South Africa. Nor was either species recorded during the comprehensive 1979 count[6].

Cormorants

The two most abundant of the three cormorant species, reed and Cape cormorants, show significant increases in summer counts (Table 9.3), although the winter Cape cormorant counts are also suggestive of an increase in recent times. Counts covering the entire 30 - year period show that overall both species are significantly more abundant during winter (Table 9.2). The significant summer increases in both species over time acts to diminish this seasonal difference. This is particularly apparent for reed cormorant, with summer counts increasingly approaching and even overlapping with winter counts over time. Summer counts of Cape cormorants were especially low until 2001, after which a notable overall increase is evident. The counts may underestimate the numbers of Cape cormorants as this species typically flies out of the estuary through The Heads in the early morning before the

Figure 9.22 This African sacred ibis scavenging offal at a picnic site at Leisure Isle, was accompanied by several conspecifics, as well as a large number of kelp gulls. It is an example of how several of the waterbirds that have recently colonized the estuary get at least some of their food from surrounding habitats outside the estuary itself (Photograph: © David Allan).

counts are initiated (L. Watt personal observations). It is interesting to note these increases in these fish-eating cormorants, along with other piscivorous birds such as African spoonbill, grey heron and little egret, in the face of apparently quite high human fishing pressure on the system.

The population of Cape cormorant in South Africa has shifted away from the west coast and towards the south coast over approximately the past three decades, following similar displacement of their main prey in South Africa, the epipelagic anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*[30]. The observed significant increase in Knysna Estuary is congruent with this overall population shift.

It is interesting to note that Smithies[10] suggested that in 1944 white-breasted cormorant was the most abundant cormorant occurring in numbers of up to "Three hundred or more" and apparently outnumbering reed and Cape cormorants. The maximum number recorded during CWAC counts was 119 (Table 9.1).

Kelp gull

Winter counts of kelp gull have decreased significantly (Table 9.3). Summer counts also suggest a long-term but less marked decrease. Counts covering the entire 30-year period show that overall this gull is significantly more abundant during winter (Table 9.2). The significant long-term decrease in winter counts acts to diminish this seasonal difference, with winter counts increasingly dropping closer to, and even below, summer counts over time.

Population trends by seasonality

The overall number of waterbirds on the estuary in summer has decreased (Figure 9.23), primarily due to decreases in Palearctic migratory waders, most notably curlew sandpiper. A major flood in November 1996 reduced waterbird numbers by about one-third in the following January 1997 count[7] as clearly evident in Figure 9.23. Major river flooding is known to remove the leaves of submerged estuarine plants such as eelgrass and to temporarily deplete both fish and invertebrate numbers in estuaries. By contrast, waterbird numbers in winter have increased driven mainly by winter increases in species such as Egyptian goose, African oystercatcher, blacksmith lapwing, African sacred and hadeda ibises, and African spoonbill. As a result of these opposing trends, the earlier pattern of summer abundance of waterbirds greatly exceeding winter abundance has been extensively narrowed over time and, if continued, shows indications of even reversing, as actually occurred for the first time in 2016 (Figure 9.23).

The long-term trend in waterbird population numbers at Knysna Estuary reflect an overall

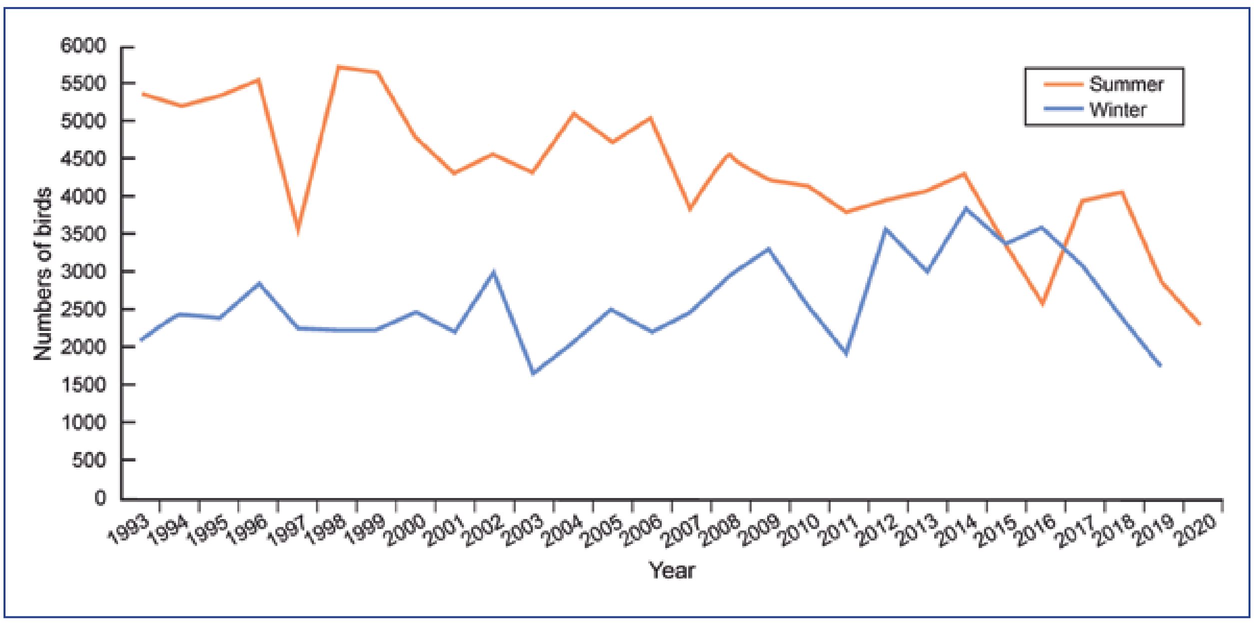

Figure 9.23 Long-term population trends by season for all waterbird species combined at Knysna estuary based on CWAC counts.

Figure 9.24 View of the Coney Glen Cape cormorant breeding colony in January 2022 when an estimated 105 pairs were actively nesting. The white staining of the upper rocks stems from cormorant excrement and reflects the long usage of this site by the birds (Photograph: © David Allan).

decrease, with the decrease in summer counts being greater than the increase in winter counts. Thus, there are fewer waterbirds present on the estuary as time passes. The last year considered in this review for which there was both a summer and a winter count (2019) had the lowest number of waterbirds ever counted, with a combined summer and winter total of 4 657 individuals, compared with the highest number of 8 439 in 1996.

A key point coming out of the discussion above though is that some of the most pronounced changes in abundance (related to both increases and decreases) by key species seem linked to regional and even global causal factors rather than being related to any obvious changes in the ecology of the estuary itself.

9.9 Breeding

Barring a few species, relatively little attention has been paid to the breeding status of the waterbirds of Knysna Estuary. There are 29 species that have been confirmed breeding and three are suspected breeders (Table 9.1 and African black duck as mentioned above), although supporting details are typically sparse or absent. There are several 'resident' species which seem likely to breed but for which nesting apparently requires confirmation, e.g. African rail, water thick-knee, three-banded plover and malachite and giant kingfishers.

Several breeding species, i.e. African darter, reed cormorant, African sacred ibis, African spoonbill, western cattle and little egrets, and grey and black-headed herons, typically nest colonially and there are a few such breeding colonies situated inland of the estuary shoreline (L. Watt personal observations) but these have not received detailed attention.

Breeding by several species is worthy of particular note, as discussed below.

African oystercatcher

The number of breeding pairs of African oystercatchers has increased in parallel with the increase in the total numbers counted[29,31]. Regular annual counts of breeding pairs over 25 years show a steady increase from 8 - 12 pairs in the first five years (1997-2002) of these counts to 16 - 28 pairs during 2016-2021[32].

The key breeding grounds comprise the Ashmead region north of Leisure Isle and the associated Thesen Island area[1,8]. It has been claimed that the increase in breeding pairs around Thesen Island is due to restricted access and hence reduced disturbance[33] but this requires confirmation as the human population on the island has greatly increased.

Threats to successful breeding include disturbance from fishermen, bait collectors and holidaymakers, and predation from kelp gulls, domestic

Table 9.4 Details of regional and global Red Data waterbird species recorded at Knysna Estuary. Migratory status; Mig. = Migratory, Res. = Resident. Numerical data come from CWAC counts; nc = not recorded during CWAC counts.

Red Data species	Red Data status regional	Red Data status global	Mig. status	% of counts	Summer avg.	Winter avg.	Overall avg.	Max.
Greater flamingo	Near-threatened	Least Concern	Res.	4%	0	0	<1	3
Eurasian curlew	Near-threatened	Near-threatened	Mig.	39%	2	0	1	8
Bar-tailed godwit	Least Concern	Near-threatened	Mig.	4%	0	0	<1	1
Red knot	Least Concern	Near-threatened	Mig.			nc		
Curlew sandpiper	Least Concern	Near-threatened	Mig.	71%	1 329	10	694	3 205
Caspian tern	Vulnerable	Least Concern	Res.	50%	1	1	1	6
Yellow-billed stork	Endangered	Least Concern	Res.			nc		
Black stork	Vulnerable	Least Concern	Res.	2%	0	0	<1	1
Cape gannet	Vulnerable	Endangered	Res.	2%	0	0	<1	5
Cape cormorant	Endangered	Endangered	Res.	96%	104	367	231	1 052
African marsh harrier	Endangered	Least Concern	Res.			nc		
Half-collared kingfisher	Near-threatened	Least Concern	Res.	9%	0	0	<1	4

dogs, feral cats and rats. Flooding of eggs during incubation by the occasional combination of strong winds and spring high tides, and runoff from storm-water drains during floods is a further threat. Hatching success was considered low, due to flooding, high-tide events and moderate levels of predation, but fledging success was high despite high levels of human disturbance.

Kelp gull

There is an early account of kelp gulls nesting from September-November on a "rocky island" at Knysna Heads[34], likely the Coney Glen offshore stack just off Eastern Head but this record lacks numbers or a precise date. Eight pairs bred in January 1979 at a Knysna "mainland" location corresponding with Western Head ("34° 05′ S, 23° 03′ E")[35,36]. A single pair bred at Thesen Island in October - December 1999 prior to its development[8] and another pair bred on Western Head in October 2012[36,37]. CWAC counts reflect breeding in most years during the period 2000-2022, with up to four pairs present.

Caspian tern

A record of apparent confirmed breeding dated 4 February 2004 from the CWAC counts is of note for this Red Data species but no further details are available and this record perhaps requires further substantiation.

Cape cormorant

The first record of Cape cormorants nesting on Coney Glen is from 1973 (number unrecorded) and the first record of nesting on Western Head is from September 2008 when 282 pairs nested[30,37]. The highest number of breeding pairs recorded on Western Head is 435 pairs in October 2012. The highest number of breeding pairs recorded on Coney Glen is 105 pairs in January 2022 (Figure 9.24)[37].

White-breasted cormorant

The first record of white-breasted cormorants nesting on Western Head is from November 1969 (three

Figure 9.25 Greater flamingo, a Red Data species, is an example of the large number of rare vagrant waterbirds that have been recorded at the estuary over time. It was recorded on only 4% of counts, with never more than three individuals being present (Photograph: © David Allan).

pairs), with 29 pairs in March 1981. The highest number of breeding pairs recorded on Western Head is 30 pairs in January 2022[37]. The first record of nesting on Coney Glen is from 1973 with 11 pairs, the highest number recorded at that locality[37,38].

9.10 Red Data species

Twelve of the waterbird species occurring on Knysna Estuary are Red Data species at a global and/or regional scale (Table 9.4)[39]. Three of these, red knot, yellow-billed stork and African marsh harrier, have not been recorded during regular CWAC counts and a further four species, greater flamingo (Figure 9.25), bar-tailed godwit, black stork and Cape gannet, have been recorded during less than 5% of counts. All of these seven species can be considered as rare vagrants.

Typical habitat for half-collared kingfisher, a species most frequently occurring in riverine areas along clear, fast-flowing rivers, is restricted to the uppermost reaches of the estuary and this species is therefore fairly marginal to the system as a whole. It has been recorded in only 9% of counts and is neither widespread nor abundant at Knysna Estuary. Eurasian curlew is a rare and highly localized bird in South Africa. It has been recorded on a surprisingly high proportion of counts on Knysna Estuary (39%), although never in numbers exceeding eight birds. Caspian tern has been recorded on 50% of counts but never exceeding six birds. Knysna Estuary cannot be considered a major stronghold of these three species.

The estuary supports, or at least in the past has supported, impressive numbers of the remaining two Red Data species, curlew sandpiper and Cape cormorant (Figure 9.26). Curlew sandpiper (globally 'Near-threatened') has decreased catastrophically. By contrast, Cape cormorant ('Endangered' both regionally and globally) has increased and in addition has significant breeding localities in The Heads area. The 435 breeding pairs at Western Head in 2012 represents nearly 1% (0.8%) of the current estimated South African breeding population[30].

Although not currently a Red Data species, African oystercatcher (Figure 9.27) was listed in the 2000 regional Red Data book[40] as 'Near-threatened' but was re-assessed as 'Least Concern' in the latest revision[41]. It is resident and has been recorded on every count. The average number counted is 65 birds, over 1% of the estimated global population of 5 000 - 6 000 individuals, and with a maximum of 148 present. Up to 29 breeding pairs are recorded annually[32]. Knysna Estuary thus provides critical habitat for this endemic and highly habitat-specific southern African shorebird.

9.11 Potential Important Bird and Biodiversity Area and Ramsar status

Knysna Estuary is not listed as either a global or subregional Important Bird and Biodiversity Area (IBA)[42,43] nor is it listed as a Ramsar site (https://www.ramsar.org/). However, elements of its waterbird populations meet criteria for inclusion in both these listings.

The regular occurrence, including increasing abundance and local breeding, of Cape cormorant as a globally Endangered species would qualify the estuary as a global IBA, especially given the relatively large numbers of birds involved. The same likely no longer applies to the curlew sandpiper, which, although still regularly present, now only occurs in relatively low numbers.

Relevant to non-threatened waterbird species, the criteria for global and subregional IBA status are determined by numerical thresholds: (https://wpp.wetlands.org/explore?publication=5). The average number of African oystercatchers counted, 65 birds (Table 9.1), exceeds the global threshold of 55 birds or 1% of the global population. The average number of kelp gulls, 370 birds, exceeds the subregional threshold of 350 birds. Counts of black-winged stilt have 'regularly' (defined as more than once in five years) exceeded the subregional threshold of 105 birds. It should be noted that numbers of curlew sandpiper exceeded the subregional threshold of 2000 birds in nine of the first 12 years of summer counts during 1993-2004 but not subsequently.

The Ramsar Convention also employs criteria relevant to waterbirds in terms of both threatened species (although only those classed as Vulnerable, Endangered or Critically Endangered) and numerical thresholds in assessing wetlands of international importance. These waterbird criteria overlap with the global IBA criteria and both Cape cormorant and African oystercatcher populations at Knysna Estuary meet Ramsar criteria. That Knysna Estuary is a National Park would seem to further motivate for its listing under both schemes.

Figure 9.26 The endemic Cape cormorant is a globally threatened species and the estuary provides critical habitat for this species. It has increased at the estuary concomitant with a shift in its population from the west coast of South Africa to the south coast. There is an important breeding colony established in The Heads area (Photograph: © David Allan).

Figure 9.27 This handsome African oystercatcher, on the intertidal flats in the Ashmead Channel area, is a flagship waterbird of the estuary. Knysna estuary supports a globally important population of these endemic birds, which have increased in abundance and breed regularly and successfully (Photograph: © David Allan).

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Clouds and sky reflected in the Knysna Lagoon (Photograph: © George Branch).

Chapter 10 : Climate change and the Knysna Estuary

Nicola James, Lara van Niekerk & Stephen Lamberth

10.1 Introduction

Estuaries are shallow coastal environments that are influenced by both tidal action and freshwater inflow. As a result of the mixing of marine and fresh waters, estuaries are naturally dynamic, unstable environments with physico-chemical conditions oscillating on hourly, daily, seasonal, yearly and decadal scales[1]. Climate change is expected to modify the physical structure and biological functioning of estuaries, by changing the magnitude of these oscillations, as well as changing long-term average physico-chemical conditions (such as average temperature, salinity and dissolved oxygen levels). In addition to rising temperatures, climate change in the coastal and estuarine environment also incorporates changes in temperature variability (land and sea), winds and ocean currents, freshwater flow (rainfall), extreme weather events, sea level and ocean acidification; all of which will have profound consequences for species living in estuaries.

In this chapter these different drivers of change, such as temperature, rainfall and hydrology, floods and droughts, sea level rise, storm surges and ocean acidification are reviewed with a focus on the effects of these drivers of change on the Knysna Estuary.

10.2 Temperature

Estuaries are affected by changes in air, river and sea temperatures. Globally, the average surface temperature has increased by 1.1°C compared to the average temperature in 1850 - 1900, which is the hottest level since 125 000 years ago[2]. Land-based air temperatures have been rising significantly over Africa; with temperature increases over subtropical southern Africa (which have increased by 3.2°C in the last 100 years) more than twice the global land-based air temperature increase[3]. Annual air temperatures over the coastline of South Africa are predicted to be between 2.5 and 4°C warmer in 2100 than they are today[3] (Figure 10.1).

A Representative Concentration Pathway (RCP) is a greenhouse gas concentration trajectory adopted by the Intergovernmental Panel on Climate Change (IPCC). For example, RCP 8.5 refers to the

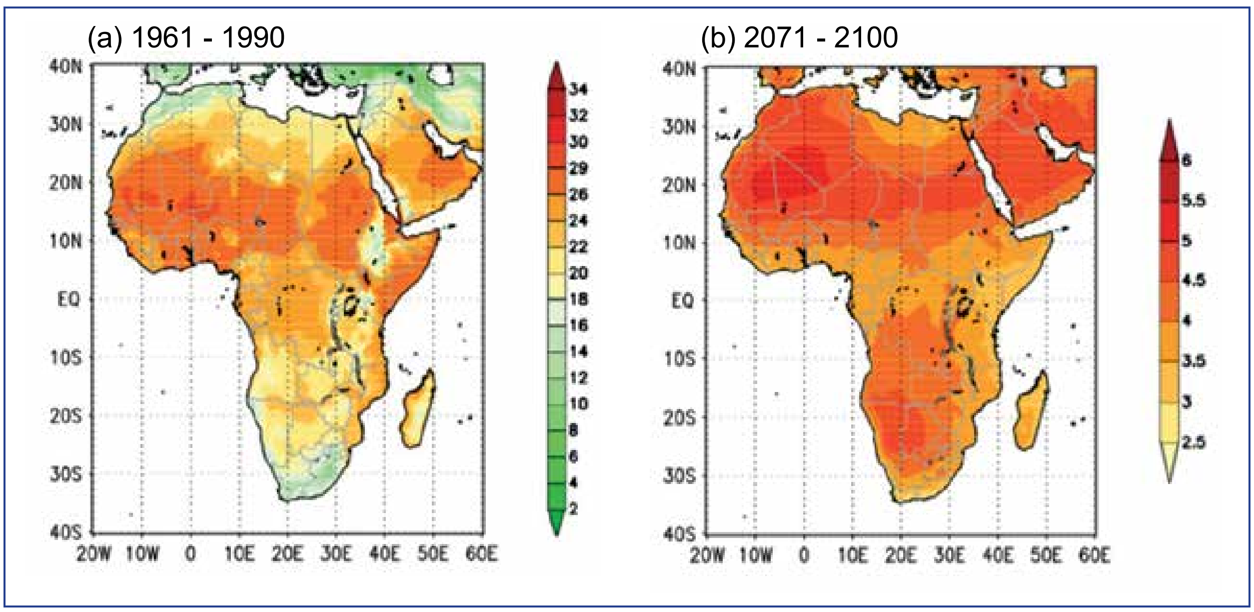

Figure 10.1 Modelled (a) average annual maximum air temperatures (°C) for 1961-1990 and (b) projected change in annual average temperature for 2071-2100 relative to 1961-1990 (after Engelbrecht et al.[3]).

concentration of carbon that delivers global warming at an average of 8.5 watts per square meter across the planet. To provide some indication of the potential increase in temperatures predicted for the Knysna Estuary, Table 10.1 below summarises the findings for Representative Concentration Pathways 4.5 and 8.5 (RCP 4.5 and 8.5) downscaled for South Africa as part of the 'Green Book' project based on Englebrecht et al.[3]. The model simulations span the period 1960 - 2100, with the period 1960 - 1990 representing the baseline, 2021 - 2050 mid-future and 2070 - 2099 far-future. RCP 4.5 is a high mitigation scenario, whilst RCP 8.5 is a low mitigation scenario. These projections show that even under future scenarios with substantial climate mitigation interventions as represented here by RCP 4.5, predicted increases in average monthly land temperatures will vary between 1.1°C and 1.9°C in the mid-future, increasing further to between 1.3°C to 2.6°C in the far-future. While under the RCP 8.5 low mitigation scenario temperatures increase by between 1.4°C and 2.4°C for the mid-future and 3.4°C and 4.1°C for the far-future.

Rising air temperatures will likely be beneficial to some tidally inundated salt marsh species in estuaries, with their productivity predicted to increase in response to rising air temperatures until an upper threshold temperature is reached. In contrast, rising air temperatures may inhibit the germination of other plant species and thus cancel out the beneficial effect of increasing productivity[4].

As surface air temperatures increase, so do sea, estuary and river water temperatures and by the beginning of the next century, sea temperatures globally may have increased by 2°C relative to temperatures at the beginning of this century[5]. Temperature is one of the biggest drivers of change affecting marine animals, mainly because marine animals are ectotherms (their temperature regulation comes from outside their bodies), with water temperature determining their distribution on a global and regional scale. In South African estuaries, at a regional scale, the distribution of estuary-associated marine biota is strongly linked to marine water temperatures rather than estuarine water temperatures[6].

The coast of South Africa has four distinct biogeo graphic zones, a tropical transition zone, a subtropical zone, a warm-temperate zone and a cool-temperate zone[7]. Sea temperatures decrease from the tropical region (northern KwaZulu-Natal) to the cool-temperate region on the Atlantic west coast, with inshore water temperatures decreasing markedly southwest of Algoa Bay. In this region, the continental shelf broadens into the wide Agulhas Bank and the warm Agulhas Current (which flows along the edge of the continental shelf) is located further offshore (Figure 10.2).

Inshore waters in this region in summer can be substantially cooler than water in the warm Agulhas Current when upwelling occurs. Upwelling occurs when southerly winds drive cooler water from the deep towards the surface. Upwelling can result in rapid temperature changes, with inshore waters at least 5°C cooler than the surrounding Agulhas Current shelf water[8]. In contrast, water temperatures are often similar in estuaries throughout South Africa. For example, in mid-summer, temperatures in estuaries in Durban may be very similar to those recorded in the Knysna Estuary.

Few species occur in all estuaries in South Africa, with many species occurring within specific biogeographic zones. Harrison[9] recorded differences in the fish found in estuaries around the South African coastline, with a gradual decrease in the number of species recorded in estuaries from east to west, mainly as a result of the decreasing number of tropical marine species recorded in warm- and cool-temperate estuaries. Cool-temperate estuaries are mainly dominated by cool-water endemic (i.e. occur only in southern Africa) species and temperate species. Warm-temperate estuaries are dominated by warm-water endemic species that also extend their distribution into subtropical estuaries, as well as cool-water endemic species. Tropical and subtropical estuaries are dominated

Table 10.1 Predicted increase in ambient atmospheric average temperature (°C) for RCP 4.5 and 8.5 under mid- and far-future scenarios.

Average temperature increase	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
RCP 4.5 Mid-future	1.6	1.3	1.3	1.7	1.1	1.8	1.4	1.3	1.5	1.5	1.3	1.9
RCP 4.5 Far-future	2.0	1.8	1.5	1.9	1.3	1.8	2.1	2.2	2.4	2.2	1.7	2.6
RCP 8.5 Mid-future	1.9	1.6	1.4	2.0	1.5	2.4	2.1	1.7	1.9	2.3	2.2	2.2
RCP 8.5 Far-future	4.0	3.5	3.6	3.6	4.1	4.1	3.8	3.4	3.6	3.7	3.8	3.7

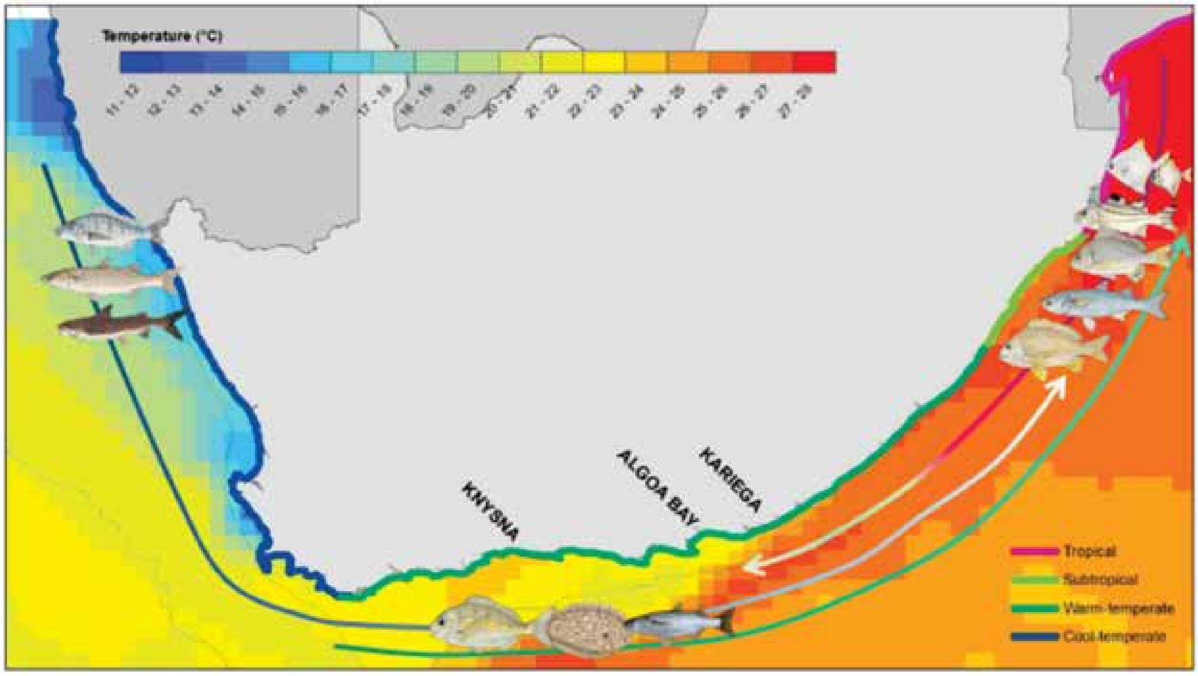

Figure 10.2 Summer sea temperatures, biogeographic regions and the distribution of tropical, warm-water endemic and cool-water endemic fish in South African estuaries (modified from James et al.[6]).

by subtropical species that occur in both subtropical and warm-temperate estuaries, as well as tropical Indo-Pacific species[10]. Prior to the past 30 years, tropical Indo-Pacific species were rarely recorded in temperate estuaries beyond Algoa Bay.

For most estuary-associated marine animals, larval development takes place in the marine environment, with the tolerance of biota to temperatures often being much lower during the adult and larval phase than during the hardy juvenile phase that occurs in estuaries. Warming marine temperatures associated with climate change have already resulted in an increase in the occurrence of tropical fish and invertebrate species in warm-temperate estuaries[1,11]. When tropical species extend their distribution into temperate estuaries, winter survival is often the bottleneck in the establishment of populations in these waters. Elevated winter temperatures associated with climate change may allow tropical species to overwinter and become established in these temperate systems.

The above said, we cannot associate all new occurrences or increases in abundance with rising temperatures. Many of the warm- and cool-temperate occurrences of tropical and subtropical estuarine associated species coincide with the unavailability of estuarine habitat in the subtropical region during extended drought periods and estuary mouth closure. More recently, extreme events such as floods and marine heatwaves seem to play a role in forcing fish and invertebrates southward.

Invertebrate species with a primarily tropical distribution (such as mud crab *Scylla serrata*, the peregrine paddler crab *Varuna litterata* and the mangrove snail *Cerithidea decollata*) are good indicators of global warming in the Knysna Estuary. Mud crabs occur in the Knysna Estuary but are absent from cool temperate estuaries (for biogeographic zones see Figure 10.2). Low water temperatures affect mud crabs, with feeding and movements stopping in temperatures lower than 12°C[11,12]. Warming water temperatures, particularly in winter in the Knysna Estuary, may increase the amount of habitat available for this species leading to an increase in the abundance of mud crab in the estuary—albeit confined to the areas of high mud distribution (e.g. Belvedere). The mangrove snail, as its name suggests, is associated with mangroves throughout its main range. This species has extended its distribution into the Knysna Estuary, where it escapes the high tide by climbing the rush *Juncus kraussi* rather than the trunks of mangrove trees[11]. On the other hand, the presence of *Varuna litterata* in Knysna Estuary does not seem to be primarily in response to rising temperatures. This crab has extended its range all the way to estuaries in the cool-temperate

False Bay, with an established population in the Zeekoeivlei Estuarine Lake. More recently, it has been recorded to the west of Cape Point in the Rietvlei Diep Estuary in Table Bay. Its occurrence in Knysna and estuaries to the west coincides with an increase in the frequency of eddies generated by the Agulhas Current, which carry and entrain warmer water species westwards to the cool-temperate coast.

An increase in the frequency and intensity of upwelling in the coastal nearshore in summer may, however, prevent range expansions of tropical species into the Knysna Estuary (by killing the larvae of tropical species before they can recruit into the mouth of the estuary). Duncan et al.[19] found that the intensity of upwelling has increased in recent years along the nearby Tsitsikamma coastline. Upwelling can affect water temperatures in the mouth and lower reaches of permanently open estuaries. Indeed, van der Walt et al.[14] measured thermal variability in the lower reaches of the Kariega Estuary on our southeast coastline (Figure 10.2) and found that when upwelling occurs in the marine environment the influx of cold upwelled water on the high tide can rapidly decrease water temperatures in this region of the estuary from 22°C to 17°C (difference of 5°C). In the middle and upper reaches of the estuary,temperatures did not drop below 24°C[14], with these reaches offering a refuge to animals from extreme temperature variability. The middle and upper reaches of the Knysna Estuary may also provide an important thermal refuge to species in the estuary as well as those from the marine environment, with fish such as baardman *Umbrina robinsoni* finding refuge inthe warmer waters of the estuary during upwelling events (Chapter 8).

During the estuarine phase of their life cycle, biota are able to tolerate both very high and very low temperatures and it is unlikely that warming will impact the distribution of biota already resident within the estuary. Temperatures within estuaries fluctuate hourly, with temperatures of up to 30°C recorded in the shallow littoral zone in the lower reaches of the warm-temperate Kariega Estuary in summer[14]. During their juvenile stage, when fish use estuaries as nurseries, fishes are very tolerant of high temperatures. Bennett[15] found that approximately 70% of juvenile tropical fishes (44 species) inhabiting shallow water nursery areas (mangroves, seagrass and tide pools) around Hoga Island in Indonesia are able to tolerate temperatures above 40°C. In the Kariega Estuary, juvenile mullet and sparids, with a predominantly temperate and subtropical distribution (e.g. southern mullet *Chelon richardsonii* and Cape stumpnose *Rhabdosargus holubi*) are able to tolerate temperatures up to 35°C, which is five degrees above the maximum water temperature recorded in the estuary[14] (Figure 10.3).

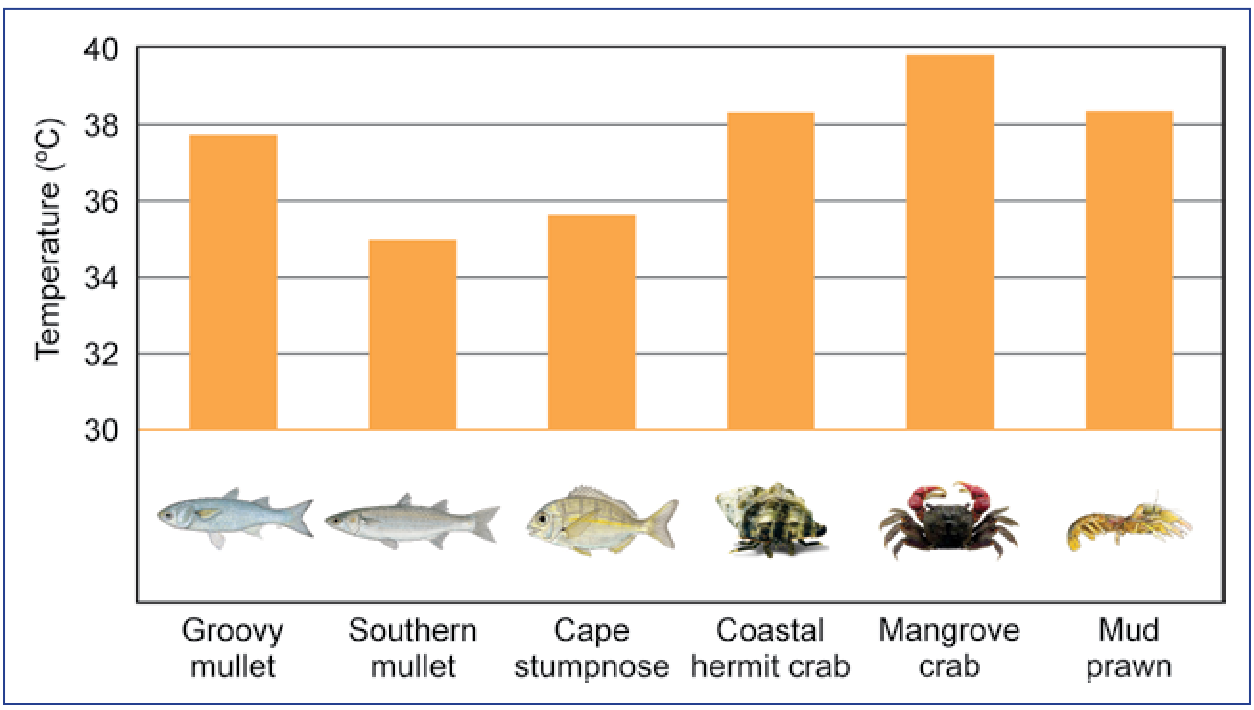

Figure 10.3 Critical thermal maxima (orange bars) limits of fish and invertebrates and maximum water temperature (orange line) in the warm-temperate Kariega Estuary.

These species, which are abundant in the Knysna Estuary, are also tolerant of low temperatures in winter and can tolerate temperatures as low as 5°C, which is well below the 12°C minimum winter temperature recorded in the estuary[14] (Figure 10.4). Resident estuarine species, such as clinids and gobies may be even more tolerant of extreme temperatures (e.g. above 40°C).

Van der Walt et al.[14] also found that the adults of three common estuarine-associated invertebrates; coastal hermit crab *Clibanarius virescens*, mangrove crab *Parasesarma catenatum* and mud prawn *Upogebia africana* from the lower reaches of the Kariega Estuary are able to tolerate temperatures as high as 39°C in summer and as low as 4°C in winter (Figures 10.3 & 10.4). The broad temperature tolerance of many marine intertidal rocky shore invertebrates is well known, with several species able to depress their metabolism to cope with the stresses associated with tidal emersion and exposure[14]. However, similar information on estuarine intertidal invertebrates of mud and sand flats is much less well known.

Although estuarine water temperatures may continue to be within the temperature tolerance of estuarine biota, warmer water associated with global warming (and particularly extreme temperatures during heatwaves) may still be stressful for them when outside the temperature optima for that species and can lead to species declines. In the San Francisco Estuary in America, population declines in the endangered delta smelt (*Hypomesus transpacificus*), which is a small shoaling fish, have been linked in part to warm temperatures during summer heatwaves[16]. Warm water was associated with behavioral changes in delta smelt. Warm water increased the swimming speed of delta smelt and changed their schooling behaviour so that they swam further apart and were less protected in a group. These behavioural changes made these fish easier for predators to attack, with double the number of fish injured and preyed on in warmer water[16].

Similarly, Mvungi & Pillay[17] when working on the combined effects of warming and eutrophication on seagrass *Zostera capensis* from the Langebaan Lagoon in the Western Cape found that eutrophication and temperatures higher than 24°C negatively affected plant size, density and growth. They suggested that this was likely as a result of nutrient enrichment and warming induced bio-fouling (Figure 10.5), which negatively impacted photosynthesis. *Zostera capensis* is a temperate seagrass species that is widespread in South Africa and a particularly important habitat-forming species in Knysna. Studies have shown that temperatures higher than 25°C can also have negative effects on other temperate seagrass species[17].

It is extreme temperatures (rather than gradually

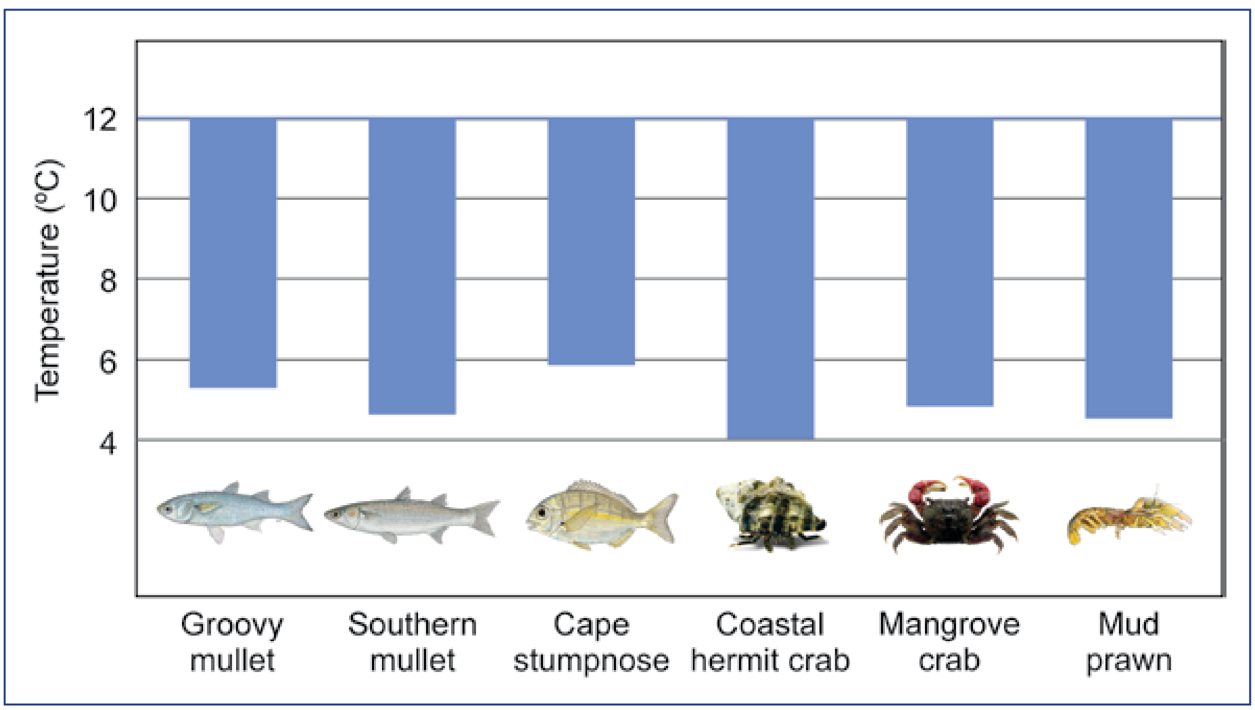

Figure 10.4 Critical thermal minima (blue bars) limits of fish and invertebrates and minimum water temperature (blue line) recorded in the warm-temperate Kariega Estuary.

Figure 10.5 Biofouled eelgrass *Zostera capensis* in the Swartkops Estuary
(Photograph: ©Thembani Mkhize).

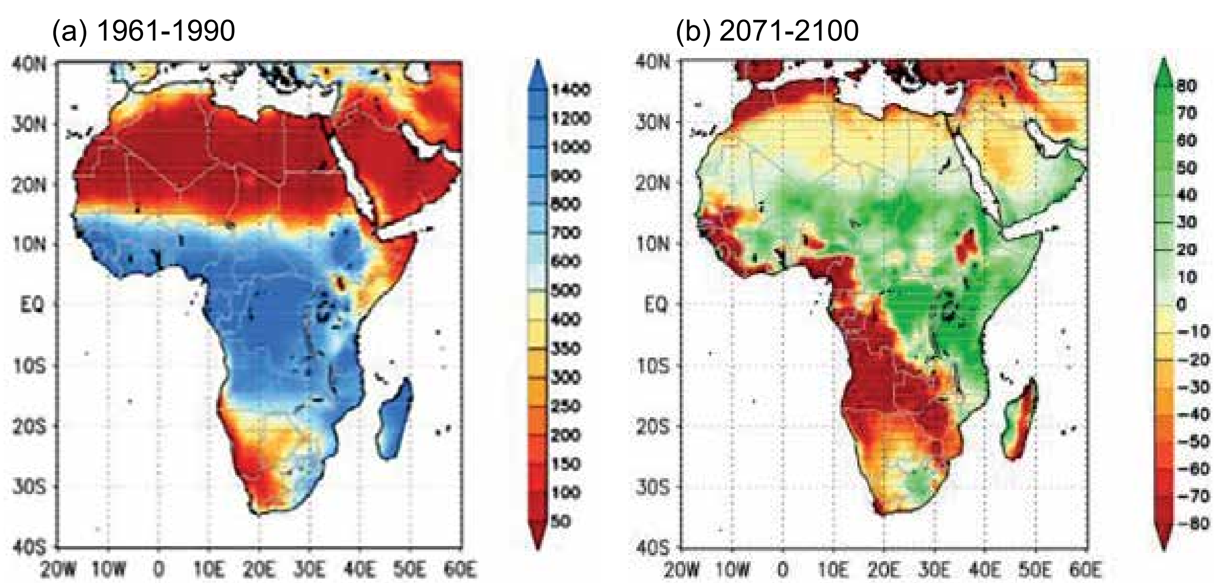

Figure 10.6 Modelled (a) annual average number of heatwave days for 1961-1990 and
(b) projected change in annual average number of heatwave days for 2071-2100 relative to 1961-1990
(after Engelbrecht et al.[3]).

increasing average temperatures) that animals and plants do not cope with well. Southern Africa already has more heatwave days per year than the rest of Africa, with the number of heatwave days predicted to increase by the end of the century[3] (Figure 10.6). In the marine environment, marine heatwaves along the warm-temperate coastline (which includes Knysna) are more intense and of longer duration than those along the cool-temperate and subtropical coastline[18]. Marine heatwaves in this region arise from deviations in the Agulhas Current bringing warm water inshore, as well as the shape and extent of the shelf in the region. Within a recent five-year period (2013 – 2018), 16 marine heatwaves occurred in the inshore region of the warm-temperate Kenton-on-Sea, with the hottest marine heatwave attaining 28.4°C, and the longest heatwave lasting 18 days[19].

Extreme variability in temperatures is often lethal to fish. A recent regionally extensive marine heatwave event was recorded along the South African east coast at the end of summer 2021, coinciding with a >120 km meander of the Agulhas Current driving warm surface as well as cold upwelled water inshore. In this event, temperatures as high as 24.0 – 26.0°C occurred for several days, followed by an upwelling event, with temperatures rapidly decreasing to as low as 10°C. Thermal shock from the temperature difference, stunned fish and invertebrates, resulting in extensive fish and invertebrate washouts and kills[19,20]. There were also reports of aggregations of fish, sharks and rays finding refuge from both warm and cold water in estuaries and the nearshore.

The heatwave also resulted in dieback of the spined kelp *Ecklonia radiata* near Wavecrest on the Wild Coast and bleaching of red algae (*Plocamium corralorhiza*) in shallow rocky areas around Gqeberha (Figure 10.7). The latter species is also found in rocky areas of the Knysna Estuary. Although the effects of extended heatwaves have not been recorded in South African estuaries, an increase in these events may have severe consequences for estuarine plants and animals, especially in the extensive intertidal areas that are characteristic of the Knysna Estuary.

10.3 Rainfall and hydrology

Climate change is already altering rainfall patterns, with changes in rainfall affecting the amount and timing of freshwater entering estuaries. These changes are exacerbated in estuaries where humans have modified freshwater delivery through freshwater abstraction[1]. Average monthly rainfall in the Knysna region is between 600 and 700 mm per year, with this region predicted to be drier (an increase in dry days and rainfall variability) by the end of the century[3,21] (Figure 10.8). Historical estimates of flow reduction indicate that the natural mean annual runoff of 83.2×10^6 m^3 a^{-1} has been reduced by less than 20%, but of concern is that most of this impact resulted from a loss of baseflows[22]. This observation, and more recent data, indicate these global change impacts are greater than previously estimated[23]. This is concerning as freshwater inflow into the Knysna Estuary has shown a clear decreasing trend with time, with low flow conditions (<2.0 m^3 s^{-1}) occurring 80% of the time during the period 2005 - 2018.

While the estuary is naturally marine dominated (meaning that there is not much gradient between salty and freshwater) due to its extensive tidal amplitude, conditions in which there is no gradient are estimated to have increased from 6% to 45% of the time[23] (depicted in Figure 10.9). As the impacts of global and climate change intensifies, marine conditions may become the dominant state for the estuary. For example, Cullis et al.[24] indicate that the median flows are likely to decrease by about 10%, with low flows decreasing even more by between 12 and 15% and floods by about 5%. These predicted changes do not include the amplification effects of ongoing and escalating abstraction.

Largier et al.[25] defined three different water regimes in the estuary: the “bay regime” which is characterized by marine salinities above 34 ppt; the “estuary regime” which, although also marine dominated (salinities between 30 – 34 ppt), is warmer due to water retention in a shallow basin; and the “estuary regime” where river inflow influences salinity and temperature. This regime is characterized by lower salinity water (salinities <30 ppt). Further decreases in river inflow will further shrink the “estuary regime” and restrict it to just the uppermost region of the estuary during periods of river inflow. Under drought conditions, even this small gradient is lost and the system becomes an arm of the sea throughout, losing its estuarine character.

Effluent from the wastewater treatment works is discharged into the Ashmead Channel. In response to these growing discharges, water quality in the channel has been deteriorating over time, with eutrophication, low dissolved oxygen concentrations, and the development of nuisance macro and microalgal blooms becoming a more common occurrence[23]. A decrease in rainfall associated with climate change, as well as warming of estuarine waters, could also exacerbate poor water quality in this region of the system.

Further decreases in freshwater flow threaten

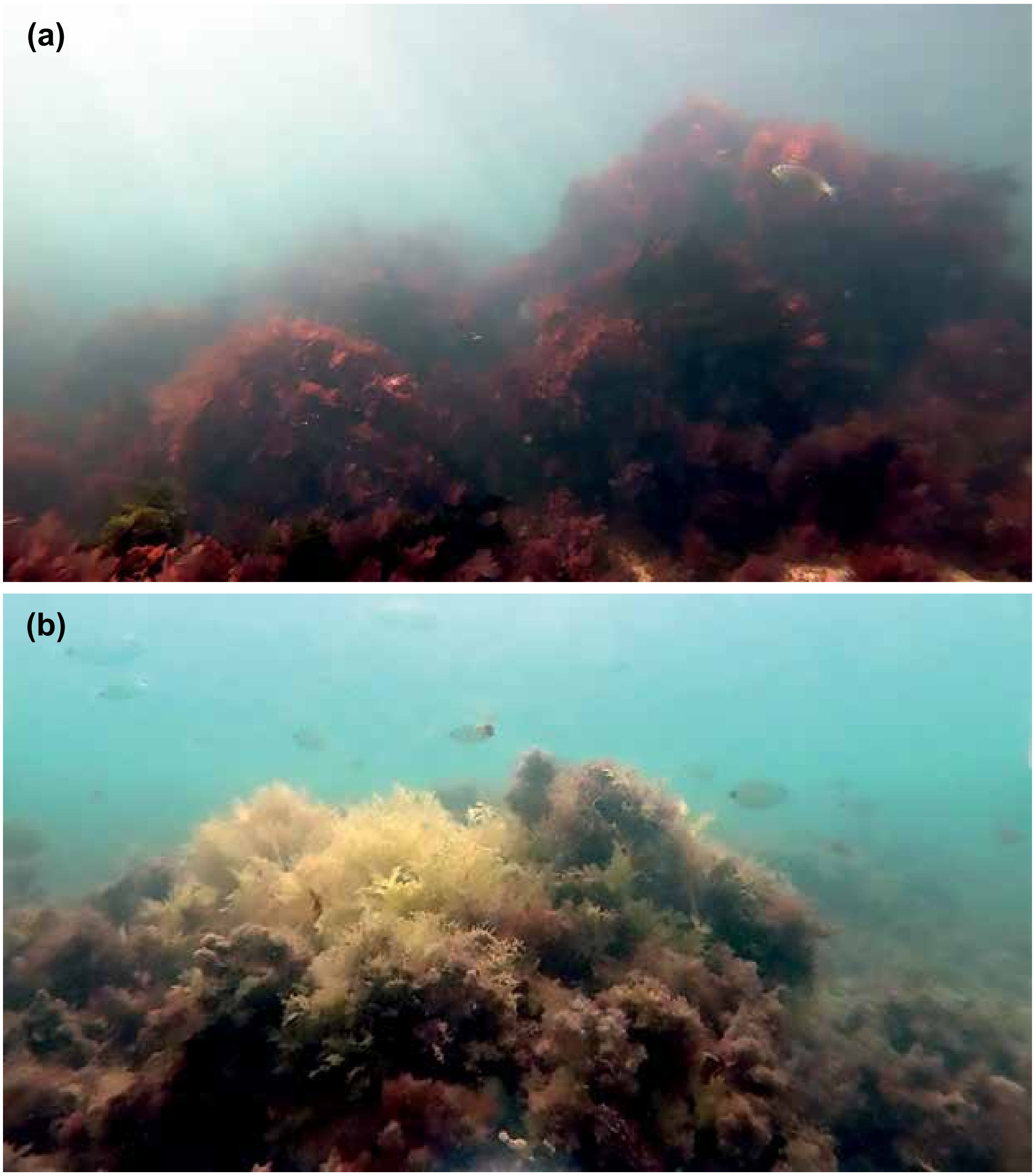

Figure 10.7 Healthy *Plocamium corallorhiza* (a) and bleached *P. corallorhiza* (b). This red alga is found in The Heads region of the Knysna Estuary and may also be susceptible to bleaching due to extended heat waves in the future (Photographs: © Mihle Gayiza).

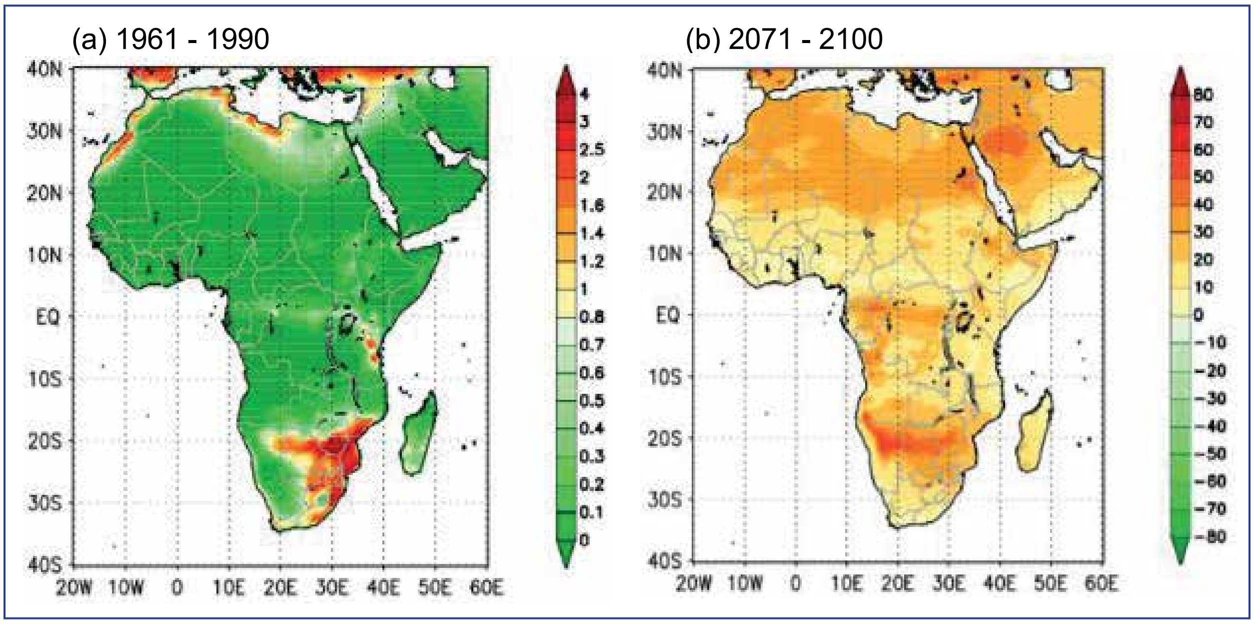

Figure 10.8 Modelled (a) annual average rainfall totals (mm) for 1961-1990 and (b) projected change in annual average rainfall (mm) for 2071-2100 relative to 1961-1990 (after Engelbrecht et al.[3]).

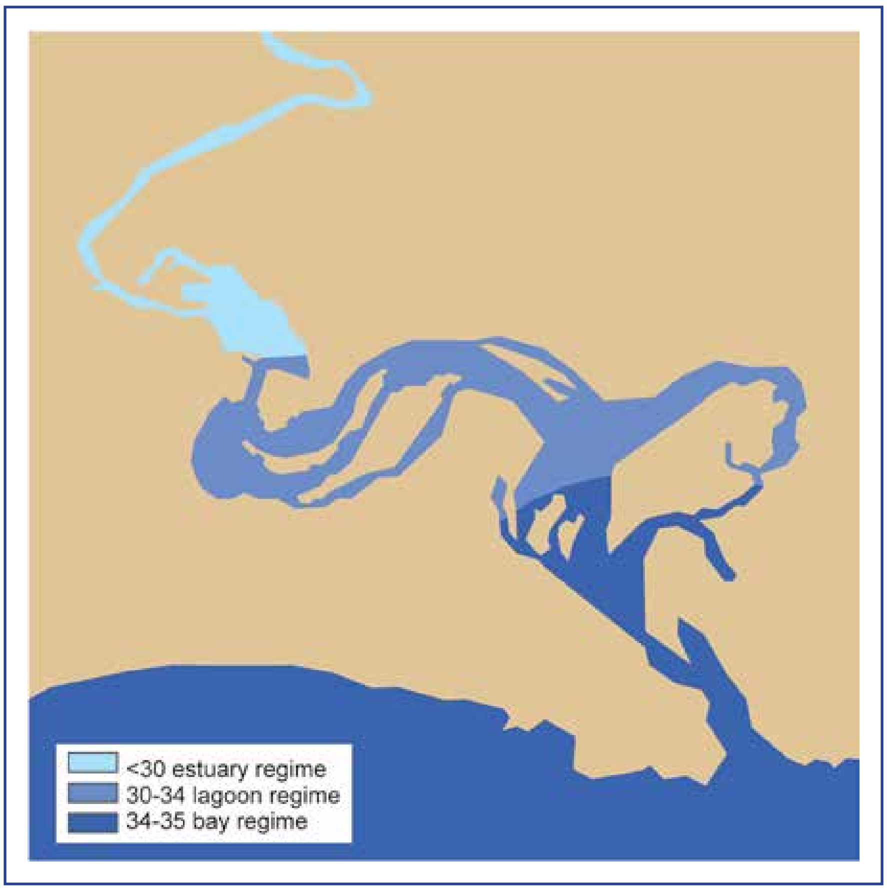

Figure 10.9 Average monthly surface salinity from 2016 to 2018 (data from Claassens et al.[21]).

the ecological functioning of the estuary, particularly in the upper reaches, where there is no longer a river estuary interface zone[23]. Salinity gradients in estuaries, that are directly dependent on freshwater flow, are regarded as one of the key determinants of estuarine species composition and productivity. The juveniles of marine fish species are adapted to a wide range of salinities and dominate estuaries throughout the salinity gradient, but are particularly abundant in the fresher middle and upper reaches. In contrast, marine stragglers that cannot tolerate the fluctuating salinities are confined to the lower reaches. Indigenous freshwater fish species such as Cape kurper *Sandelia capensis*, Cape galaxias *Galaxias zebratus* and redfins *Pseudobarbus* spp. occur in the river immediately above the estuary but only the non-native and salt tolerant mosquito fish *Gambusia affinis* has been recorded in the Knysna Estuary shallows.

A study of demersal fish assemblages in the marine-dominated Kariega Estuary following a major river flood event demonstrated the importance of adequate freshwater flow for estuarine productivity and functioning[26]. Similar to Knysna, the Kariega Estuary receives a proportionally limited amount of freshwater on a daily tidal basis, primarily because of both freshwater abstraction and prolonged drought conditions in the Kariega catchment. Although species richness is high in this estuary, with many marine straggler species recorded, the abundance of juvenile estuarine-associated species — particularly the important fishery species spotted grunter (*Pomadasys commersonnii*) and dusky kob (*Argyrosomus japonicus*) — is low. Following a major 1 in 100 year flood in the estuary, a normal estuarine salinity and turbidity gradient was re-established, and zooplankton productivity increased substantially in response. Euryhaline marine fish species responded to this increase in turbidity and productivity, particularly the early juveniles which prey on zooplankton. This led to a strong recovery in the populations of spotted grunter and dusky kob within the Kariega Estuary[26]. These results highlight the importance of maintaining river flow into the Knysna Estuary where these fishery fish species are also present.

10.4 Floods and droughts

The frequency and intensity of extreme events, such as droughts, sea storms and river floods is already increasing along the southern African coastline[1]. When large floods occur in the Knysna system, low salinity water extends all the way to the mouth and out to sea[25]. During floods, a considerable amount of polluted nutrient-rich stormwater discharge also enters the Ashmead Channel via the Bongani catchment[23]. An increase in the occurrence of extreme discharge events such as floods is likely to increase silt, nutrient input and turbidity to the system and could impact *Zostera capensis* beds in the estuary. Flooding can also result in the temporary loss of seagrass, which will have a direct impact on species using this important habitat such as crustaceans, gastropods and juvenile fish, including the critically endangered pulmonate limpet *Siphonaria compressa* and the Knysna seahorse *Hippocampus capensis*.

During droughts, river inflow is negligible and as a result, the estuary regime zone shrinks so that it occupies only a small proportion of the uppermost estuary[25]. The water residence times also increases in the estuarine and lagoon regime during drought conditions, potentially enhancing the effect of increased land surface temperatures and leaving the system more vulnerable to pollution and potentially resulting in warmer upper reaches.

In estuaries where sampling has been conducted after major flooding, recovery of the zooplankton, invertebrate and fish to pre-flood conditions (in terms of species composition and abundance) was fairly rapid. However, after consecutive flood events, recovery was less rapid[27]. Significantly, where floods and droughts result in prolonged loss of available habitat (habitat squeeze), species declines occur. In the much smaller intermittently open East Kleinemonde Estuary a decline in the abundance of marine species over a 20-year period was attributed to an increase in the intensity and duration of floods and droughts affecting the availability of subtidal habitat for fishes[28]. Similar responses (loss of subtidal habitat) can be expected in the Knysna Estuary under the increase in extreme events (drought and floods) predicted for a hotter climate.

10.5 Sea level rise and storm surges

Several climate models project an accelerated rate of sea level rise over the coming decades, with tide gauge data from the southern Cape showing that sea level has risen by approximately 1.57 mm per year[29]. Of all climate-induced changes sea-level rise, in combination with anthropogenic impacts on sediment supply, is seen as the greatest threat to salt marsh habitats in estuaries[30]. Salt marshes on a local scale are capable of responding to this threat by maintaining surface elevation using sediment accumulation. However, some salt marsh habitats fail to keep pace with changing sea-level when rates of subsidence (the sinking of the land) and sea-level rise are not balanced by accretion (sediment accumulation)[31]. In the absence of sediment inputs from

Figure 10.10 Salt marsh monitoring sites and vulnerability to sea level rise. Red stars indicate salt marsh habitat losing surface elevation and very vulnerable to sea level rise, orange stars indicate sites gaining surface elevation but not fast enough to keep pace with sea level rise (moderate risk), and yellow stars indicate salt marsh habitat gaining surface elevation at a rate fast enough to keep pace with sea level rise (low risk) (adapted from Raw et al.[28]).

catchments, salt marshes will move inland in response to rising sea level, retaining a constant position relative to the shifting tidal frame. This is how salt marshes have adapted to previous sea level rises. However, inland migration may be prevented by local topography, artificial embankments and infrastructure development, which thus cause a loss of salt marsh habitat (particularly supratidal salt marsh) through coastal squeeze[31].

Raw et al.[30] assessed surface elevation change and relative sea level rise experienced at salt marsh sites in the Knysna Estuary. Using tide gauge data for the period 1960 to 2017, they calculated relative sea level rise (the height of the sea relative to the land) of 2.19 mm per year. Salt marsh habitats in the middle reaches of the estuary (shown in red in Figure 10.10) are losing surface elevation, through either erosion or subsidence (sinking of the ground), and are not keeping pace with sea level rise. Worryingly, these habitats are surrounded by developed land, which will prevent landward migration of the supratidal salt marsh. Some salt marsh habitats in the upper and lower reaches (orange in Figure 10.10) are gaining surface elevation but not at a rate fast-enough to keep pace with sea level rise. These sites are also impacted by coastal squeeze (development around these sites is depicted in Figure 10.11), which will prevent local adaptation to sea level rise. However, two salt marsh sites in the upper and lower reaches (green in Figure 10.10) are gaining surface elevation at a rate faster than sea level rise and are adapting to the current rate of sea level rise[30].

Loss of salt marsh and other vegetated habitats in the estuary will ultimately affect the animals using these habitats as a food source or refugia, such as birds, fish and invertebrates. The effects of sea level rise will be exacerbated by increases in the frequency of severe storms and high tides. The South African coastline is at times affected by extreme swells and storm surges, which are predicted to increase in frequency and intensity[1] as the climate becomes hotter. These types of events cause estuarine habitat loss. For example, in the Mbhashe Estuary, a major storm surge deposited marine sediment in the lower reaches of the estuary that smothered the pneumatophores of some mangroves and resulted in dieback of a patch of mangrove trees[27]. Sediment deposition may temporarily or permanently cover sandprawn, mudprawn and other invertebrate burrows, resulting in a loss of habitat and refuge for gobies, shrimps and other burrow symbionts.

Figure 10.11 Developments on Thesen Island will prevent landward migration of salt marsh habitats during a rising sea-level scenario (Photograph: © Alan Whitfield).

10.6 Ocean acidification

From pre-industrial times (1750) to 2019, the atmospheric concentration of CO_2 has risen by 47%[2]. Approximately 30% of this man-made CO_2 has been absorbed by the oceans and one of the primary impacts of introducing huge amounts of CO_2 into the ocean is that water becomes more acidic (pH decreases), in a process referred to as ocean acidification. When CO_2 dissolves in seawater, a series of chemical reactions occur (referred to as the carbonate system). The addition of large amounts of dissolved CO_2 shifts the balance of the carbonate system, ultimately resulting in an increase in hydrogen ions (H^+) and HCO^{3-}. Over time this lowers pH and uses up carbonate ions in the water column. Calcifying organisms, such as crabs and prawns, use carbonate ions to maintain and make calcium carbonate, which is the building block for the shells of many organisms.

The reduction in pH and carbonate ions that accompanies elevated CO_2 concentrations in seawater holds severe implications for some coastal organisms[32]. It is estimated that the pH of surface waters in the open ocean will decrease by 0.3 units (from a current average of 8.1) by 2100 as atmospheric CO_2 levels continue to increase[2]. Several laboratory-based studies where animals have been exposed to pH levels predicted for the open ocean at the end of the century have shown that both non-calcifying organisms (like fish) and calcifying organisms invertebrates) may be adversely impacted by ocean acidification[32]. The structures of calcifying organisms are made of calcium carbonate, which will start to dissolve and, as carbonate ions are reduced, it requires more metabolic energy for an organism to deposit calcium carbonate. Ocean acidification may also adversely affect the mortality and calcification of some fish species[33]. For example, when larval dusky kob *Argyrosomus japonicus* were reared in low pH water (pH 7.78) the growth, bone development (ossification — shown in red in Figure 10.12) and survival of larvae was significantly lower in the low pH treatment compared to larvae reared in seawater with a pH of 8.1[34].

Changes in bone development can have severe implications for dusky kob and spotted grunter and

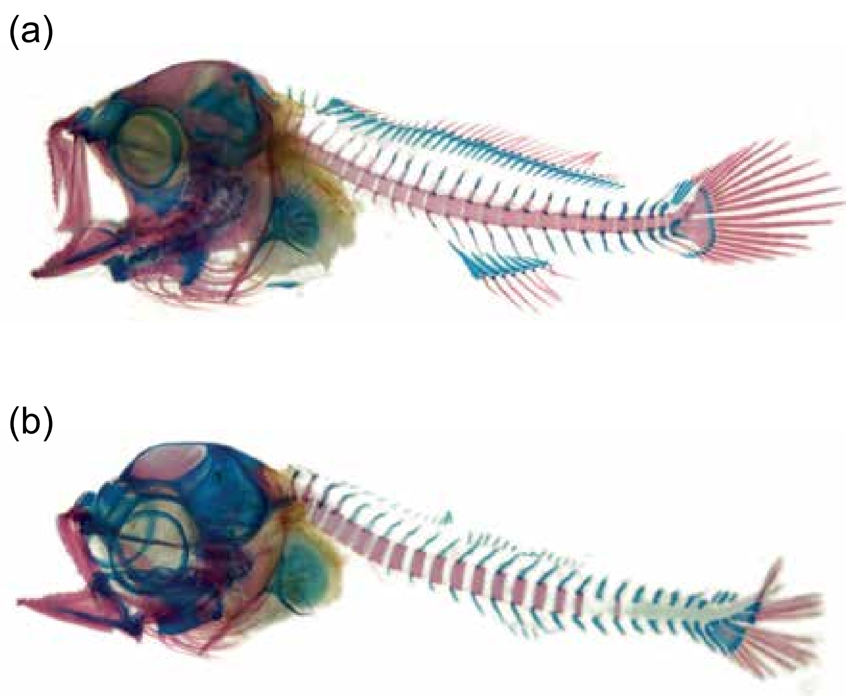

Figure 10.12 Bone (red) and cartilage (blue) development in larval dusky kob (*Argyrosomus japonicus*) reared in seawater with a pH of (a) 8.15 and (b) 7.78. Note that a small change in pH can result in major changes in cartilage and bone development in fish larvae (images from Erasmus[32]).

other soniferous fish that rely on sound and hearing for foraging and communication. Changes in earbone (otolith) structure results in hearing loss and may see fish switch from sound to visual foraging. Changes in sound-producing structures such as the pharyngeal teeth of spotted grunter, may cause complete loss of vocalization or sounds not familiar to others of the species. This and loss of hearing ability may play havoc with courtship and spawning.

The conditions predicted for the open ocean in 2100 may not, however, reflect what is going to happen in coastal ecosystems. Changes in pH in estuaries may be caused by ocean acidification (and the intrusion of CO_2 high seawater into the estuary) as well as a multitude of other (natural or anthropogenic) factors. These include nutrient enrichment, freshwater inflow, locally elevated atmospheric CO_2 from industry and agriculture, upwelling in the coastal environment and photosynthesis and respiration of plants and animals[35]. These factors cause much greater pH variability in estuaries than in the open ocean, and can result in greater fluctuation in pH and even more acidic conditions than in the open ocean[36]. This is a particular threat for the biota of the Knysna Estuary since the river water entering the estuary already has a low pH of approximately 5 and currently relies on the higher pH marine water in the system to act as a convenient buffer.

Nutrient enrichment can alter the pH of estuarine water through enhanced biological respiration and photosynthesis. Photosynthesis increases pH in the surrounding water and decreases dissolved carbon by taking up CO_2 and HCO^{3-} (bicarbonate). In contrast, respiration by marine animals and plants (at night) decreases pH and dissolved carbon because of the release of CO_2 in this process[37]. The pH of river inflow into estuaries is influenced by characteristics of the catchment such as geology and vegetation, as well as eutrophication and pollution in the river caused by anthropogenic activities such as the use of fertilisers, thus increasing natural pH variability[38]. The Knysna catchment comprises mainly Table Mountain Group sandstone and the dominant vegetation of temperate forest and fynbos can make the incoming river water acidic (median pH = 5.3, range 3.6-8.4)[38]. An increase in the intensity of marine upwelling, which is linked to climate change, may further influence acidification of the Kynsna system.

It is difficult to predict the pH of coastal systems in the future because we do not know enough about average coastal and estuarine pH values and their variability[35]. Recent research programmes have started to shed light on just how variable pH and carbonate chemistry is in estuarine and coastal environments. Rosenau et al.[36] monitored pH in the lower region of seven estuaries along the coast of America. They found that pH in the lower reaches of the study estuaries varied between 7.16 and 8.32. In contrast, surface water open ocean pH typically varies < 0.1 inter-annually[35]. In shallow water with dense seagrass and seaweed beds pH can fluctuate daily by more than 1 pH unit[37]. The pH in the Knysna Estuary ranges between 6.6 and 8.1[39]. In the future, an increase in eutrophication in the estuary, along with the intrusion of low pH seawater (from upwelling) could result in an increase in pH variability and acidification in the lower and middle reaches of the estuary, which are strongly marine influenced. In addition, should the river baseflow be removed from the estuarine system due to increased abstraction, the natural pH gradient observed in Knysna Estuary may also be lost.

Under elevated atmospheric CO_2 scenarios dissolved CO_2 and HCO^{3-} will increase, while $CO_3^{\ 2-}$ is set to decrease. This change, coupled with increasing temperatures, is likely to benefit productivity in seagrass[40]. Elevated atmospheric CO_2 concentrations may also increase productivity of some salt marsh species[4]. While lowered seawater pH caused by ocean acidification can have substantial impacts on seagrasses and seaweeds, these species can in turn also affect seawater pH. For example, seagrass and seaweed can raise pH on a local scale by taking up carbon through photosynthesis[41]. These localised zones of elevated pH associated with seagrass and seaweed beds could potentially serve as ocean acidification refugia[42]. For example, Wahl et al.[43] found that dense beds of brown algae and seagrass in the Western Baltic increased the overall mean pH of the surrounding water by as much as 0.3 units relative to other similar habitats with no macrophytes and also imposed strong diurnal pH fluctuations (due to photosynthetic activity). This allowed mussels (*Mytilus edulis*) to maintain calcification even under acidified conditions, thus reducing the impact of ocean acidification on organisms living in these habitats. Seagrass beds in the lower and middle reaches of the Knysna Estuary (Figure 10.13) may counteract the effects of ocean acidification (by raising the overall pH of the surrounding water) and serve as ocean acidification refugia for the animals living within them.

Figure 10.13 Extensive seagrass beds may raise the pH of the surrounding water in parts of the Knysna Estuary, thus protecting the associated biota from ocean acidification trends (Photograph: © Alan Whitfield).

10.7 Summary of climate change effects on the Knysna Estuary

Sea-level rise, shifting temperatures, changes in rainfall, extreme events and changes in currents and wind regimes may see biogeographical regions and habitats shrinking, subjecting estuarine plants, fish and invertebrates to one or more of coastal, habitat and temperature squeezes.

In the Knysna Estuary, climate change will exacerbate anthropogenic stressors, such that the estuary regime will be reduced. Poor water quality (eutrophication and acidification), nuisance algal blooms and reduced productivity in the upper reaches (estuary regime) may be exacerbated by warming, low rainfall and droughts. Remaining salt marshes in the warmer lagoon regime (middle reaches) are at the greatest risk of habitat loss due to sea level rise (and coastal squeeze) and floods. Warming in this region of the estuary may result in an increase in the abundance of tropical species. However, temperature changes in this regime may have negative consequences on the growth and health of important seagrass habitats and associated temperate species (summarized in Figure 10.14 and Table 10.2).

Decreased productivity (associated with low rainfall and habitat squeeze through a reduction in the estuary regime) may also affect the nursery function of the estuary for estuary-associated marine species. Increased floods may result in poor water quality and habitat loss in the estuary regime. The bay regime may be impacted by coastal storms, which are increasing in frequency and intensity, as well as an increase in temperature variability and the intrusion of low pH seawater associated with an increase in the frequency and intensity of upwelling events (Figure 10.14 and Table 10.2).

In summary, the Knysna Estuary faces an uncertain future under a hotter and dryer climate, with rainfall events being less evenly spread and more erratic, both in magnitude and periodicity. These changes will impact negatively on an already stressed biotic community that is having to cope with existing human pressures.

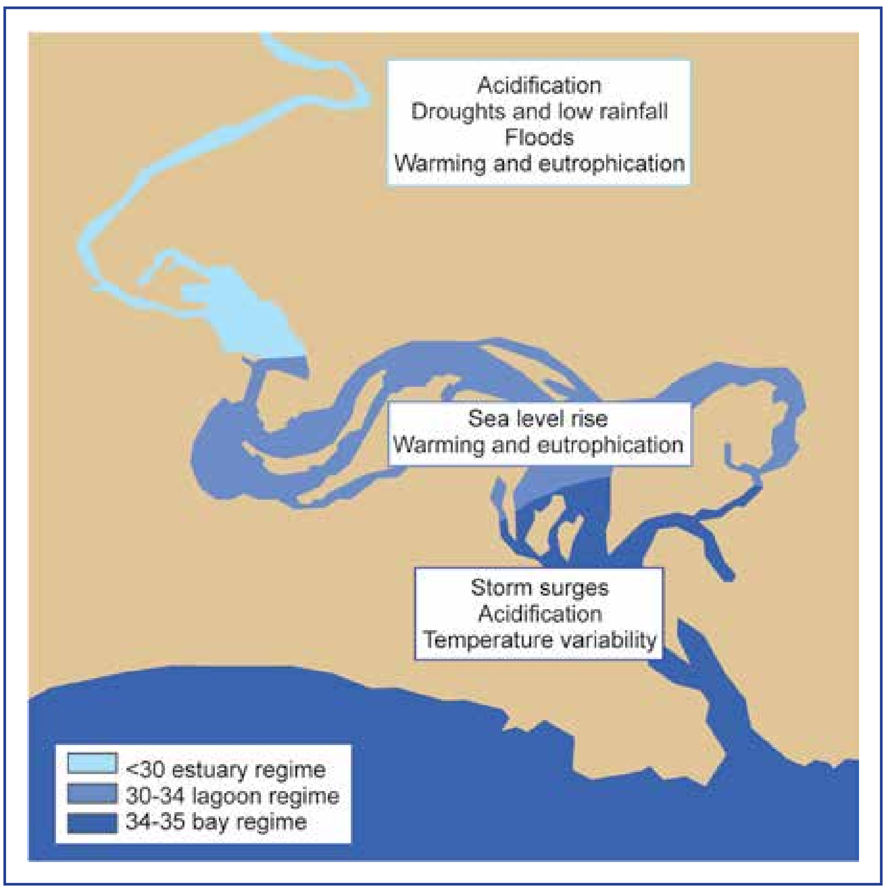

Figure 10.14 Categories of climate change impacts expected in the different sections of the Knysna Estuary. Surface salinity regime data from Claassens et al.[21].

Table 10.2 Summary of the expected intensity of climate change drivers and broad vulnerability of the Knysna Estuary to climate change. The more intense the colour, the greater is the expected intensity of change.

Intensity of change	Climate Change Driver	Marine zone	Lagoon Regime		Estuarine Regime
		Lower reaches	Middle Reaches	Ashmead Channel	Upper reaches
↑ Agulhas (off shore) ↓ Upwelling (inshore)	Sea Temperatures				
↑↑ 1 – 4 °C	Land Temperatures				
↑ Droughts ↓↓ Baseflows Flows ↓ Floods	Rainfall				
↑ 0.5 – 2.0 m	Sea level rise				
↓ pH ↑ pH	Acidification - Ocean - Catchment				
↑ Storms	Coastal storms				

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Knysna Waterfront restaurants and harbour (Photograph: © Robin Runck).

Chapter 11 : Knysna Estuary — Collaboratively Governing and Managing a Shared Resource

Dirk Roux, Stef Freitag, Ian Russell & Megan Taplin

"We are fallible humans studying fallible human behaviour within institutional structures constructed by other fallible humans. We should not act as if we know for certain how to achieve sustainable development. We can, however, recognise our growing capabilities and those of the individuals we study to experiment with rules, learn from the experiments, and, if the broader institutional and cultural milieu facilitates, gradually improve outcomes so they are sustainable over time." (Elinor Ostrom[1])

11.1 Introduction

Falling within the Garden Route National Park, Knysna Estuary comprises four distinct hydrological regime areas: the marine embayment (The Heads to Railway Bridge), Ashmead channel (with shallow warmer waters and distinctive hydrology), lagoon (Railway Bridge to White Bridge) and upper estuary (upstream of the White Bridge) (see Figure 1.4 in Chapter 1). As an area of high national biodiversity importance and included in the management system of a national park, conservation is an automatic objective. However, it is also an open-access common-pool resource, shared and used by many and owned by all. As such, it contributes to a multitude of social and economic benefits to diverse user groups, with many and varied ecological and social challenges.

This chapter critically reflects on the current governance and management of Knysna Estuary and focuses on the challenges of and requirements for governing the estuary as a common-pool resource. It also makes suggestions as to how governance and management of Knysna Estuary might be improved to promote achievement of both conservation and socio-economic objectives.

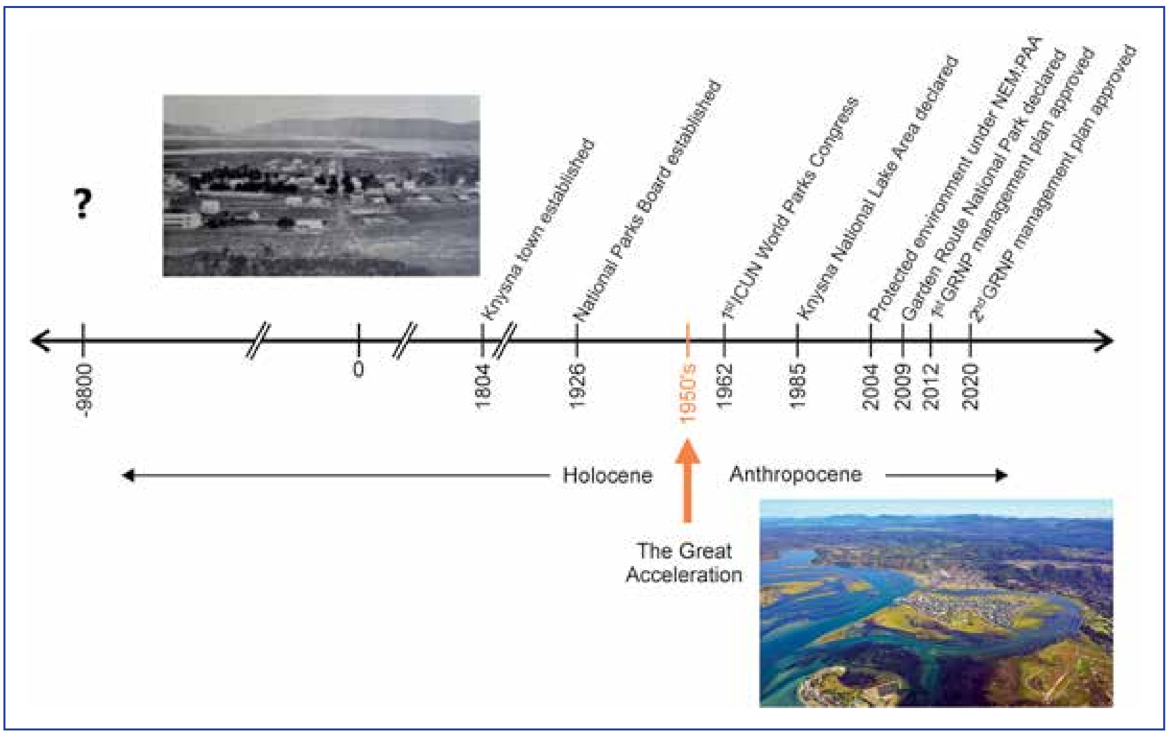

Figure 11.1 Timeline of important events and changes in governance arrangements for Knysna Estuary in the context of the Anthropocene.

WHAT DOES 'COMMON-POOL RESOURCE' MEAN?

Common-pool resources are relatively large systems like groundwater basins, fishing grounds, communal grazing areas, lakes and Earth's atmosphere. They face potential overuse and user conflict because it is typically difficult to control access to these resources (i.e. excludability); their multiple users may have diverse interests and values; and each user could subtract from the ability of the next user to benefit from the resource (i.e. subtractability)[1,2]. It is well documented that free-for-all or open access usually leads to unsustainable outcomes by overharvesting or resource degradation.

Effective governance of common-pool resources is critical to safeguard their sustainability and promote equitable benefits to users. This requires viewing people and the environment as interdependent components of one 'social-ecological system' and acknowledging that interactions between these may cause unpredictable outcomes resulting in uncertainty regarding overall system behaviour. Thus, collaborative approaches to learning about and managing these systems are necessary to promote a common purpose and adaptive capacity in the face of uncertainty and ever-changing contexts[2,3].

11.2 Knysna Estuary in multi-scaled context

Human influence over geological time-scales

The past 11 700 years, known as the Holocene Epoch, were characterised by relatively stable climatic conditions on Earth. This period also witnessed the remarkable development of humans, including worldwide migrations, rise and fall of civilizations, various revolutions (agricultural, industrial and technological) and a transition towards urban living. However, Earth has now entered into a new, still unofficial but widely recognised epoch, the Anthropocene, characterized by humans dominating change to its climate, landscapes, ecosystems, ecological processes and distributions of organisms[4,5]. The proposed start of the Anthropocene is the mid-20th century, a time referred to as the Great Acceleration due to sudden and dramatic changes in socio-economic (e.g. human populations, urbanization and fertiliser consumption) and Earth system (e.g. increasing atmospheric CO_2 concentration, ocean acidification and tropical forest loss) trends[6].

Recent governance and management history

Within the Anthropocene context, formalised governance and management arrangements for the Knysna Estuary have been a very recent consideration (Figure 11.1). Before 1985, management responsibility was shared by several authorities, including the Knysna Municipality and Outeniqua Divisional Council for sport, recreational boating and mooring facilities, and Department of Environmental Affairs for resource utilisation through the Sea Fisheries Act. The Department of Constitutional Development and Planning were responsible for land use and development issues and the Cape Provincial Administration for urban and marine development and environmental conservation in areas above the high water line[7].

In 1985, Knysna Estuary and some surrounding lands were proclaimed as the Knysna National Lake Area with associated regulations for its management promulgated under the Lake Areas Development Act (Act No 39 of 1975). Responsibility for implementing these regulations was assigned to the then National Parks Board (NPB; later South African National Parks or SANParks). The next 10 years were challenging and contested, with significant tensions between NPB personnel and stakeholders around the implementation of new regulations associated with recreational usage and biological resource extraction. Tensions between co-governing agencies focussed primarily on development, resource usage and pollution. This culminated in a period when the complete withdrawal of NPB as the primary management agency for Knysna Estuary was internally proposed and explored. This was however abandoned when no willing alternative management agency could be identified, pleas by residents sought to reverse the decision, and concerted efforts were made to improve cooperation and engagements on all fronts.

The Lake Areas Development Act was repealed in 2004 with the promulgation of the National Environmental Management: Protected Areas Amendment Act (Act No 31 of 2004), and with it the reassignment of Knysna Estuary as a Protected

Environment. This was followed, five years later, by the declaration of the Garden Route National Park (GRNP) in 2009. In the same year, regulations were gazetted for the management of the Knysna Protected Environment, under the ambit of SANParks as designated management agency on behalf of the now named Department of Forestry, Fisheries and the Environment (DFFE). Ministerial approval of the first management plan for the GRNP was received in 2012 with Knysna Estuary managed as an integral component of the national park since then. Recent revision of the management plan for the park, approved by the Minister of DFFE in 2020, recognised Knysna Estuary as an important and unique element, managed within a holistic social-ecological systems approach for this park.

Contextualising Knysna Estuary within the recent Anthropocene

In the Anthropocene, human activity impacts manifest in closely intertwined social and ecological changes. There is an interplay between an increasing human population with rapidly rising wealth and consumption and extensive land use changes and degradation of ecosystems and their services. This now threatens to destabilize critical biophysical systems and erode the "safe operating space" of humanity[8]. In essence, we are damaging the planetary conditions essential for sustaining our well-being[6], which has been referred to as a "profoundly existential crisis"[9].

Protected areas have become 'vital organs' in Earth's biophysical support system, critical to the future of humans in the Anthropocene. But, many factors hinder the protected area estate from achieving its potential[10], including rapid loss of options for future protected areas and declining investment in existing areas. Further, a third of global protected land is under intense human pressure within its boundaries[11] and areas are increasingly expected to demonstrate that they both conserve biodiversity and provide social benefits[10,12,13,14]. The highly fragmented and largely unfenced GRNP is one such protected area, consisting of forest, fynbos, lake, riverine, estuarine and marine ecosystems, all juxtaposed with semi-urban, commercial forestry and agricultural areas (Figure 11.2). The national park is embedded in a multifunctional landscape, which offers a diverse array of 'ecosystem services' that humans both rely on and alter, for better or worse. These landscapes serve various purposes and fulfil several needs at the same time, also maintaining people-nature connections. However, for different land uses to complement each other and result in synergistic and sustainable outcomes across economic, social and environmental objectives, coexistence alone is not enough. Rather, inhabitants need to interact and find ways to avoid abuse of resources by some and secure the cooperation required to enable sustainable use by all.

Knysna Estuary is a classic example of an open access common-pool resource with inherent challenges and dilemmas for its management to achieve biodiversity conservation, while also providing diverse direct and indirect benefits to all (Figure 11.3). This is accommodated in the framing of SANParks' vision ("a world class system of sustainable national parks reconnecting and inspiring society") and mission ("to develop, protect, expand, manage and promote a system of sustainable national parks that represents natural and cultural heritage assets, through innovation, excellence, responsible tourism and just socio-economic benefit for current and future generations"). However, giving effect to and reconciling management and governance challenges and the diversity of stakeholder wants, needs, perceptions and expectations, requires viewing Knysna Estuary as a complex social-ecological system. Further, this calls for investment of time, trust, cooperation and ongoing learning. Trust and cooperation are founded on sound relationships which may be challenging to achieve and which require time and effort invested from all sides.

> Society's primary response to Earth's 'existential crisis'…has been through setting aside selected areas of land and sea for protection[15,16]. Coincidentally (or not), around the onset of the Anthropocene, the International Union for Conservation of Nature (IUCN) was established on 5 October 1948, holding its first World Parks Congress in 1962[10].
>
> Since the 1960s the global number of protected areas has grown rapidly to more than 200 000 in 244 countries and territories[17]. Protected areas now cover 14.7% of land on Earth, and conservation represents the second largest form of land use after food production[18].

Figure 11.2 Map showing the fragmented and largely unfenced GRNP and location of the open access Knysna Estuary (blue circle). The national park straddles two provinces, two district municipalities and four local municipalities. GRNP's 164 600 hectares (ha) consists of approximately 43 800 ha indigenous forest; 85 320 ha fynbos; 4 050 ha rivers, wetlands, lakes and estuaries; 30 300 ha marine; 250 ha beach; 470 ha rocky outcrop or cliff; 410 ha infrastructure and other disturbance (e.g. fire belts).

11.3 Understanding Knysna Estuary as a complex social-ecological system

People and nature are intertwined social-ecological systems

How society understands and frames its relationship with nature has changed significantly over the past 60 years[21], and this is likely to continue changing. The biggest shift came about in the 1990s with a move from viewing nature as separate from people to acknowledging a tight coupling of natural and social systems. Since then, emphasis has changed from a utilitarian perspective (nature provides people with services and benefits) to one that recognises a two-way dynamic relationship between people and nature[21]. This subtle shift in emphasis is also evident in the change in wording of the desired state (vision/mission) for the GRNP from 2012 to 2020 (Figure 11.4).

The latter framing recognises the interdependence between nature conservation and human well-being, and the resilience of this linked social-ecological system (SES) at different scales—from the planet to the local estuary. The term 'social-ecological systems' emerged in the 1990s[22] to emphasise the intertwined and interdependent nature of human and natural systems. Since then, SES scholarship has developed into a prominent discourse in the scientific literature[23] and multiple frameworks have been proposed for studying and analysing SES[24]. In essence, SES thinking asserts that the delineation between social and ecological systems is artificial and arbitrary, and that studying any one system in isolation from the other will not be sufficient to guide society towards sustainable outcomes[22].

Addressing SES problems requires bringing together understanding of human social systems with knowledge of the natural world. For Knysna, many social and economic drivers and their outcomes are

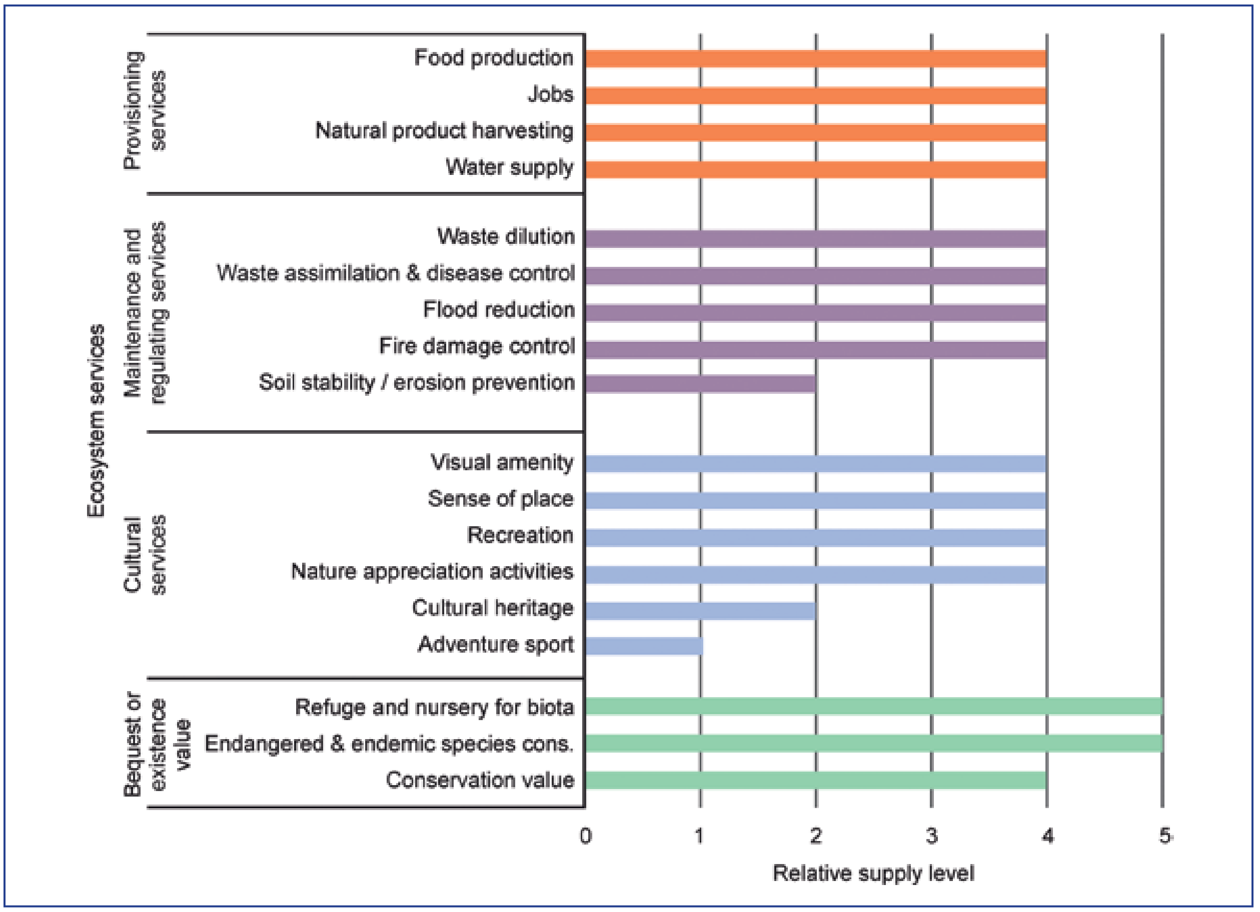

Figure 11.3 Knysna Estuary provides and delivers a range of direct and indirect benefits, also termed ecosystem services. These include a diversity of provisioning, maintenance and regulating, cultural and existence value services[19]. Relative supply levels range from low (1) to high (5). The annual monetary value of these services was estimated at around R 1.2 and R 1.3 billion in 2005[20]. Ecosystem services highlight the material and non-material benefits and connections between people and nature, as well as providing a basis for considering the tensions and trade-offs between these. The bequest or existence value highlights a basket of non-use values associated with perpetuity for future generations and knowing that the ecosystem and its associated biodiversity exists.

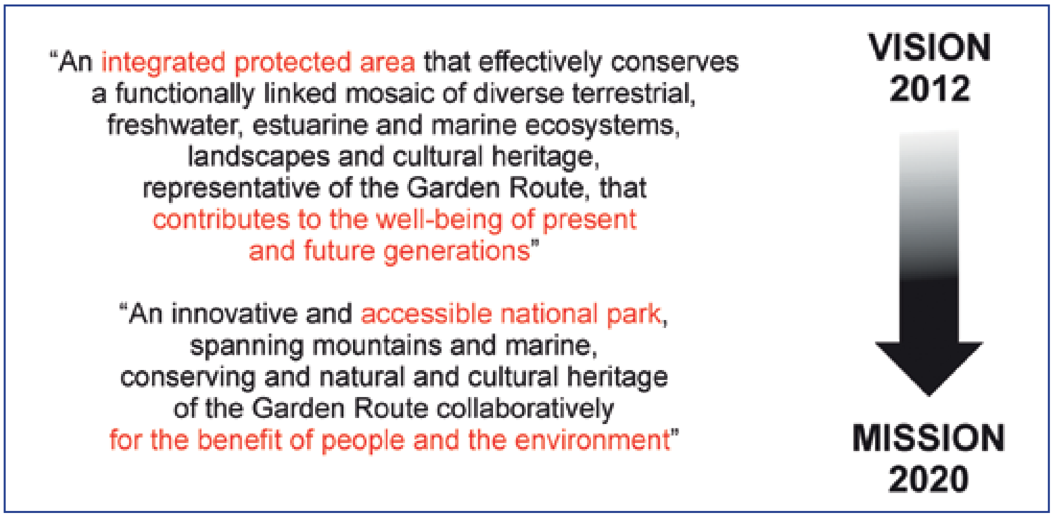

Figure 11.4 Wording of the vision/mission statements for the Garden Route National Park since its declaration in 2009 mirrors the global shift in people-nature relationships from a utilitarian emphasis in 2012 to one recognising interdependence of people and nature in 2020.

intertwined with and interdependent on the environmental and ecological health and delivery of services by the estuary (Figure 11.5). Characteristic reciprocal feedbacks between social and ecological system parts give rise to complex patterns of behaviour not evident when system parts are studied individually[25]. Thus, Knysna's key economic engine, a flourishing tourism and adventure activity industry, is inextricably dependent on this unique estuary.

Social-ecological systems are complex and evolve in unpredictable ways

Systems can broadly be classified into those that are complicated and 'knowable', and those that are complex with inherent uncertainty[30]. Complicated knowable systems, such as circuit boards or aeroplanes, have many different parts that function in a predictably repeatable way relative to each other. They can therefore be disassembled and reassembled into identical products with the same function, i.e. the whole is the sum of the parts. On the other hand, constituent parts of complex systems interact in an interdependent and evolving manner, leading to unpredictable behaviour and a degree of 'irreducible uncertainty' in terms of their response to interventions[31]. Examples include the human brain, anthills, economies and climate.

In social-ecological systems, complex behaviour arises from interactions between parts within the social and ecological systems respectively, but also from interactions between parts across these systems. Knysna Estuary is an example of a SES that is in constant flux as its beauty and sense of place attract more people which leads to rising development and waste production, which impacts the environment and water quality (sewage, solid waste and sedimentation), affecting biodiversity and then starts to negatively feedback on diverse basic livelihoods (e.g. subsistence fishing, water recreation; Figure 11.6). Complex systems are thus more than the sum of their parts. Their overall response cannot be known by only studying individual parts in isolation from one another as there are many interactions between these parts; relationships and feedback loops between them may be non-linear, are affected by their histories and can be influenced by factors outside of the system (Table 11.1; Figure 11.7). This limits our understanding of the behaviour of such systems[32] as they are ever changing.

Acknowledging uncertainty and limits to understanding is uncomfortable as the frequent lack of clear cause-and-effect relationships means there are no standardised responses to problems[30]. However, treating complex systems and problems as if they are fully knowable, either through reductionist science and/or command-and-control management, may lead to its own problems. In the case of the estuary, better mapping or understanding

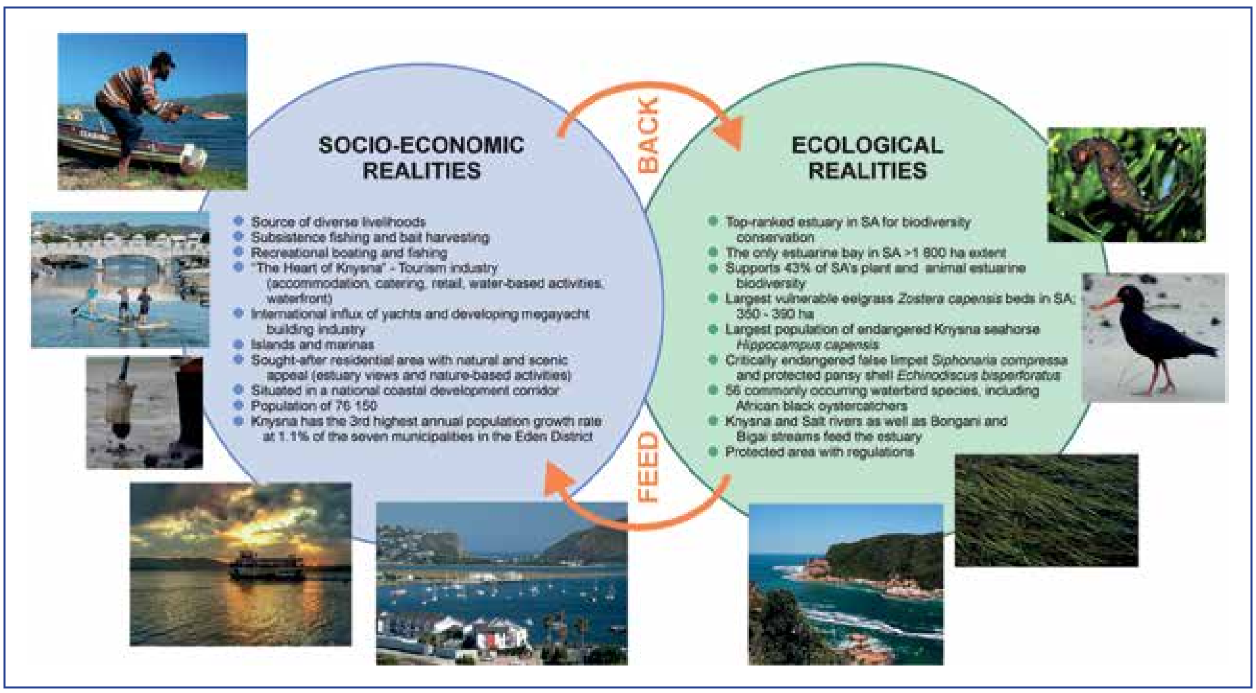

Figure 11.5 Some socio-economic and ecological realities[26,27,28,29] of the interconnected Knysna Estuary social-ecological system.

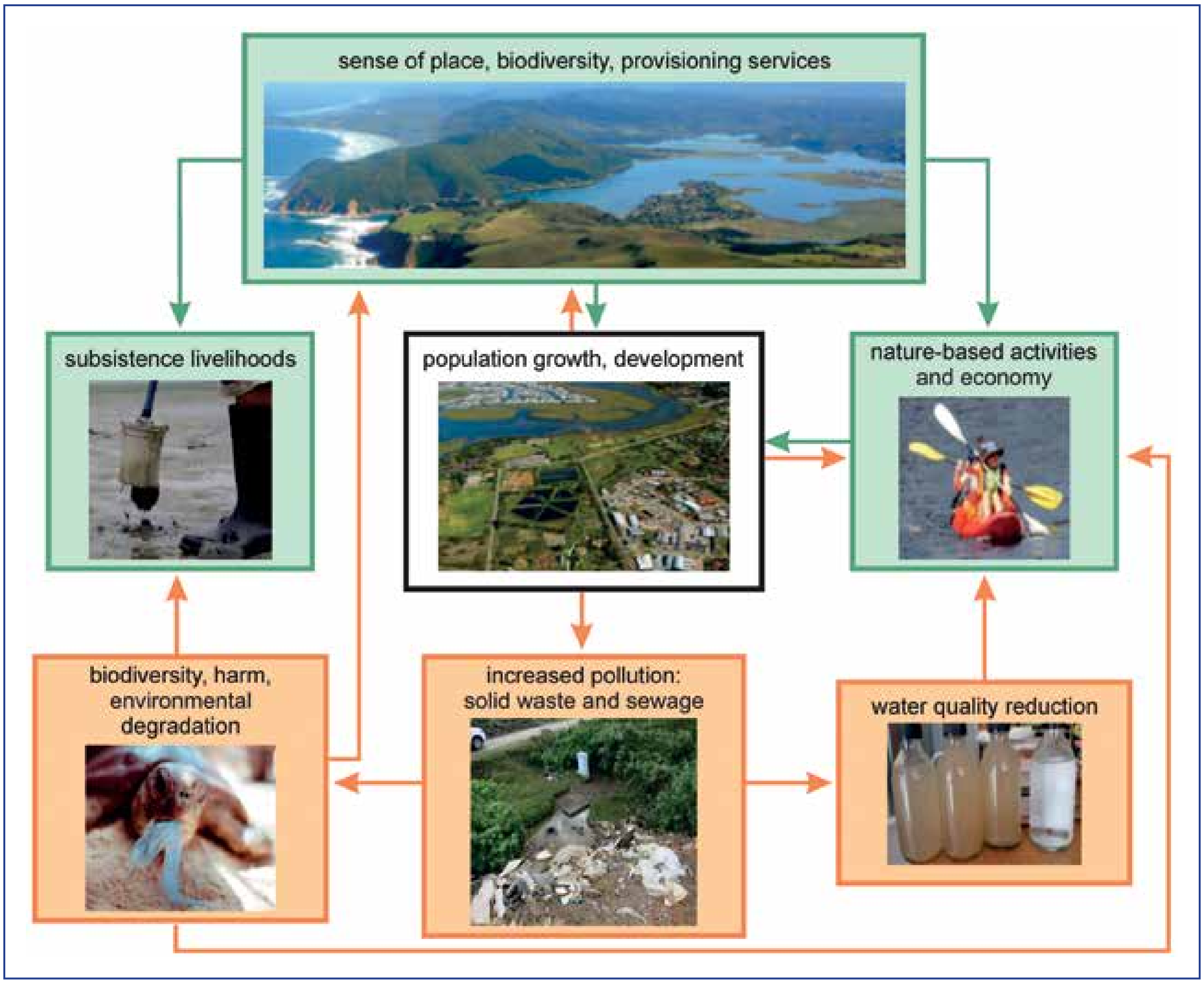

Figure 11.6 Simple rendering of some connections and feedbacks between social and ecological system parts for Knysna Estuary SES (orange arrows are negative feedbacks, green arrows are positive feedbacks), demonstrating interconnectedness. There are 111 streams, drainage pipes, ditches, culverts and the waste water treatment works that drain directly into the estuary from the industrial area, residential areas and catchments of Knysna. These outlets carry human effluent, fertilisers, herbicides and pesticides, sediment, plastics and general litter into the estuary. The estuary thus becomes the drain and sink for all these anthropogenic influences, inputs and toxins.

biodiversity (e.g. fish diversity and eelgrass beds) or estuary impacts (e.g. sewage pollution and sedimentation of the Ashmead channel) may illustrate biological and physical changes in the system, and even guide some management actions and monitoring. However, such knowledge may not lead to improved livelihoods for all or mitigate conflicts between users, and has not yet resulted in substantive and proactive investment in the replacement of inadequate and failing waste and storm water management infrastructure. Thus, the puzzle of a social-ecological system can never be fully solved by only studying the pieces[32], but requires integration of knowledge from a range of disciplines encompassing the system.

11.4 Managing Knysna Estuary as a complex SES

Knysna Estuary is a social-ecological system, which underlies the complexity of its management. Figure 11.7 depicts a framework for bringing together the subsystems of Knysna Estuary SES based on conceptual models[35,36]. The framework shows the four key subsystems with examples of their variables and layers:

- the resource system — Knysna Estuary as part of Garden Route National Park, but also as a component of the catchment basin. This is one of South Africa's most biodiverse estuaries with the highest conservation value in the country[37]. Thus, human

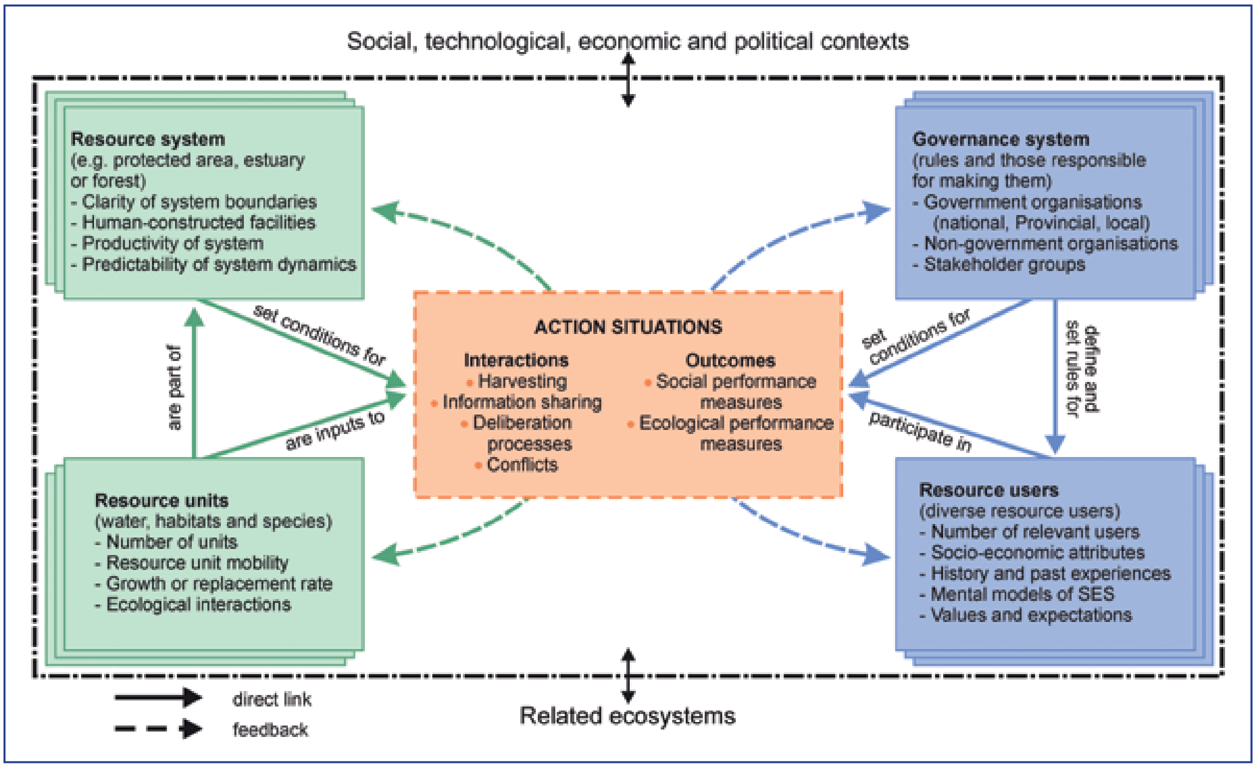

Figure 11.7 Conceptual model for the complex Knysna Estuary social-ecological system. Four solid boxes denote the high-level system components, with examples of variables in each. The orange action situation box is where interactions take place and inputs are transformed by the actions of multiple resource users into outcomes. Dotted lines show that boundaries are porous and that external influences from related ecological systems or social, technological, economic and political factors and contexts can affect any component of the system[35,36].

pressure on its resources exerts pressure on management to maintain a healthy system.

- resource units — including the estuary's biophysical features, habitats and species.
- the governance system — encompassing the rules at various scales (such as national, organisational, local) and the institutions responsible for making them. SANParks manages the estuary and activities that occur on it but does not control many of the influences on the estuary such as waterborne and solid waste pollution from urban areas and drainage systems.
- the diverse users of the estuary — with their variable contexts, histories, expectations and demands. This can lead to conflicting user needs and wants e.g. subsistence fisher people and bait collectors versus recreational fishing versus commercial fishing charters, or preservationists pushing for non-motorised vessels versus business people of offering high speed adventure boating.

The sub-systems are relatively distinct but interact to produce outcomes at the SES level, which in turn feed back to affect the subcomponents, their variables and other systems[35]. Because social-ecological systems are complex with interactions, often non-linear, and feedback loops between their many social and ecological parts and with external systems (Figure 11.7), system behaviour cannot be readily predicted and is seldom reversible[33]. Also, common-pool resources often have multiple stakeholders with divergent world views, expectations, values and ways of accessing and interpreting information. In the case of Knysna Estuary, these stakeholders too are diverse, and are engaged with through multiple platforms and forums (Figure 11.8).

How then should such systems, where uncertainty is a given and the stakes often high, be managed? This challenge led to the development of adaptive management in the 1970s[38,39] and since then, has become a foundation of effective environmental management[40]. It treats management of the system as an experiment by asking questions, implementing decisions, monitoring system responses and adapting actions based on learning from the experience. An adaptive management approach does not delay decisions until the consequences of actions are fully understood (full understanding is impossible in complex systems). Rather, it combines the need for immediate action with a plan for

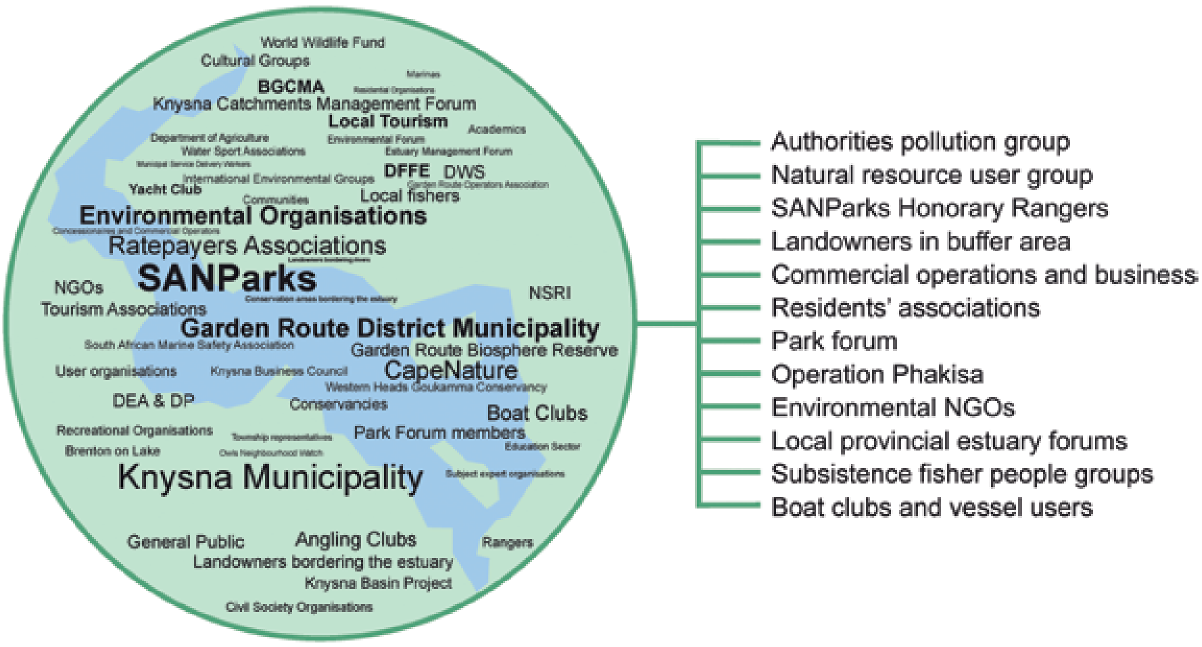

Figure 11.8 Illustrative schematic showing the diversity of stakeholder groups and types, with an interest in the outcomes of governance and management of Knysna Estuary (left), and an example of the engagement platforms and forums interacting with SANParks on issues related to Knysna Estuary (right).

learning[41]. Further, adaptive management is based on synthesis of relevant information, from different disciplines and perspectives, to inform the problem(s) to be addressed and better understand the system and its interrelated parts. Selected actions are then implemented, followed by purposeful monitoring, learning and adaptation as necessary. The combination of having an explicit structure (including carefully identified objectives, a conceptual model or hypothesis to reflect current understanding, decision options for advancing any particular objective, and experiments and monitoring to test outcomes) and being resolute about incorporating new learning into decisions, distinguishes adaptive management from blind, aimless or ad hoc trial and error management.

In South Africa, strategic adaptive management (SAM) has become central to thinking, planning and decision-making within SANParks where it was developed in response to river conservation challenges in the Kruger National Park[42]. A form of common-pool resource situated within social-ecological catchment systems, river health and biodiversity in Kruger National Park are dependent on policy and upstream practices. SAM helped bring about improvements in river flow patterns through development of a participative vision and objectives that facilitated collaboration of upstream water users[41,43]. Over the past two decades, SAM has been applied to the management of many complex ecological problems, from fire regimes to elephant populations, and for the development of management plans for the 19 national parks, including GRNP.

Broadly, SAM consists of five key steps (Figure 11.9 A) with strong elements routed in four subprocesses (Figure 11.9 B), namely adaptive planning, implementation, evaluation as well as governance. In addition, there are a number of important feedback loops for learning between these sub-processes. In order to understand the management of Knysna Estuary, we assess how well these four sub-processes are applied in GRNP with specific reference to Knysna Estuary.

What does adaptive governance mean in the context of Knysna Estuary?

As a common-pool resource, Knysna Estuary is prone to overuse as potential users are difficult to control, and conflicts may arise as users affect each other's ability to benefit from the estuary. It is well documented that free-for-all or open access almost always leads to unsustainable outcomes. Effective

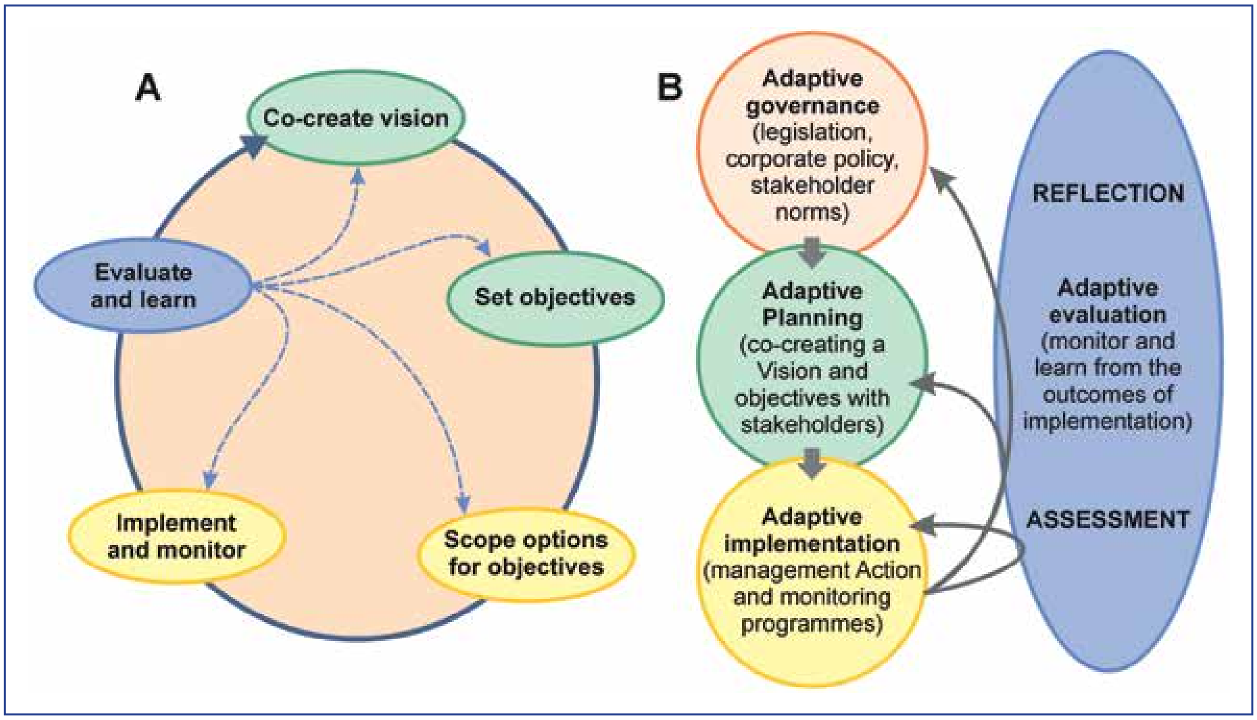

Figure 11.9 Steps in Strategic Adaptive Management (A) and how these relate to the four interdependent adaptive processes outlined in B. Corresponding colours in A and B show how the main steps of SAM in A relate to adaptive governance, planning, implementation and evaluation in B. Blue dotted lines in A indicate learning feedbacks[44] while grey arrows in B indicate sequential dependencies (downward arrows) and learning feedbacks (curved arrows)[45].

governance is therefore critical to safeguard resource sustainability and promotes equitable benefits to users.

'Adaptive environmental governance' refers to a form of governance suited to social-ecological systems and common-pool resources where complexity and uncertainty prevail[1,2,46]. Adaptive governance takes place through a range of interactions between stakeholders, social networks, organizations and institutions in pursuit of a desired state[47]. Its focus is on adaptation to changing situations in collaboration with multiple stakeholders operating at different levels of governance and with varying values and needs through cross-scale networks for collective action, knowledge integration and ongoing learning[3,47,48]. This is especially desirable in the Anthropocene, with its increased uncertainty and higher probability of frequent and extreme environmental, social and economic change—take for example the range of uncertainties and unexpected knock-on effects of the COVID-19 pandemic and how these have affected everything, globally to locally in Knysna.

Adaptive governance provides an essential enabling context for adaptive management, especially where multiple governance regimes overlap (e.g. legislation from national, provincial and local government as well as different policy sectors) and where broader ownership of rules, decisions and responsibilities are desirable. A case study on adaptive governance, focussed on Knysna Estuary, was initiated in 2020. Four common principles of adaptive governance — polycentric institutions, collaboration, social learning, complexity thinking —provided a basis for dialogue with stakeholders representing various local and provincial government departments, business, NGOs, boat and yacht owners, residents and homeowners, and fishers. Outputs from anonymous online questionnaires and an online discussion session recognised a diversity of challenges regarding the management of Knysna Estuary (Table 11.2). Through dialogue, eight indicators were co-developed with stakeholders to promote adaptive governance of the estuary (Table 11.3). These represent idealised conditions believed to support collaborative rule-making to promote sustainability of the estuary.

Table 11.1 Four fundamental attributes of complex systems[25,33,34] and what this means for Knysna Estuary.

Attributes of complex systems	What does this look like for Knysna Estuary?
Complex systems are defined by rich interactions among many parts • any part influences and is influenced by a number of others; • interactions are usually between neighbouring parts and each part is ignorant of the system as a whole; • the system is defined by interactions among constituent parts rather than by the parts themselves	Untreated effluent from ageing and failing waste and storm water infrastructure and underserviced developing areas contributes to both the nutrient load in the estuary, which can result in algal blooms that in turn can displace eelgrass, as well as the bacterial load which can pose a health threat to recreational users. Each of these 'constituent parts' will have their own cascading effects on other components.
Complex systems are characterised by non-linear relationships and feedback loops • at least some, often many, interactions between parts are non-linear; small causes or perturbations can have large effects; • some interactions create feedback loops, which can be positive (amplifying / reinforcing) or negative (dampening / counterbalancing); • a system is held in a particular state at a particular time by enhancing or inhibiting feed backs, or may reach another state with different identities, functions and relationships between parts when it passes a threshold.	A large open estuarine system with extensive sea-grass and marine algal beds supports a diverse fish community with high species abundance as part of the complex food web. Abundant fish results in intensive fishing pressure which reduces species abundance and alters population structures. Sustainable fishing however promotes livelihoods and enhances enjoyment and appreciation of the estuary and encourages protection. A negative feedback can result when high nutrient loads from sewage influx promote algal blooms, which reduces oxygen availability in estuarine water. This negatively affects growth of other plant and faunal components within the ecosystem.
Complex systems are dynamic with histories and legacy effects • parts of the system interact, to result in 'emergent' system-level behaviour; • they change over time, with histories and memories of their past — the past defines the present state and affects future trajectories (legacy effects).	Knysna's historical timber economy and associated developments has contributed to shaping the estuary of today (boating access, Thesen Island factory and later developments). Similarly, the construction of multiple bridges and causeways across the estuary, and hard infrastructure along much of the shoreline, continue to have legacy effects on the estuary's sediment, flow and flooding dynamics. A decision in the 1980s to assign responsibility for managing the estuary to SANParks has also created a specific management legacy.
Complex systems are open to external influences and nested within a larger system • system boundaries are permeable, allowing flow of energy, information and matter between the system and its surroundings. Thus, interactions and feedbacks occur between system parts and between parts and the external environment; • complex systems are often connected to, or nested within, a hierarchy of systems representing different scales; interactions at one scale can spread to have consequences across scales.	Knysna Estuary, with its location at the bottom of the catchment basin, is part of a bigger landscape and influenced by activities in its catchment, such as fire increasing sedimentation, alien trees reducing runoff and agricultural activities inputting nutrients, herbicides and pesticides. Similarly, ecological conditions and human impacts within the estuary affect certain fish populations in the coastal zone (as the estuary functions as an important nursery site). The estuary is also affected by provincial, national and global developments, e.g. national legislation and global climate change or a pandemic. Global events including wetland loss along waterbird fly-ways and hunting pressures along migration routes affect the abundance and use of the estuary by migratory waterbirds. The estuary is also open to 'visits' by people and biota, via land or sea, including non-native species that may be introduced by visiting watercraft and may become invasive.

Table 11.2 Diversity of challenges around managing Knysna Estuary as identified by stakeholders through an online anonymous questionnaire administered during 2021. These have been grouped into four broad categories as they refer to ecological, social and economic, governance and management and social-ecological aspects.

ECOLOGICAL
Ecological health (ecosystem processes, functioning, habitats)
Pollution
Utilization (overexploitation) of natural resources
Development of infrastructure with ecological impact
Water quantity
Biodiversity/species management
Sedimentation due to erosion

GOVERNANCE and MANAGEMENT
Policing and enforcement of present legislation/policies
Co-operative management team to achieve balanced,shared and broad vision to reach practical, objective and measureable goals
Accountability and tracking compliance and state of system over time by those legally responsible
Unpopular short-term decision to enable long-term sustainability for all users
Balance private and public interest
Consider the expanded area influencing the Estuary
Water quality standards
Better stormwater management
Environmentally-friendly approaches by boat operators
Agroecological farming practices

SOCIAL and ECONOMIC
Creating and securing social and economic opportunities
Employment aspects & livelihoods
Affordability (e.g. licencing to fish, even if very infrequent)
Health services/Human health
Safety
Recreational uses (e.g. boating)
Tourism
Infrastructure development
Education
Socio-economic status of residents (gini-co-efficient)
Sustainable housing & homeless people around the estuary
Historical spatial and settlement planning resulted in reduced sense of equitable social ownership of estuarine resources
Equity, fairness and social cohesion
Public coastal access

SOCIAL-ECOLOGICAL
Balance between preserving the ecological and the recreational and economical demands of the public who use the estuary
Balance between livelihoods of those who harvest resources, and leaving enough to repopulate stocks
Social-ecological resilience

Adaptive planning for GRNP and Knysna Estuary

Contemporary adaptive management approaches acknowledge stakeholder participation as central to framing the management problem and identifying management outcomes or goals[49]. Stakeholder engagement through adaptive planning in SAM (i.e. visioning and objective-setting; Figure 11.9 A) led to the first publically mandated plan for a national park in South Africa in 1997, namely for Kruger National Park. Since then this has been embedded in national legislation (National Environmental Management: Protected Areas Act No. 57 of 2003) and adaptive planning with stakeholders has become a well-honed process in SANParks, including engagement during approximately 10-yearly revision of management plans.

In 2018 a process was initiated to revise the GRNP management plan of 2012. Over two years, more than 500 stakeholders participated in seven 'desired state' workshops and 14 thematic focus group meetings (Figure 11.10). The outcome of this extensive adaptive planning process is a co-created mission and objectives hierarchy for GRNP (Figure 11.11), forming the basis for the revised park management plan approved in January 2020[50]. The objectives hierarchy consists of seven high level objectives supporting the mission for the park and a cascade of lower-level objectives with ever-increasing detail that end in actionable sub-objectives (Figure 11.11).

The Estuarine Management Programme falls within the natural heritage objective ('to conserve the diverse terrestrial and aquatic ecosystems of the park on a landscape scale through adaptive,

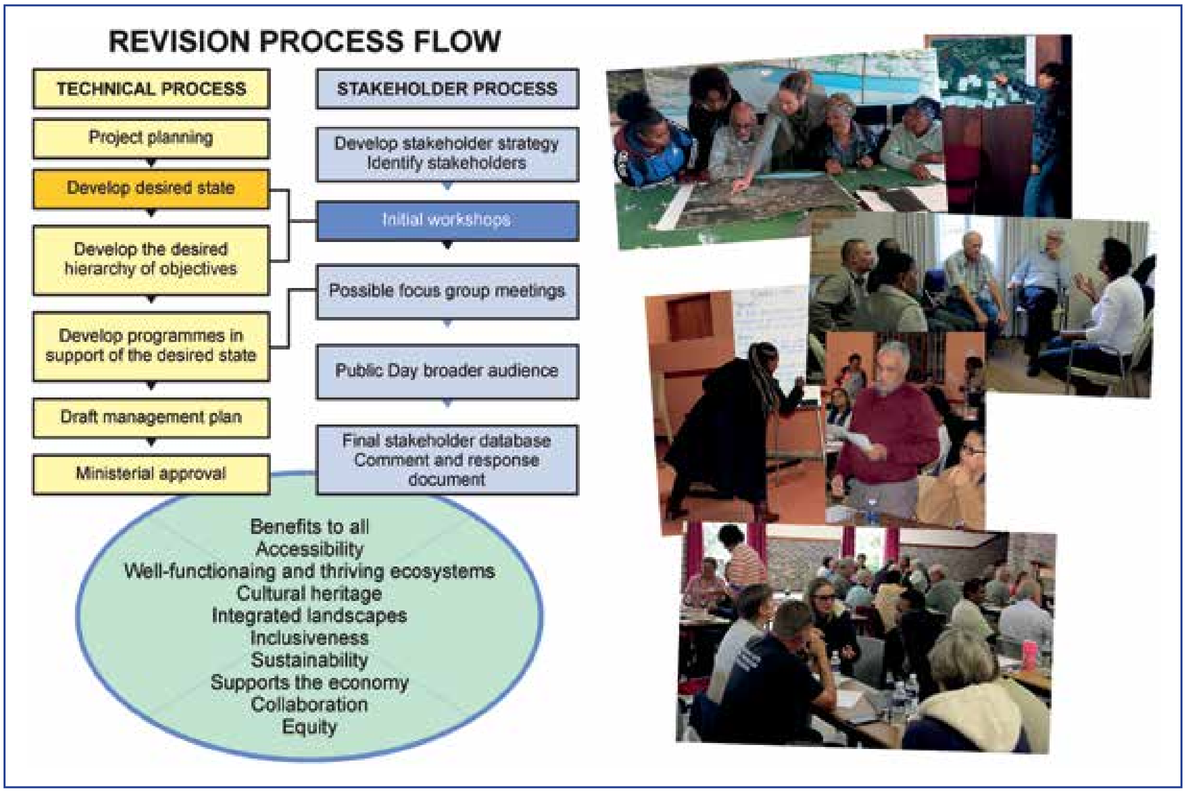

Figure 11.10 Over 500 stakeholders participated and engaged with SANParks during the 2018-2020 revision of the park management plan for GRNP. This included seven desired-state workshops across the region, 14 thematic focus group workshops and written responses to the draft plan.

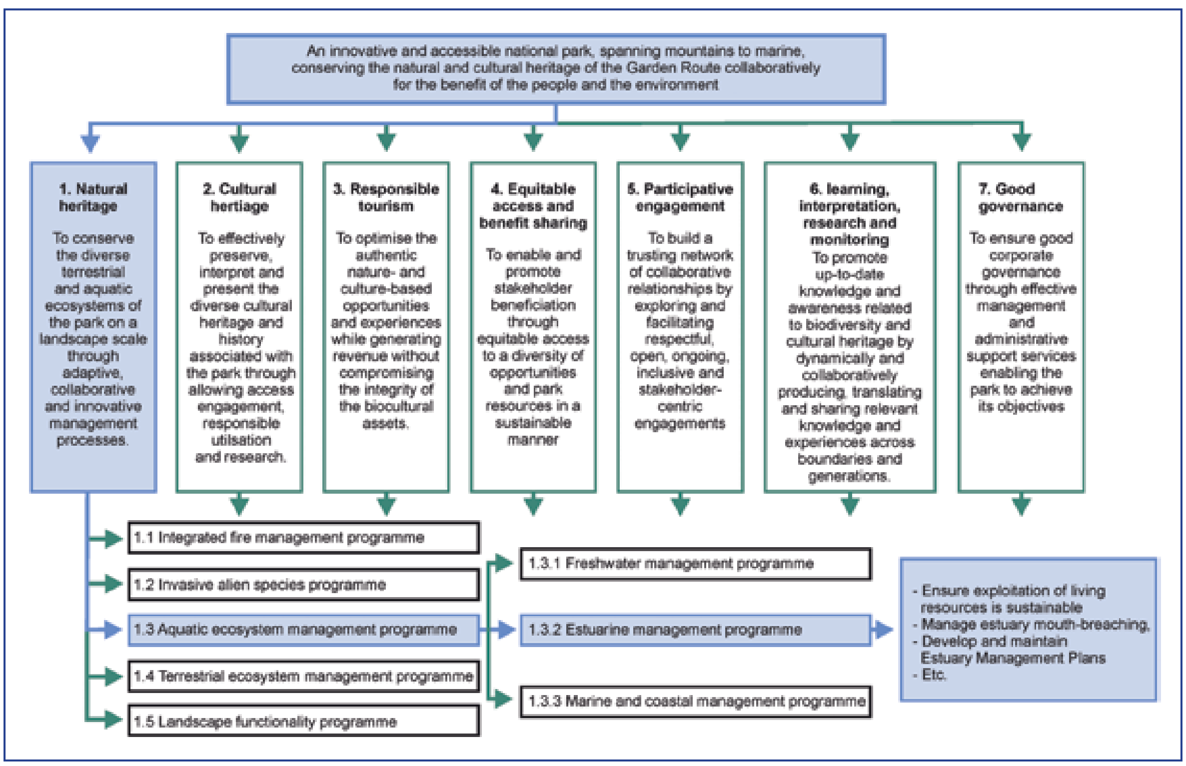

Figure 11.11 Partial objectives hierarchy for the Garden Route National Park, tracing the incorporation of estuary management from the vision to detailed operational actions for estuaries in this park[50].

GOVERNANCE and MANAGEMENT
Governance ≠ management

Governance has to do with social context (e.g. rulemaking, emergent leadership, assigning of responsibilities, agreeing to collaborate, developing trust, maintaining a collective vision) that enables management.

Management is the operationalization of a collective vision through resource allocation to implement selected actions and initiatives.

The SES approach considers governance and institutions as integral parts of the system[2]. The assumption is that improved governance leads to more effective management, which ultimately results in desirable outcomes such as a clean estuary.

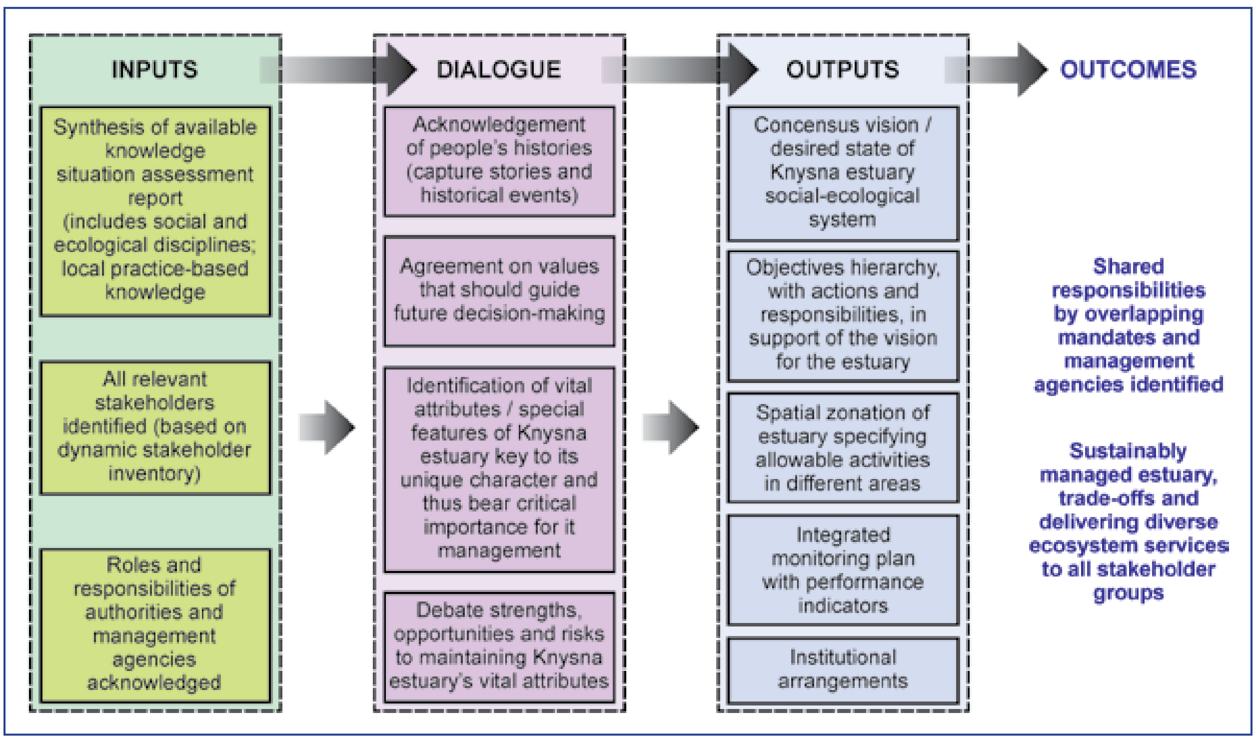

Figure 11.12 Main steps of adaptive planning as proposed for the development of a legally mandated estuary management plan for Knysna Estuary.

collaborative and innovative management approaches'). One sub-objective of the GRNP's estuarine management programme requires development and implementation of Estuary Management Plans in line with relevant legislation, namely the National Environmental Management: Integrated Coastal Management Act (Act No. 24 of 2008) and in accordance with the recently revised and published national Estuarine Management Protocol. Development of the Knysna Estuary Management Plan has commenced and is due for completion by March 2023. A carefully designed and executed adaptive planning process is a critical condition for the development of such a plan (Figure 11.12), reconciling stakeholders with different values and expectations and forging lasting partnerships.

Achieving a shared understanding among all stakeholders can be challenging[51]. Nevertheless, it is anticipated that partnerships for the governance and management of Knysna Estuary will be enhanced by respectful adaptive planning processes. Dialogue in carefully designed social learning spaces should facilitate shared understanding of estuary challenges and complexities, and lead to consensus around and co-development of a vision for this social-ecological system. Social learning spaces (see indicators 5 and 6 of Table 11.3) promote diverse and inclusive participation, well-facilitated and ongoing sequences of dialogues among stakeholders enable evolution of understanding over time, and articulation of collective understanding into explicit forms and products that are truly owned by all[52].

Adaptive implementation of management actions and monitoring in Knysna Estuary

Adaptive implementation entails operationalizing the vision and objectives through management actions in conjunction with research and monitoring programs. Implementation is informed and guided by various objectives and their diverse operational actions for the GRNP (Figure 11.11) and the greater Knysna catchment area as well. Not only does this require an understanding of the legislative requirements and governance context, it also requires embracing a complex social ecological systems perspective for the estuary (Figure 11.7). Currently, management within the estuarine waterbody is mainly SANParks' responsibility as the designated management authority for Knysna Estuary. It is driven by organisational processes engaged in water quality evaluation and pollution control (waterborne pollutants and/or discharge of non-compliant water from Waste Water Treatment works and storm water drains, solid waste management), regulation of recreational and commercial vessels, activities and resource use on the estuary, inputs to coastal developments and combatting of illegal and/or inappropriate development and associated environmental damage (including habitat transformation, mechanical impacts of harvesting and boating activities), inputs on freshwater usage, environmental allocation and possible bulk water storage, safety and signage, environmental education and awareness. This is done in conjunction with various forums (e.g. the Park Forum, Estuary Authorities Pollution Committee) and supporting structures and expertise (Honorary Ranger corps, various law enforcement authorities, NGOs, environmental or community lobby groups).

SANParks' SAM is designed to engage stakeholders and their perspectives, needs and visions. However, decision-making and implementation of actions within the estuary (not the catchment) still primarily rests with SANParks who then carries the responsibility, and by default, most of the risks[44]. In unfenced and common-pool resource situations such as the Knysna Estuary, with complex governance arrangements and overlapping mandates, this approach is insufficient. Rather, it requires collective action, with decisions boiling down to the costs and benefits of cooperation[51]. While there is a continuum of degrees of cooperation, from SANParks exploring options with stakeholders prior to making its decision (i.e. adaptive management) to co-productive development and ownership of decisions by the authority and stakeholders (i.e. adaptive co-management), the latter has not yet been tried. Legislation makes provision for adaptive co-management arrangements in national parks (NEM: PAA) and SANParks should actively explore this as a management paradigm for the Knysna Estuary. However, it will depend on the degree to which authorities and stakeholders are willing to share the responsibilities and risks associated with decision-making. While co-management processes lead to enhanced legitimacy of decisions, it often comes with the cost of significant personal stress arising from both logistical and social/emotional demands of participation in these processes[53].

Monitoring is critical for measuring the impact of implementation and identifying lessons for future actions and policy (Figure 11.9). Some monitoring programmes should evolve dynamically to align with management objectives[54] and actions, tracking their outcomes. However, this has proven difficult in practice where initiating new programs is hampered by resource and capacity constraints, and terminating existing programs to free-up capacity for others is difficult[41]. A number of long-term background monitoring and/or monitoring through research takes place on Knysna Estuary

Table 11.3 Four principles of adaptive governance, with two outcome indicators for each that can serve as beacons for stakeholders indicating some of the governance conditions that are conducive to effective management of the estuary. Quotations in blue provide reflection on how stakeholders perceive the current governance arrangements.

Adaptive governance principle	Stakeholder quotes from the dialogue process describing the current status quo	Outcome indicator for Knysna Estuary
Polycentric institutions = how decision-making is spread vertically across government levels (i.e. local, provincial, national and global) and horizontally across policy sectors (e.g. conservation, fisheries, water and sanitation), and between multiple organisations and actors. In theory these organisations, entities and interest groups are connected through rules that interact across hierarchies and structures so that problems can be addressed swiftly by the right people at the right level.	'There is shared responsibility on paper, but not in practice' 'The problem is bigger than just wastewater treatment, it is the entire catchment' 'Tensions occur because priorities differ between Knysna Municipality (with a focus on service delivery) and SANParks (with a focus on conservation)' 'Decision-making centres tend to work in silos and not all are pulling their weight	**1.** Decision-making centres and those playing critical supporting roles are clearly identified, spanning institutional levels local, provincial, national) and organisational forms (government, NGO, private). **2.** Decision-making centres and those with supporting roles are connected and take each other into account in competitive and co-operative relationships with mechanisms and resources for resolving conflicts and ensuring coordination across the system.
Collaborative governance = achieving coherence across diversity by acknowledging that no single party has all the answers and a lack of collaboration has negative consequences for all.	'The visitors coming on their annual holiday are completely uninformed / indifferent and show little respect for local rules and practices' 'Everyone may have a common understanding of what needs to be done, but sadly not much is being done' 'The Park Forum has been the best attempt to coordinate action' 'If we mess up the estuary everyone loses'	**3.** Decision-making centres have a shared understanding of key management challenges, agree on the need for collaboration, and cooperatively contribute towards a shared vision for the estuary. Broad buy-in reinforces a culture of compliance with rules. **4.** A leadership body plays an active and dynamic role in co-ordinating collaborative actions towards achieving the collective vision. This is done in a way that enables stakeholders to contribute and promotes trusting relationships.

Social learning = when individuals who care to make a difference participate freely to share their knowledge, expectations and uncertainties. Through deliberate and sustained interaction between diverse stakeholders, perspectives convergence and contribute to improved trust and decision-making.	'Existing forums are not sufficiently inclusive of the diversity of people that live in the catchment' 'The same people attend all the forums and get meeting fatigue, and don't send information on to others down the communication line.' 'Need to have different ways of engaging. What is available currently are long and boring forum meetings' 'Rather than having 14 meetings, how can we have one meeting? 'There needs to be a coordinating space to reflect on adaptation—this is a critical component for success'	**5.** Formally-coordinated social learning spaces are resourced and enable deliberate and sustained learning among multiple and diverse stakeholders **6.** Participation in social learning spaces contributes to integration of diverse forms of knowledge as well as the uptake of new knowledge in policy and decision-making.
Complexity thinking = acknowledging that outcomes in complex SES are poorly predictable and uncertain, and governance systems assuming predictability are likely to go wrong. Further, SES cannot be understood solely by studying individual parts of the system or through individual expertise, but rather require broadened and diversified participation at multiple interconnected levels, openness to new ideas, sharing of information, experimentation, learning, monitoring, evaluation and frequent adaptation.	'The Estuarine Management Protocol acknowledges social-ecological systems complexity, and the need for flexibility and adaptation' 'It is difficult to knit together the diverse flexible and inflexible legislative requirements. Coordinating across different mandates can sometimes compromise our ability to adapt and various institutions themselves often aren't adaptable' 'Monitoring happens at smaller or sporadic scales, and is primarily ecological. There is scope for more interdisciplinary research and monitoring' 'We do not have adequate understanding of the different mental models that exist across the stakeholders'	**7.** A holistic perspective underpins mental models (beliefs and assumptions about how the estuary works) and decision-making about Knysna Estuary. Appropriate systems models are used to explore interrelatedness between social and ecological components, identify key feedbacks and explore how changes to the system may influence the flows of services and disservices from the system. **8.** Management of Knysna Estuary is informed by sustainability science, i.e., research dealing with the interactions between natural and social systems with the aim of advancing the sustainability of the overall system.

(Table 11.4). Results and trends from some of these programmes are regularly disseminated to specific stakeholder groups, e.g. water quality parameters including *E. coli* counts are presented to the Estuary Authorities Pollution Committee and Park Forum. Nevertheless, transdisciplinary research and citizen monitoring programmes should play an increasingly valuable role in fostering stakeholder involvement in broad-based learning. This should include monitoring of key social-ecological feedbacks and critical slow variables, including trust, to also inform hypotheses of change and possible regime shifts.

Considerable research effort has been directed at Knysna Estuary over time, much of which is evident in this book. Strikingly, much has focussed

Table 11.4 Monitoring and research undertaken in the Knysna Estuary since 2018 that could form the basis of aspects of measuring and interpreting changes in aspects of the SES within an adaptive management system.

Monitoring undertaken in the Knysna system
Water quality in estuarine waters (three programmes) • Water quality of Wastewater Treatment Works and storm-water outlets • River flow • Water heights • Meteorology • Recreational and subsistence fishery—use and compliance • Acoustic tracking of tagged fish • Waterbird abundance
Recent research undertaken that could form the basis of future monitoring
• Ecology and diversity of seagrass beds • Meta barcoding of seagrass communities • Dynamics of saltmarsh and seagrass meadows • Saltmarsh elevation and response to sea level rises • Fish assemblages – spatial and temporal variability and habitat usage • Knysna seahorse status • Mud prawn standing stock and population structure • Alien species – status and trends • Underwater soundscapes • Recreation boat utilization

on specific parts or variables of this social-ecological system (Figure 11.7), primarily environmental studies focussed on estuarine biota and processes, the recently developed draft Situation Assessment Report for Knysna Estuary cites 210 references. While such knowledge forms important building blocks for understanding (e.g. ecology of Knysna seahorse, eelgrass and moonshine worms, fish diversity, etc.), these constituent parts cannot alone explain the overall behaviour of, flows from and/or tensions and trade-offs arising within Knysna Estuary's SES. Existing disciplinary research and understanding must be complemented by a systems perspective (Figure 11.7) to improve understanding of dynamics of the whole system[3] to inform management decisions.

Consideration of where the Knysna Estuary SES boundary (however porous) should be, will inform the 'unit of analysis'[2]. Studies can then be designed to consider ecological (resource system and resource units) and social (governance system and resource users) variables as well as those describing connections between these systems (interactions and outcomes) as shown in Figure 11.7[25]. There is very limited evidence of interdisciplinary studies (that draw on and integrate knowledge from across scientific disciplines) or transdisciplinary research (that also incorporates local and practice-based knowledge and involves non-academic stakeholders in a process of co-learning) for Knysna Estuary, at least in the formal scientific literature. However, one participatory assessment for the Knysna Catchment[19] forms the basis for presenting the relative supply of this estuary's diverse ecosystem services (Figure 11.3). The concept of tangible and intangible benefits or ecosystem services presents a unifying social-ecological concept to further understand and learn about the beneficiaries of the estuary's diverse services, how these are mobilised, appropriated and valued, and where conflicts arise and how trade-offs might be made. Nevertheless, how this research and learning is conceptualised, structured and shared with stakeholders needs thought and attention to facilitate social learning and complexity thinking which is essential for the management of Knysna Estuary (Table 11.3).

Adaptive evaluation of management and stewardship of Knysna Estuary

Monitoring, evaluation and learning are interrelated and often used together. We dealt with monitoring under adaptive implementation as one of its main challenges is resourcing and effective implementation. While learning is often depicted as an outcome of evaluation (feedback loops in Figure 11.9), important learning also occurs during all SAM steps or sub-processes and social learning is an explicit principle and aim of adaptive governance (Table 11.3). However, desired state workshops and focus group meetings and dialoguing during adaptive planning also enable stakeholders to learn about available knowledge, societal values and diverse expectations. Further, adaptive implementations provide opportunities to learn from management actions, research and monitoring. Creating awareness amongst stakeholders about the results of research and monitoring is vital to ensuring buy-in to the actions that result from it.

Formal and informal evaluation of management plan implementation takes place through various platforms in SANParks. These include a formal midterm review (after five years) with colleagues from the national Department of Forestry, Fisheries and Environment, semi-formal evaluation during science management meetings to discuss and reflect on implementation issues, and informal evaluation during quarterly stakeholder forum meetings. In addition, numerous compliance-based reporting tools exist (e.g. the Management Effectiveness Tracking Tool55). These assessments should be complemented with deeper reflection and evaluation. However, in practice, assessment-type learning tends to dominate and inadequately link to reflection in SAM[56]. Adaptive evaluation for Knysna Estuary should be strengthened by reflecting more purposefully and doing so in collaboration with stakeholders. Insights derived from deliberating deep questions (see box) should be captured as part of the institutional memory, and used to adapt the vision, objectives, management actions and monitoring protocols as and when required. Adaptive management will realise its potential when reflection takes place in combination with reflexivity, i.e. the ability of a group to adapt or reconfigure itself in response to reflection on its performance[57]. Indeed, a reflexive culture is acknowledged as an important virtue of adaptive environmental governance, which is even more urgent in the Anthropocene[58].

Purposeful reflection with stakeholders should include deep consideration of questions such as:

- is understanding of Knysna Estuary SES based on a robust systems model and is this under standing shared by stakeholders?
- is monitoring adequate, cost effective and feasible?
- have intended plans of operation materialized?
- were selected actions appropriate?
- were predicted outcomes correct and, if not, why?
- were outcomes actually acceptable?
- even if the predicted outcomes were correct and are acceptable, are the objectives and vision being met?

Adaptive management provides a context and model to guide natural resource decision making[59] yet problems associated with its implementation remain "legendary"[40]. These include, though are not limited to, an inability to invest meaningfully in and maintain financial and technical support for a required complex decision making framework; failure to engage meaningfully with all stakeholders in decision making; resistance to acknowledging uncertainty and the belief that all solutions are already known; risk aversion; emphasising short-term gains and losses over long-term benefits and costs; and importantly the lack of institutional commitment to initiate and maintain appropriate monitoring and assessment after adaptive decision-making[60]. It is also important to recognise that adaptive management may not be necessary for all resource problems, notably those where there is good understanding of the response of natural resources to management, and equally engagement or monitoring by itself is not enough to make a project adaptive[60]. Learning from the failings of past attempts from all around the world to implement adaptive management will help prevent the repetition of errors and fatal flaws, and increase the likelihood of successful collaborative decision-making.

Successful adaptive management in a multi-stakeholder environment rests on three abilities, namely to develop a robust and shared conceptualisation of the system (e.g. based on Figure 11.7); monitoring key variables to shed light upon this conceptualisation, and collective learning from the experience[32]. We add two further abilities, namely implementing actions that enable learning from their outcomes, and learning and reflexivity to adjust actions, strategies, policies and behaviour. All five abilities require investment of time and energy, honest and willing engagement and listening to all perspectives, and trust.

11.5 Conclusion

For all the wonderful biodiversity, beauty and sense of place that defines Knysna Estuary, conservation of this common-pool resource ultimately rests in the hands of people and their actions embedded in a complex social ecological system. Knysna Estuary is a public good delivering a wide range of material and non-material ecosystem services to a diversity of stakeholders, all of whom have a right to benefit from the estuary. Challenges include diverse and changing societal expectations, ongoing trade-offs, maintaining the diversity of relationships and trust, 'outsiders' who choose not to engage but criticise from the perspective of their own vested interest, maintaining ongoing learning and reflection, non-adaptive governance and funding mechanisms, and fatigue of authorities and stakeholders.

We also acknowledge ecological challenges from increased pressure on the estuary due to rapid development and expansion of Knysna, under-capacitated and failing municipal waste management infrastructure and climate change effects. The latter has many and compounding effects on an estuary such as Knysna leading to complex outcomes, which together with anthropogenic pressure may result in significant change to the system. This will likely include loss of some habitats due to sea-level rise, increased potential for alien invasion, and impacts on local species assemblages as water temperatures and salinity levels change under modified rainfall and runoff regimes and rising global temperatures, and species changes due to unsustainable use. We know that standardised solutions will not work but must rather take into account the local culture and institutional environment specific to Knysna Estuary[1], and that existing disciplinary environmental research must be broadened to also include more systemic social-ecological transdisciplinary enquiries.

So where do we go from here?

Numerous constructive engagement forums with different stakeholders exist including the park forum, the estuary authorities' pollution committee, Garden Route and provincial estuary forums, subsistence fisher forums and boat club/vessel users forum where issues are raised and ways forward sought.

However, the governance and management of Knysna Estuary is a multi-mandated and complex issue, which spans many interconnected social, political and ecological realities. This requires trade offs, and is an area of ongoing management engagement across these sectors. In Knysna, as elsewhere globally, there are tensions and trade-offs between conservation (as opposed to preservation) and human well-being objectives (which includes basic livelihood tangible benefits, recreation and a host of other non-material benefits). These realities pose challenges bigger than what can be solved or addressed by any one organisation. SANParks is heavily engaged with and working on numerous fronts to advance governance of Knysna Estuary, with the understanding that improved polycentric and collaborative governance as well as social learning and complexity thinking will lead to improved management.

Adaptive environmental governance relies on relationships, trust and ongoing co-learning among stakeholders, and the past two years have provided overwhelmingly positive experiences with many stakeholders who have chosen to participate in the process. We have also learned, in line with case studies from all over the world, that effective engagement requires involving diverse perspectives, acknowledging that no one has full understanding of the complex whole, that there is no one right perspective or solution, and that people start to learn together once they are comfortable with putting their own uncertainties on the table and respectfully listen to the uncertainties of others.

A beacon of hope for SANParks in the ongoing challenge of managing the complex Knysna Estuary system, is the recent rise of community activism — local individuals and groups who are passionate about making a positive difference through their individual and collective action and who are using innovative ways of doing so, together with SANParks. This is the first step in individuals taking responsibility for their own impacts, a vital step towards co-management of the estuary and towards the local Knysna community taking collective responsibility for the jewel of Knysna.

Further, we are embarking on the development of the Knysna Estuary management plan, as mandated by the national Estuarine Management Protocol. While SANParks takes the lead in this process, it requires extensive collaboration and cooperation from co-responsible authorities to take joint responsibilities for outcomes through their own mandates and actions. It will also include stakeholder engagement to develop a common vision, broad accountability and collaborative action. We hope that constructive engagements from all stakeholders and responsible authorities will result in both a better understanding of the context, challenges and management commitments, as well as allocation of the will and resources to act on these.

We recognise that stakeholders have many and varied expectations of the estuary and its management, which can pull in different directions based on individual values and needs. It is our hope though, that together and with concerted effort and energy, willingness to engage and collaborate, respectfully listening to all perspectives, and ongoing development of relationships and trust, we can collectively pool available resources and capacities to make a difference for all.

"For the Knysna area, the exquisite miniature landscapes of lakes, deep-cut gorges and headlands will need critical new sympathies from those that are beginning to understand their futures. On the economic side, the precise blend that prosperity should take in such a fine wild area will need to be analysed with the greatest care. Will this still be an Eden of South Africa in a thousand years' time?"

(extracted from the preface of A.V. Hall in *The Knysna Story* by Arthur Nimmo, 1976)

Sunset over the Knysna Estuary (Photograph: © Duran De Villiers).

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Chapter 12 : The Way Forward

Charles Breen & Alan Whitfield

"A beacon of hope for SANParks in the ongoing challenge of managing the complex Knysna Estuary system, is the recent rise of community activism — local individuals and groups who are passionate about making a positive difference through their individual and collective action and who are using innovative ways of doing so, together with SANParks. This is the first step in individuals taking responsibility for their own impacts, a vital step towards co-management of the estuary and towards the local Knysna community taking collective responsibility for the jewel of Knysna."[1]

12.1 Introduction

In this chapter we highlight major management issues raised by the authors in other chapters of this book. We also explore co-management arrangements and suggest how this can be realized for the Knysna Estuary. In addition, we identify management issues that offer opportunity for initiating co-management, an approach that offers considerable options in a way forward for this estuary.

If we are to "develop and apply goals for future sustainability, we must consider what people care about and what motivates them to engage in solving sustainability issues[2]". This draws our attention to the importance of understanding the relationship between caring, motivating and engaging in promoting sustainability.

What determines whether or not we care about a place such as the Knysna Estuary? And how can we use an understanding of 'care' to enable us to motivate residents and visitors to steward their use of the estuary in ways that enable progress toward sustainability? These are important questions that will guide us on mapping the way forward.

Because strong positive feelings of attachment to a place create a sense of rootedness, belonging, or an intense feeling of being at home, the deeper the sense of attachment we feel to the Knysna Estuary, the greater should be our commitment to care for it. But it goes further than this because the sustainability of communities is also a reflection of strength of attachment to place. This attachment to place is not something that has only recently become part of our being — it is something that was probably also part of the early *Homo sapiens* who made Knysna their temporary or permanent home.

But what then determines our sense of attachment? When we look at the three photographs in Figure 12.1 it becomes clear that for some, a subsistence fisher for example, attachment may be molded by dependence on the resources that can be harvested from the estuary. For others, it is a place of work or a place that can satisfy important needs such as recreation and relaxation. Place dependence therefore conveys an instrumental connection between people and place; people-place relationships that permit the achievement of needs and goals.[2]

For others though, the Knysna Estuary conveys something less tangible, more personal, how they identify with a place through for example, the imagery the estuary and surrounds evoke. For example, the sense of belonging, or the sense of place one may feel watching the tide surge through The Heads, or quietly observing a beautiful sunset or looking for interesting creatures along the shore. Through these connections, we become attached not simply to the place itself, but to the meanings that it holds for us. Place attachment and place meanings can be considered as dimensions of Sense of Place (SoP) (Figure 12.1). While place attachment emphasizes people-place bonds, Sense of Place refers to people's attachments and meanings associated with place, both individual or shared[3].

Because individuals and groups can hold quite different preferred meanings while exhibiting equally strong place attachment, their ideas about what is important about the estuary and how it should be used and managed can differ in fundamental ways. The meanings and attachment that people feel toward an estuary, shape their place-related behaviour. This link between Sense of Place and positive behaviour towards a particular natural environment, system or habitat, provides an opportunity for development and implementation of stewardship strategies[4].

12.2 Stewardship

Stewardship is the careful and responsible management of something entrusted to one's care, while management on its own is the 'act' or 'skill' of controlling and making decisions.

As we strive to secure the future of the estuary, and the benefits we derive from it, we realize that in

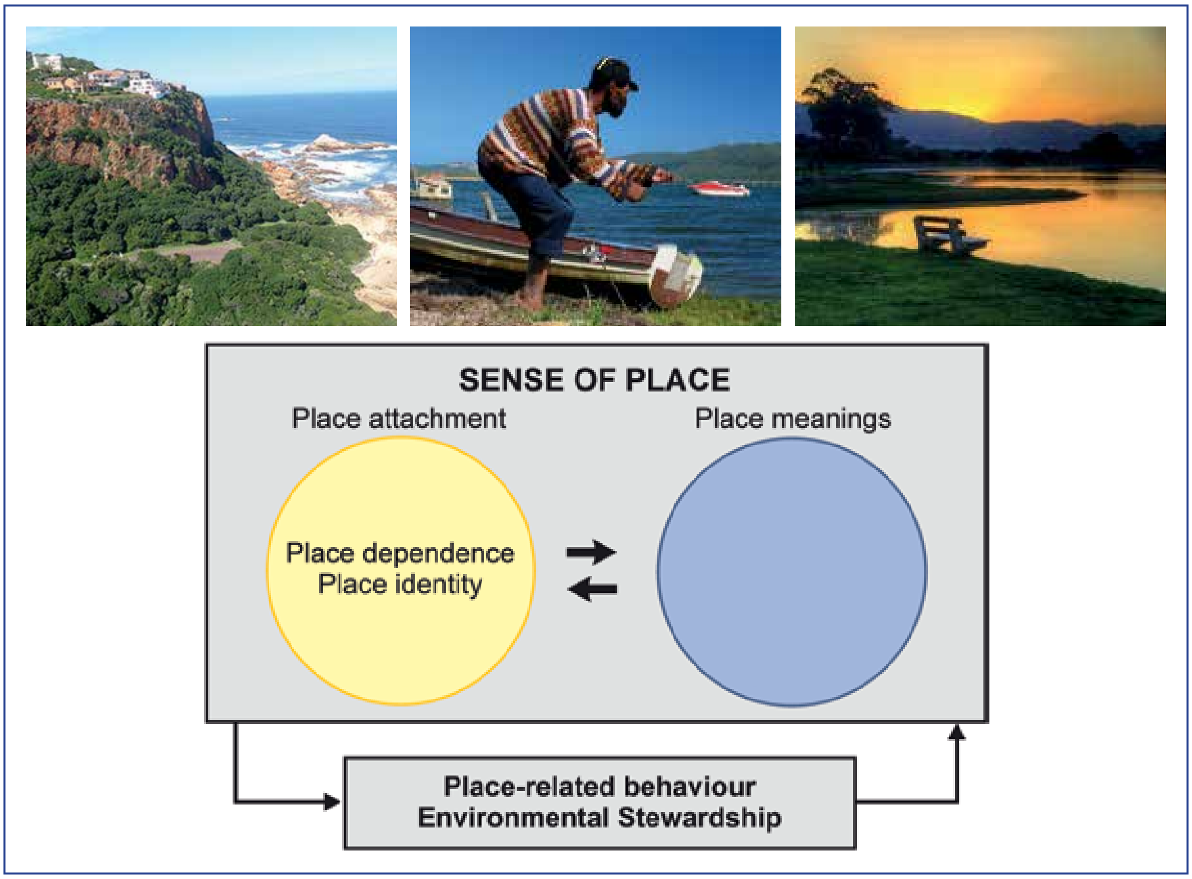

Figure 12.1 Dimensions of Sense of Place[2; 3], a concept that has relevance to the Knysna Estuary. (Photographs: Center: © Rob Tarr).

reality there is only one thing we can manage—our behaviours, individually and collectively. For it is what we choose to do or choose not do, and how we do it, that determines the state of the estuary and the services it provides. By committing to values and behaviours that direct use which accords with sustainability goals, we can create and sustain a shared long-term perspective and become individual and collective stewards of the estuary. While place attachment can provide a foundation for stewardship strategies, a diversity of place meanings and multiple kinds of attachment to place may also contribute to resilience and capacity to adapt to social change.

Local environmental stewardship has been defined as “the actions taken by individuals, groups or networks of actors, with various motivations and levels of capacity, to protect, care for, or responsibly use the environment in pursuit of environmental and/or social outcomes in diverse social-ecological contexts”[5]. Place meanings help to distinguish between different types of stewardship groups and to “describe different roles that civic engagement can take in environmental management”[6]. Intuitively we might understand Sense of Place as providing motivation for stewardship actions that promote sustainable outcomes. However, because of the multiple dimensions of SoP, it can create a spectrum of different place identities. Stewardship can develop along different pathways which may lead to different, even conflicting stewardship goals. Taking place meanings into account can help us “extend knowledge about how Sense of Place is linked to behavior, as well as better describe and understand the different pathways”[6]. The challenge in using SoP as a motivation for stewardship actions is to draw on those attributes that unite people in their commitment to place and to negotiate acceptable solutions to those political, ideological, and social issues that are contested and create conflicts about how people should interact with these places.

Stewardship is thus largely a collaborative endeavouring to bring together multiple, diverse stakeholders who may hold quite different attachments and meanings to, for example, a system such as the Knysna Estuary and the larger basin within which it is situated. In essence stewardship is driven by a shared desire for sustainability. Because of the uncertainty that characterises complex systems, it requires linking an adaptive approach to governance with an adaptive approach to management — "Adaptive governance provides an essential enabling context for adaptive management, especially where multiple governance regimes overlap (e.g. legislation from national, provincial and local government as well as different policy sectors) and where broader ownership of rules, decisions and responsibilities are desirable"[1] (see Chapter 11 for more details).

While stewardship can be personal, if it is to service the greater public good it must also occur within interactive and overlapping networks of civic, government, and private actors. Individuals need to consider themselves embedded in stewardship networks. It is through being active in such networks that people gain a sense of contributing to the local community's identity significantly and positively in ways that influence all of the possible management outcomes[1,7].

Although we are all connected through our direct and indirect use of the estuary, our needs and interests focus attention so that individually, we may be largely unaware of how and to whom we are connected and how dependent we are on the connections through which the benefits we gain from the Knysna Basin are generated. We manage for our own needs and interests and much less so for the connections through which these are serviced or for the implications our use may hold for others.

Sustainability in the long term requires that collectively we steward and manage the value chains and networks through which benefits and dis-benefits are generated and distributed. Reader[8] suggests that this requires us to see our personal roles as being caretakers, focusing on the duties that we owe other people and the organization as a whole. We must assume extended responsibility for the whole. This concept of organizational stewardship directs attention to how we establish, contribute to, and support an organization that enables and encourages a more cooperative environment focused on collective success.

Place attachment suggests a sense of 'ownership', even where an individual may not have legal ownership. There is a strong relationship between seeing our roles as caretakers and sense of ownership. Understandably, a weak sense of ownership lowers sense of responsibility and undermines development of roles as caretakers. Conversely, strengthening the sense of ownership, even where one may not have legal ownership, encourages responsible engagement and can contribute to positive outcomes, including stewardship[8].

The converse of a sense of ownership and stewardship is a perception of being disenfranchised, which can contribute to a psychology of dependency on those who are perceived to be the owners of resources[3]. We can envisage this in the context of the Knysna Estuary where a sense of being disenfranchised might prevail among those people who, for historical, social and economic reasons, feel excluded. It may also arise among those who perceive Government and its agencies to be the 'Owners' of the estuary to an extent that they are powerless, even though they may have skills and capacity to significantly contribute to long-term sustainability.

Dependence and disenfranchisement present significant barriers to engagement and our ability to capitalize on the potential of sense of place to motivate stewardship. Enabling participatory processes helps stakeholders to envisage and position themselves in natural resource-based value chains and networks, thereby facilitating participation in processes such as planning, decision making and monitoring. This helps to weaken the barriers associated with perceptions of ownership and disenfranchisement. Knowledge and understanding are, however, significant determinants of 'stewardship capacity' and the ability to engage meaningfully[5]. It is the purpose of this book to contribute to knowledge and understanding, thereby facilitating engagement.

Trade-offs, justice and legislation

Progress toward sustainability will require trade-offs. But not all stakeholders have the same influence in decision making. Turkelboom et al.[9] developed a stakeholder- centered framework of ecosystem service trade-offs to analyse ecosystem services trade-offs, drawing from 24 cases around the world (Figure 12.2). The framing identifies three categories of stakeholders:

- 'Influential users' have (significant) influence over the decisions made in relation to the trade-off, and at the same time face a negative or positive impact of the trade-off (e.g. farmers, foresters).
- 'Non-influential users' face a negative or positive impact of the trade-off, but have no or little influence on decision-making (e.g. citizens, tourists).
- 'Context setters' have a significant influence on the decision making, but do not experience directly the negative or positive impacts of the trade-off (e.g. administrations, municipalities).

In the Knysna Estuary situation, SANParks is both a context setter and influential user, thus placing this organisation in a unique position of power and influence. Furthermore, as the legal entity responsible for the management of the estuary, all options are possible. Hence, it is worth quoting from Chapter 11 of this book, namely "Legislation

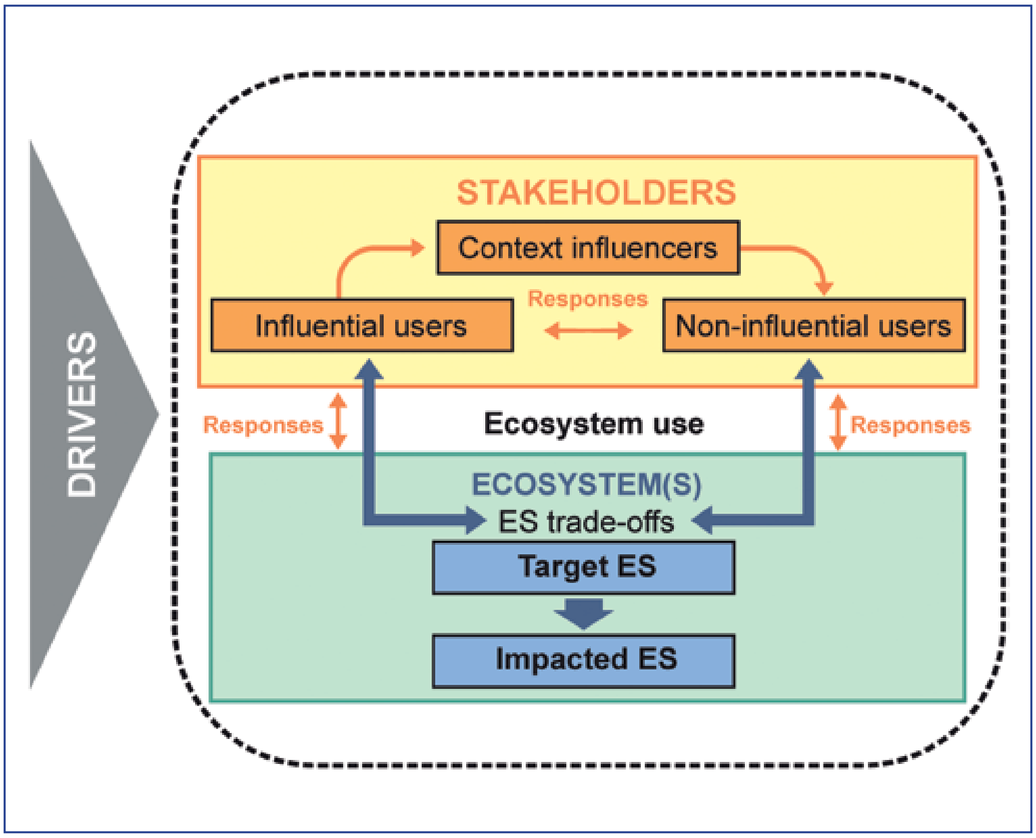

Figure 12.2 The Turkelboom et al.[9] study illustrates a stakeholder-centered framework of Ecosystem Services (ES) trade-offs.

BOX 12.1 LOCAL ASSETS AND GOVERNANCE SUPPORT FOR STEWARDSHIP CAPACITY

Local assets

- Capital: social, financial, physical, cultural, political, human and institutional

Broader governance

- Institutions: laws and policies, organizations, networks, and decision-making processes
- Structural processes: related to power and politics, economic inequality, discrimination, and exclusion from decision-making.

makes provision for adaptive co-management arrangements in national parks (NEM: PAA) and SANParks should actively explore this as a management paradigm for the Knysna Estuary"[1].

The study illustrates the complexity trade-offs, and particularly that "Influential users and Context setters are at the core of the trade-off decision making, but most of the impact is felt by Non-influential users". This leads to decisions being contested on the grounds of justice. Stewardship therefore requires careful attention to "ethically conscientious governance" that "is grounded in an explicit normative commitment to the promotion of justice"[10]. What makes this particularly challenging is the complexity of social-ecological systems (Chapter 11), the associated infrastructures, institutions and perceptions, and that new forms of vulnerability or injustice for certain social groups can emerge as complex social-ecological processes unfold across space and over time[11].

In the particular case of Knysna, O'Donohugue et al.[12] concluded that "if a city or municipality lacks the capacity to effectively respond with adaptation measures, local private wealth may dominate and result in haphazard adaptation responses to the detriment of regional adaptation planning efforts". However, the proposed Knysna Basin Compact as set out later in this chapter, should provide additional capacity and thus ongoing attention to justice that not only addresses the distribution of benefits and disbenefits, but also whether the needs of all potentially affected stakeholders are considered in the relevant processes. The Compact also needs to ensure that different stakeholders are not harming or otherwise negatively affecting others, thus facilitating a proper recognition of the needs of all. This understanding stresses the importance of implementing an adaptive approach to governance and management (see Chapter 11 for more details).

Approaches to advancing stewardship

An important first step towards securing the participation of stakeholders is broadening and deepening understanding of how, for example, the Knysna Estuary serves those who live, work and visit Knysna. Equipped with this knowledge and understanding, stakeholders are able to discern their positions in the value chains and networks. But the capacity to take stewardship actions is also enabled or constrained by local assets and broader governance factors[5].

Stewardship requires investment and planning. Biggs et al.[13] observed that in southern Africa "It is clear that many areas in the region require extensive investment to develop the necessary skills

Table 12.1 Filters mediating the flow of benefits from green and blue infrastructure to potential beneficiaries translated into an analytical framework for the assessment of GBI-related initiatives[10].

	Infrastructures	Institutions	Perceptions
Barriers	Which infrastructural barriers might have negatively influenced the realization of the initiative, and how have they been addressed?	Which institutional barriers might have negatively influenced the realization of the initiative, and how have they been addressed?	Which barriers related to the stakeholders' preferences might have negatively influenced the realization of the initiative, and how have they been addressed?
Enabling Factors	Which infrastructural factors might have positively influenced the implementation of the initiative, and how have they been strengthened?	Which institutional factors might have positively influenced the implementation of the initiative, and how have they been strengthened?	Which factors related to the stakeholders' preferences might have positively influenced the implementation of the initiative, and how have they been strengthened?
Trade-offs	What trade-offs have been considered, and how have they been solved?	What trade-offs have been considered, and how have they been solved?	What trade-offs have been considered, and how have they been solved?
Environmental Justice	How have the justice aspects been dealt with (here, in particular, distributional justice)?	How have the justice aspects been dealt with (here, in particular, procedural justice)?	How have the justice aspects been dealt with (here, in particular, interactional or recognition justice)?

and capacities to support sustainability transformations." Using an analysis of investment and planning initiatives in six case-study cities related to green and blue infrastructure (GBI), Kronenberg et al.[10] direct attention to the unintended consequences that "most typically resulted from the under appreciation of the complexity of social-ecological systems and — more specifically — the complexity of the involved infrastructures, institutions, and perceptions". Drawing from Anderson et al.[14], they developed an analytical framework that focuses on three "systemic filters that mediate the flow of benefits: infrastructures, institutions, and perceptions, and how they influence the ES potential, mobilization, and realization". The importance of the ENABLE framework (Table 12.1) lies in the structure it brings to identifying which questions to ask and to providing input to an informed discussion of the relevant knowledge needs that should guide planning and investment.

"In 2018 a process was initiated to revise the Garden Route National Park Management Plan of 2012. Over two years, more than 500 stakeholders participated in seven 'desired state' workshops and 14 thematic focus group meetings (Figure 11.11). The outcome of this extensive adaptive planning process is a co-created mission and objectives hierarchy for GRNP (Figure 11.12)"[1]. Implied here is that this will lead to co-management, as enabled by the National Environmental Management: Protected Areas Act, 2003. But how do we build the capacity required for and secure the resources and commitment to engage in co-management? Do those who engage these workshops see themselves as partners in a joint venture that achieves its objectives by jointly solving problems, sharing resources, cooperating, coordinating and building coalitions in which participation is governed by co-management agreements?

There are a number of examples in the literature of how stewardship capacity can be built and actioned. For example, although much larger and more complex than the Knysna Basin system, it is instructive to consider the stewardship approach instituted for Puget Sound in the USA[15]:

"After efforts to address Puget Sound's decline, former Washington Governor Christine Gregoire, through the legislature, created the Puget Sound Partnership in 2007. The Partnership's key task is to lead and coordinate ecosystem restoration and protection efforts, working with a range of partners including tribal, state, federal, and local governments. Although a non-regulatory agency, the Partnership collaborates with a range of partners to monitor and manage recovery. The Partnership is governed by an environmental governance regime known as the Management Conference, which includes the aforementioned partners and overseeing bodies, that include the Leadership Council, Ecosystem Coordination Board and Science Panel, all of whom embody different roles and responsibilities. For example, the Science Panel is comprised of regional scientists and ensures the Partnership develops a science-based recovery plan for the region."

"Vital signs (indicators) are a key aspect of the Partnership's efforts. These indicators measure both biophysical attributes of ecosystem health and environmentally specific social indicators of human well-being. Biophysical indicators include abundance of chinook salmon, Pacific herring, and orca whales, for example, whereas human well-being indicators include average general public rating of their sense of place, and frequency with which the general public engages in environmental stewardship activities. This work contributes to regional research focused on sense of place in the region, including paralleled indicator work that has highlighted the distinct sense of place among the region's indigenous population. Unlike the biophysical indicators that are monitored and updated by external partners, many of the human well-being indicators are monitored by a regional general public human well-being survey conducted every two years to track change or recovery goal progress over time."

"The Washington State Legislature created the Puget Sound Partnership to coordinate and lead the effort to protect and restore Puget Sound through a strategic, prioritized, science-based Action Agenda that addresses all of the complex connections among the land, water, web of species, and human needs. The Action Agenda charts the course for effective collective action. Benefits of the Action Agenda include:

- Identifies regional priorities to ensure resources are being invested in actions that drive recovery outcomes.
- Describes the recovery resource needs locally, regionally, and nationally.
- Provides a credible plan to make funding decisions more efficient and effective."

The Puget Sound Partnership may assist in providing a foundation or guide for developing a Way Ahead or Action Agenda for the Knysna Basin.

Knysna Basin stewardship

Just as the health of the estuary is strongly influenced by marine drivers, it is increasingly apparent that estuary health also reflects how effectively land-based processes are stewarded and directed toward long-term sustainability. If the Knysna Estuary is to remain the 'Jewel of the Garden Route', our stewardship concept and practices must extend to encompass the basin as an integrated, complex social and ecological system (see Chapter 11 for details). But it is not only about spatial scale; our stewardship actions must be directed at the long term, particularly given the anticipated trends in climate change and biodiversity loss[16], and all parties must commit to serving the greater goal.

The South Florida's Compact for local climate change solutions[17] provides an example of how this can be achieved at a larger scale than the Knysna Basin. The notion of a Compact is important because it reflects the formal agreement among parties that they are committed to, and will work in partnership to promote resilience. As we raise our collective goal, the more opportunities we create for inclusivity in our stewardship endeavours and the better positioned we are to prepare for, mitigate and adapt to climate change and other forces that undermine resilience.

Drawing from the examples above, we can anticipate that there will be barriers to achieving collective stewardship among citizens and other stakeholders, and these can also confound attempts by government and its agencies to promote and share capacity for collective stewardship. This explains the significance that should be attached to the processes adopted for constituting the Puget Sound Partnership and the South Florida Compact, and for establishing supporting governance and operational procedures. While a 'traditional' approach has been to look to the regulatory agencies to lead and coordinate efforts to promote estuary management, what is required is a non-regulatory agency, the Knysna Basin Partnership, formed through a Compact among interested and affected parties.

The purpose of the Compact would be to initiate and sustain collective stewardship within the Knysna Basin and further afield, as may be required to promote resilience in the face of climate change and other forces that pose a risk to sustainability. When the NGO InterAction launched its Climate Compact Committing to Environmental Action and Sustainability on Earth Day 2020, it had this to say about the Compact: "With commitment from Members, it will start collective action, generate dialogue and learning, quickly advance initial actions,

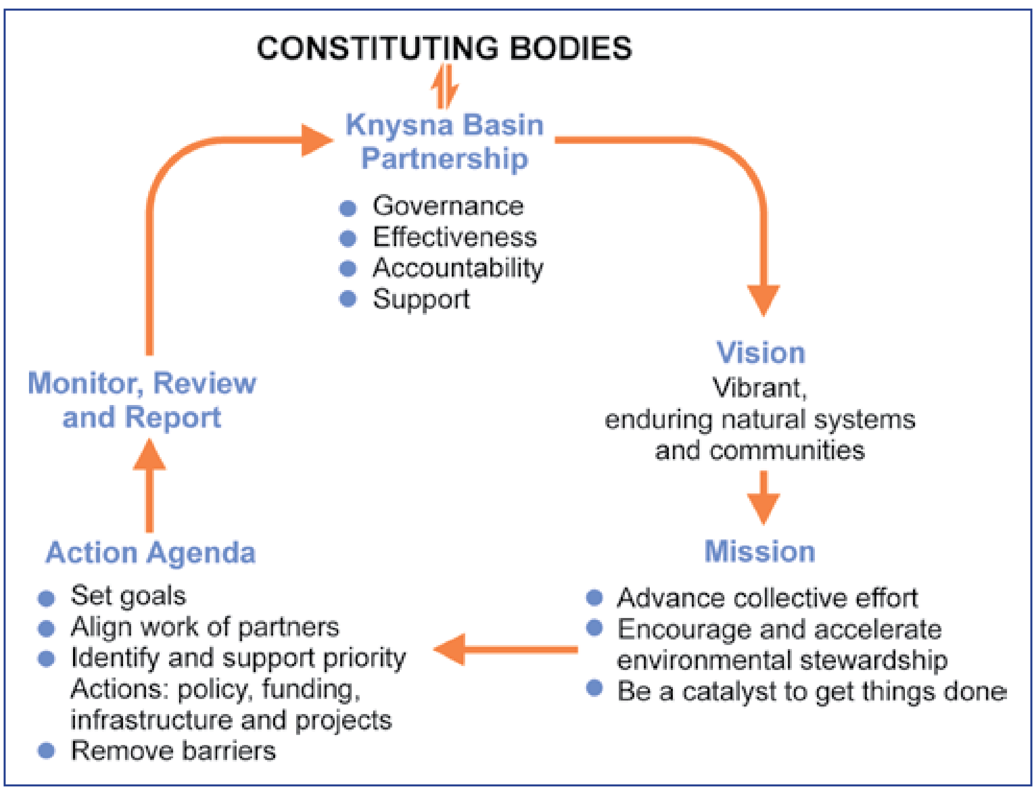

Figure 12.3 Concept diagram showing the elements required for a Knysna Basin Partnership that promotes actions to ensure a 'healthy' estuary for all.

and kick-start initiatives that will lay the groundwork for more behaviour and attitudinal shifts in the years to come"[18]. Similarly, the proposed Knysna Basin Compact would work to connect and leverage the efforts of individuals and organizations working on a shared mission to secure the social and ecological health of the Knysna Basin by setting goals and achieving them through actions specified in the common framework of a Knysna Basin Action Agenda (Figure 12.3). What are some of the matters that would be considered for the proposed Action Agenda? It is helpful to consider these in at least two categories: those requiring long term investment in the Partnership, such as climate change, and those where the goals can be achieved in much shorter time scales.

Stewardship for climate and global change resilience

What is a jewel without its setting? While the Knysna Estuary is unique within South Africa and even further afield, it is within the Garden Route that the jewel finds its maximum expression, giving it a strong, timeless identity. However, this identity is threatened by both climate and global changes that afflict many of the estuarine systems around South Africa's coast (Chapter 10). Examples of global change impacting on the Knysna Estuary are habitat degradation, sedimentation, pollution, invasive species proliferation and resource over-exploitation.

According to the Knysna Municipality, the estuary and surrounds "have suffered almost all of the climate-driven disasters anticipated in the Western Cape and South Africa as a whole." Climate change resilience must therefore be understood as an integrated collective effort at basin and larger scale. While the Eden District Climate Change Adaptation Plan is "primarily adapting to climate change it also highlights that the key mitigation aim for the Eden District Municipality is to invest in ecological infrastructure to ensure that current ecosystem services are not lost or reduced." The Adaptation Plan also stresses the "need for increased awareness campaigns and education programmes in the Eden District Municipality regarding climate change and its predicted effects". A key barrier to responding to climate change in this municipality is the need to enhance institutional capacity and capacity-building (including in disaster management) as well as financial resources at both the district and local municipality levels."

Paul Allen[19] observed that inaction and apathy do not stem from ignorance or even indifference. Rather it is a result of a lack of leadership (both cultural and political) and the lack of a framework that supports change and inadequacies in the way we are encouraged to see the challenge in relation to our own lives. He goes on to stress that "Positive action unites us, and encourages those who don't yet see the need to act. And, positive stories of collective action can counter feelings of helplessness, scepticism or detachment, and show that others care".

The Knysna Basin Partnership through its Programme for Climate and Global Change Resilience (Figure 12.4) will actively collaborate with the Knysna Municipality, the Eden District Municipality, South African National Parks, and other interested and affected parties to promote a Resilience Pathway that is structured around delivering

BOX 12.2 PROPOSED KNYSNA BASIN PARTNERSHIP PROGRAMME

Knysna Basin Partnership Vision

- Resilient environmental and ecological systems
- Resilient people and livelihoods
- Resilient businesses and economies

Knysna Basin Resilience Workshop Programme

Introduction

- Session 1: Situation Assessments
- Session 2: Climate Risk Assessments
- Session 3: Global Change Assessments
- Session 4: Mitigation and Adaptation Strategies
- Session 5: Climate and Global Change Compact
- Session 6: Action Plan

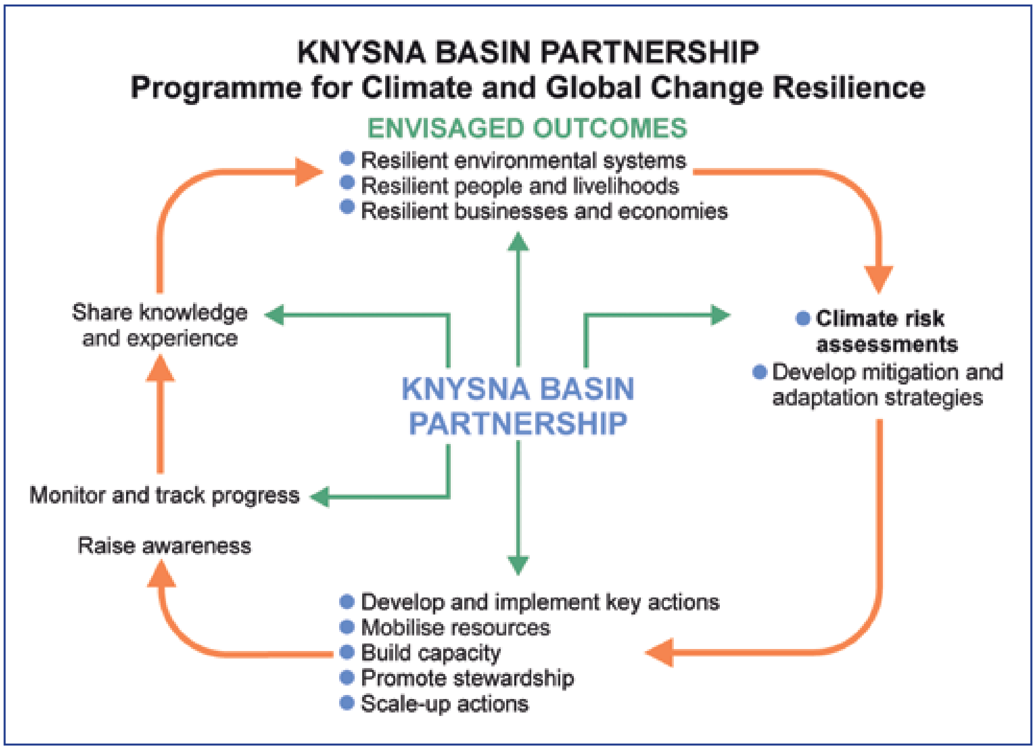

Figure 12.4 Diagrammatic representation of the cycle of partnership activities required to promote resilience of the Knysna system to climate and global change pressures.

the overall vision and through three outcomes: resilient people and livelihoods; resilient businesses and economies; and resilient environmental and ecological systems. It will provide leadership, capacity and help to develop the positive stories that will enable and advance stewardship for climate and global change resilience while also addressing more immediate management issues.

To set the platform for establishing the Knysna Basin Programme for Climate and Global Change Resilience it will be necessary to motivate for the Compact that will secure commitment among partners, develop an Action Plan and motivate investment. To this end interested parties need to promote a Knysna Basin Climate and Global Change Resilience Workshop (Box 12.2) at which the Compact and Action Plan can be developed.

Stewardship for more immediate management issues

Early success reinforces commitment. A number of Knysna specific management issues have been raised by the authors of the various chapters in this book and possible ways of addressing these have been suggested. Elimination or amelioration of some of these pressures need to be explored and action initiated by the Knysna Basin Partnership, including:

- There are many Knysna residents for whom the estuary holds little meaning — attachment to the estuary is weak and does not shape behaviour. There are others who are concerned and would like to promote stewardship but who are not empowered to engage, and feel disenfranchised. How does the Vison for the Knysna Estuary become one that is owned by all? How are more people enabled to become included in the Action Agenda and feel motivated through inclusion? This requires that specific attention is given among others, to enabling those whose homes may be far from the estuary but whose lifestyles determine the state of the estuary in significant ways, to take 'ownership' of the Vision and become environmental stewards (Figure 12.5).
- A careful assessment and response to the growing tendency of creating hard wall structures around the perimeter of the estuary in response to intertidal progression towards the supratidal zone (Figure 12.6). This natural progression of the estuary margins to create new and higher intertidal areas is likely to accelerate as a result of global warming

Figure 12.5 Widespread community involvement in helping maintain Knysna Estuary health is vital for the future of the system (Photograph: © Megan Taplin).

Figure 12.6 A failed attempt to prevent the expansion of the southern shore of the Knysna Estuary using a precast concrete fence structure. Such hard structures in selected areas should be removed to allow the estuary to follow its natural evolutionary path (Photograph: © Alan Whitfield).

Figure 12.7 The Knysna River entering the estuary. Note the Department of Water & Sanitation's water level recorder in the lower right of the picture (Photograph: © Alan Whitfield).

Figure 12.8 Bulldozed alien vegetation on the banks of the upper Knysna Estuary (Photograph: © Alan Whitfield).

and sea level rise. Research needs to be conducted to identify those littoral estuarine areas around Knysna most likely to impact on adjacent developed land, and to plan for the mitigation of both human and environmental costs associated with such water level increases. Some areas may be prioritized for hard structure protection, whereas others may be allowed to erode naturally to create new intertidal areas associated with the rising sea level.

- River flow is a vital component and driver of any estuarine ecosystem — and the Knysna system is no exception (Figure 12.7). The Department of Water & Sanitation's Water Reserve for the maintenance of the ecological functioning of the Knysna Estuary needs to be fully implemented and monitored. This will become increasingly important as the Knysna population grows, and demands on the freshwater supply from the Knysna River increase. Human pressures to impound the Knysna River will increase in the future, and any decision to build a dam on the river will have far reaching consequences in terms of river-estuarine-marine connectivity and the natural functioning of the estuary.
- The proliferation of invasive vegetation in the river catchment area needs to be controlled in a measured way that takes into account the re-establishment of indigenous plants in cleared areas (Figure 12.8). The techniques and approaches used in terms of alien tree replacement by indigenous forest species in the Pledge Nature Reserve needs to be extended to other parts of the Knysna River catchment. Alien invasive trees use large amounts of ground water, destroy natural river sponge areas, and high riverine infestations block natural river flows to the estuary. The replacement of these invasives by indigenous vegetation, including fynbos, will greatly assist the natural functioning of the estuary, both in terms of freshwater flow and reduced riverine sediment inputs. This action will require new and sustained employment of large numbers of people to undertake the catchment rehabilitation.
- Increasing sedimentation of the Knysna Estuary caused by the exposure of terrestrial sediments to water erosion, particularly during high rainfall events, needs to be reduced from current levels if the water depth of the estuary is to be maintained. In addition, sediment yields from agricultural and forestry land in the catchment needs to be monitored and disturbance of riparian areas along rivers and their tributaries kept to a minimum. Harvesting of commercial plantations needs to be carefully planned and implemented to re-

Figure 12.9 A portion of the railway bridge traversing the lower Knysna Estuary. This defunct bridge and earthen approaches need to be removed in order to restore natural hydrodynamic processes to the system (Photograph: © Alan Whitfield).

duce sediment erosion into streams that ultimately flow into the Knysna River and estuary.

- Possible removal of the now defunct Knysna rail bridge and associated landfill embankments (Figure 12.9) needs to be explored and the full hydrodynamic functioning of the estuary in this area restored. In addition, from a visual (aesthetic) perspective, the lagoon would thus be restored to its original condition. This project, although likely to be expensive, will bring much needed employment to the Knysna community.
- Water pollution in the form of waste effluent from the Knysna processing plant entering the estuary (Figure 12.10) needs to be reviewed and alternatives explored. In addition, the consequences of chemical or industrial spills entering the Knysna Estuary following accidents needs to be explored and preventative measures put in place. The close proximity of the N2 to the estuary in terms of a possible truck accident spill also needs to be recognized.
- Plastic and other waste inputs into the Knysna Estuary (Figure 12.11) need to be controlled, with litter in the intertidal and subtidal areas also being removed as part of the regular municipal clean-up programme that takes place along fringing pathways and open recreational areas.
- Eelgrass beds are a keystone habitat for many invertebrates and fishes of the Knysna Estuary. The decline in the extent of these beds is of serious ecological concern. This trend needs to be carefully monitored and the current negative pressures of destruction caused by bait harvesting methods, outboard propeller track digging and swash, and algal infestation due to eutrophication (Figure 12.12), all need to be reversed.
- Bait harvesting needs to be limited to those areas where it is specifically permitted and the legal numbers of different bait organisms harvested rigidly enforced by regular patrols. Respect for bait sanctuary areas also needs to be part of the law enforcement duties and the appointment of honorary monitors to assist SANParks in these duties needs to be implemented. The compulsory use of 'prawn pumps' that have a valve that prevents the extraction of sediment 'castles' following each 'pump' (Figure 12.13) needs to be explored.
- Strict adherence to fish bag limits and size regulations for the different species needs to be actively pursued. In addition, the education of anglers and subsistence fishermen regarding the importance of these regulations (Figure 12.14) in ensuring healthy fish stocks for the future also needs to be promoted. Catch and release angling needs to be encouraged whenever possible and fishing competitions

Figure 12.10 Foam and processed effluent water leaving the Knysna Waste Water Treatment Plant and about to enter the Ashmead Channel area of the estuary (Photograph: © Alan Whitfield).

Figure 12.11 An example of macroplastic pollution of the Knysna Estuary—in this case the dumping of a supermarket trolley into a salt marsh channel (Photograph: © Alan Whitfield).

Figure 12.12 Eelgrass (*Zostera capensis*) is visible in the top of this Ashmead Channel intertidal picture but an algal mat has smothered any eelgrass development in the central and lower sections (Photograph: © Alan Whitfield).

Figure 12.13 Sand and mud 'castles' created as a result of prawn pumping in the Knysna Estuary intertidal area. These sediments smother growing eelgrass and result in the desiccation of small non-bait invertebrates associated with the 'castle' (Photograph: © Alan Whitfield).

prevented from taking place in the Knysna Estuary.

- Disturbance of wading bird populations by unleashed dogs should be prevented and relevant local legislation promulgated to achieve that goal. This is particularly important during the summer months when Palaearctic migrants are present and are totally dependent on the Knysna Estuary for food.
- Speed boating should be discouraged in the Knysna Estuary by restricting the areas in which high-powered boats can operate to a minimum. Most of the estuary should be designated for sail boarding, canoeing, yacht sailing and rowing, with outboard powered boats only permitted to enter such areas at idle speed (Figure 12.15).

12.3 Research for the future

Monitoring of the 'health' of the Knysna Estuary (Figure 12.16) is a key action that will determine the effectiveness of any stewardship actions implemented by management authorities and the associated community. The following research needs were recently identified by a report to the Western Cape Government (Environmental Affairs and Development planning) to fill knowledge gaps and provide supplementary data for monitoring programmes that will inform management of the estuary[20]. The report suggested that SANParks, through the Scientific Services Division, approach tertiary and research institutions such as Universities, CSIR, SAIAB, SAEON and the Knysna Basin Project to create an awareness of what is required. The following projects/studies were recommended by the 2017 Knysna Estuary Management Plan[19]:

- Assess the influence of hydrodynamics on the recruitment of both invertebrates and vertebrates into the Knysna Estuary.
- Assess the influence of human disturbances on the population structure of invertebrates associated with submerged macrophyte beds, especially eelgrass, within the different reaches of the estuary.
- Examine the nutrient dynamics within the estuary, with particular reference to the role of nutrient cycling within the submerged macrophyte beds. Clearly the reduction in fresh water inflow into the estuary has been associated with decline in the overall availability of macronutrients within the system, but other point sources have increased input. This needs to be investigated further through a new study.
- Examine the potential influence of global climate change on the ecosystem dynamics within the estuary. Recent studies suggest that global climate

Figure 12.14 Fish and bait regulations are designed to ensure the sustainability of these resources for both anglers and subsistence fishers (Photograph: © Alan Whitfield).

Figure 12.15 All boat users need to pay respect to other users of the Knysna Estuary. There also needs to be awareness of the harm caused to aquatic biota by high speed power boating (Photograph: © Sooth Sayer).

change is likely to be associated with changes in the coastal rainfall and in disturbances to the oceanographic regime, including increases in sea water temperature. Such changes are likely to be associated with an extension in the home range of several species, including tropical invasive species.

- On-going monitoring of fisheries, comprising both bait and fish. Key elements include fishing/collecting effort, catch per unit effort, target fish species, catch composition, bait utilization in relation to existing regulations, motivation for using resource, economic value of the fishery, degree of compliance and conflict between different fishing fraternities. Particular attention needs to be given to monitoring and conservation strategies relating to white steenbras in the Knysna Estuary. The population of this iconic and important South African endemic species has been depleted by more than 90% compared to pristine stocks, and the Knysna Estuary is probably the most important estuarine nursery area for this species along the entire southern Cape coast.
- Invertebrate organisms primarily used for bait. Key elements should include densities (in and outside sanctuary area and in control areas), recovery periods after disturbance (collecting and trampling that alter habitat), community structures before and after disturbance, effect of pollutants in the sediment, mortality due to birds foraging after collection activities, effect on birds by bait collectors (both use same area at low tide) and larval settlement times, location along the tidal cross-section (avoid these areas at specific times).
- While the 2017 Estuary Management Plan suggests "Current efforts at determining the carrying capacity of the estuary need to be completed so that informed decisions can be made about the numbers of users from different user groups", it is now generally accepted that because of the inherent complexity and variability associated with social ecological systems, it is impractical to attempt to establish 'carrying capacity'. Rather, when implementing an adaptive management approach, managers use a series of monitoring endpoints known as thresholds of potential concern (TPC) to establish the upper and the lower levels of accepted variation in social ecological systems that can be used inform decision making. Some data can be collected as part of the ongoing monitoring programmes, but aspects such as sense of place, pollution due to engine emissions, and incidents of confrontation between user groups will need to be addressed by a dedicated project.
- A comparison between biodiversity and habitat health within the sanctuary area compared to the

Figure 12.16 This photograph shows the Department of Water Affairs & Sanitation flow gauging weir at the head of the Knysna Estuary. Regular monitoring of Knysna riverine water quality and quantity inputs, together with a range of estuarine 'health' indicators, is required for future wise management of the system (Photograph: © Alan Whitfield).

conservation areas in the rest of the system. An aspect that should be included is the response of communities (plant and animal) to freshwater pulses, instream flows and contaminants.

12.4 Some preliminary conclusions

"Legislation makes provision for adaptive co-management arrangements in national parks (NEM: PAA) and SANParks should actively explore this as a management paradigm for the Knysna Estuary[1]." This legislation establishes a platform for enabling stewardship within the Knysna Basin. But stewardship requires informed, active engagement in co-ordinated endeavour that is conscious of the complexity of social-ecological systems and the need for an adaptive approach to governance and management. Such an approach ensures justice in the sharing of benefits and consequences that arise from management actions. This presents a challenge when there is a history of disenfranchisement and when many may be unaware of how estuary goods and services influence their lives. Stewardship needs to be enabled. Experience from other parts of the world alerts us to the 'barriers' that may be experienced when initiating stewardship. We will have to commit to new ways of thinking and doing if we are to enable stewardship. If we can do this, and stakeholders become partners, we can broaden and strengthen the senses of 'ownership' and 'attachment' that are necessary to align and reinforce behaviours that are consistent with a shared Vision and Action Agenda.

Estuaries are naturally resilient ecosystems. What this means is that they are tolerant of considerable external pressures, both natural and anthropogenic, and still remain as a functional estuarine system[21] — although not as optimal as would be the case if these pressures are removed. Just because estuaries are resilient and have the ability to 'bounce back' from most perturbations, does not mean it is justified to 'abuse' these systems. If the abuse is of a structural (e.g. harbours or bridges influencing hydrodynamics) or persistent (e.g. waste water inflow) nature, then estuarine degradation is likely to become entrenched — to the detriment of both the aquatic biota and people using the estuary. This chapter summarizes a number specific artificial 'pressures' impacting on the Knysna Estuary. Removal or amelioration of these impacts will have a major positive influence on the 'health' of the system in the future, resulting in increased diversity, biomass and productivity of important invertebrates, fishes and birds associated with the estuary. These responses will benefit all people associated with the estuary.

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View over Leisure Isle towards Thesen Island and Knysna town (Photograph: © Peter Betts).

Appendix 1

Knysna Estuary Flora and Fauna

Macroalgae and Plants

Species nomenclature is in accordance with AlgaeBase (www.algaebase.org) for macroalgae and the International Plant Name Index (www.ipni.org).

FAMILY	SCIENTIFIC NAME	COMMON NAME
	MACROALGAE	
Bonnemaisoniaceae	*Asparagopsis taxiformis*	Red sea plume
Caulerpaceae	*Caulerpa filiformis*	Strap caulerpa
Cladophoraceae	*Chaetomorpha* sp.	None
Cladophoraceae	*Cladophora* sp.	None
Codiaceae	*Codium fragile*	Fragile upright codium
Codiaceae	*Codium lucasii*	None
Codiaceae	*Codium tenue*	None
Dictyotaceae	*Zonaria tournefortii*	None
Gelidiaceae	*Gelidium pristoides*	Saw-edged jelly-weed
Gigartinaceae	*Chondrus crispus*	Sea moss
Plocamiaceae	*Plocamium corallorhiza*	Coral plocamium
Rhodomelaceae	*Polysiphonia* sp.	None
Sargassaceae	*Sargassum binderi* var. *incisifolium*	Different-leafed sargassum
Scytosiphonaceae	*Iyengaria stellata*	Starred cushion
Splachnidiaceae	*Splachnidium rugosum*	Dead man's fingers
Ulvaceae	*Enteromorpha* sp.	None
Ulvaceae	*Ulva clathrata*	Tangleweed
Ulvaceae	*Ulva hookeriana*	Sea lettuce
Ulvaceae	*Ulva lactuca*	Sea lettuce
	SUBMERGED MACROPHYTES	
Hydrocharitaceae	*Halophila ovalis*	Spoon grass
Zannichelliaceae	*Zannichellia palustris*	Horned pondweed
Zosteraceae	*Zostera capensis*	Cape dwarf-eelgrass
	INTERTIDAL AND SUPRATIDAL SALT MARSH	
Aizoaceae	*Disphyma crassifolium*	Rounded noon-flower
Amaranthaceae	*Salicornia capensis*	Glasswort/marsh samphire
Amaranthaceae	*Salicornia decumbens*	Glasswort/marsh samphire
Amaranthaceae	*Salicornia littorea*	Glasswort/marsh samphire
Amaranthaceae	*Salicornia meyeriana*	Glasswort/marsh samphire
Amaranthaceae	*Salicornia natalensis*	Glasswort/marsh samphire
Amaranthaceae	*Salicornia pillansii*	Glasswort/marsh samphire
Amaranthaceae	*Salicornia tegetaria*	Glasswort/marsh samphire

Asteraceae	*Cotula coronopifolia*	Brass buttons
Asteraceae	*Poecilolepis ficoidea*	None
Caryophyllaceae	*Spergularia glandulosa*	Sea-spurry
Chenopodiaceae	*Chenolea diffusa*	Sout-bossie
Juncaceae	*Juncus acutus*	Spiny rush
Juncaceae	*Juncus kraussii*	Incema/Sea rush
Juncaginaceae	*Triglochin buchenai*	Lower tidal arrow grass
Plantaginaceae	*Plantago crassifolia*	Fleshy plantain
Plumbaginaceae	*Limnolium crustaceophikum*	Cape sea lavender
Poaceae	*Sporobolus maritimus*	Small cordgrass
Poaceae	*Sporobolus virginicus*	Seashore dropseed
Poaceae	*Stenotaphrum secundatum*	St. Augustine grass
Rubiaceae	*Galium capense*	Tiny-tots
Theophrastaceae	*Samolus porosus*	Water pimpernel
	SALT MARSH/TERRESTRIAL ECOTONE	
Aizoaceae	*Carpobrotus edulis*	Hottentot-fig
Aizoaceae	*Drosanthemum candens*	Sea dew vygie
Aizoaceae	*Aizoon secundum*	Comb brackbush
Aizoaceae	*Tetragonia decumbens*	Dune spinach
Aizoaceae	*Tetragonia fruticosa*	Kinkelbossie
Amaranthaceae	*Atriplex semibaccata*	Berry saltbush
Amaranthaceae	*Chenopodium phillipsianum*	Nama goosefoot
Asteraceae	*Gazania linearis*	Treasure flower
Asteraceae	*Nidorella ivifolia*	Bakbos
Asteraceae	*Nidorella pinnatifida*	Veldkruid
Asteraceae	*Senecio juniperinus*	None
Asteraceae	*Senecio pterophorus*	Common ragwort
Campanulaceae	*Lobelia anceps*	Angled lobelia
Crassulaceae	*Crassula biplanata*	Klipblom
Malvaceae	*Anisodontea scabrosa*	Sandroos
Poaceae	*Diplachne fusca*	Sprangletop
Poaceae	*Ehrharta calycina*	Perennial veldt-grass
Poaceae	*Pentaschistis aspera*	None
Primulaceae	*Samolus valerandi*	Seaside brookweed
Rubiaceae	*Anthospermum prostratum*	Creeping flowerseed
	REEDS AND SEDGES	
Cyperaceae	*Cyperus crassipes*	None
Cyperaceae	*Cyperus laevigatus*	Smooth flatsedge
Cyperaceae	*Isolepis cernua*	Fibre optic grass
Cyperaceae	*Schoenoplectus scirpoides*	Steekgrassie
Poaceae	*Phragmites australis*	Common reed
Polygonaceae	*Rumex* sp.	Sorrel
Typhaceae	*Typha capensis*	Cape bulrush

Invertebrates

All species nomenclature follows that given in the current World Register of Marine Species (www.marinespecies.org), as accessed during July/August 2020. Records of molluscs based only on untenanted shells are not included.

FAMILY	SCIENTIFIC NAME	COMMON NAME
	PORIFERANS (Sponges)	
Halichondriidae	*Hymeniacidon perlevis*	Breadcrumb sponge
	CNIDARIA (Hydroids, anemones, soft-corals, jellyfish, etc.)	
Actiniidae	*Actinia ebhayiensis*	Plum anemone
Actiniidae	*Bunodactis reynaudi*	Sandy anemone
Actiniidae	*Bunodosoma capense*	Knobbly anemone
Actiniidae	*Korsaranthus natalensis*	Candy-striped anemone
Actiniidae	*Pseudactinia flagellifera*	False plum anemone
Alcyoniidae	*Alcyonium fauri*	Purple soft coral
Cerianthidae	*Ceriantheopsis* sp.	Tube anemone
Eudendriidae	*Eudendrium deciduum*	None
Gorgonidae	*Eunicella albicans*	Flagellar sea fan
Halcampidae	*Halcampaster teres*	Eelgrass anemone
Hydractiniidae	*Hydractinia kaffraria*	Tick-shell hydroid
Melithaeidae	*Melithaea* sp.	Soft coral
Parasphaerascleridae	*Parasphaerasclera* sp.	Soft coral
Pelagiidae	*Chrysaora* sp.	Compass jellyfish
Pelagiidae	*Pelagia noctiluca*	Night-light jellyfish
Physaliidae	*Physalia physalis*	Bluebottle
Rhizostomatidae	*Eupilema inexpectata*	Root-mouth jellyfish
Sagartiidae	*Anthothoe stimpsonii*	Striped anemone
	XENACOELOMORPHS and PLATYHELMINTHS (Flatworms)	
Convolutidae	*Symsagittifera mcnaei*	None
Notocomplanidae	*Notocomplana erythrotaenia*	Limpet flatworm
Planoceridae	*Planocera gilchristi*	Gilchrist's flatworm
Polycladida	At least two species	Polyclad flatworms
Pseudocerotidae	*Thysanozoon brocchii*	Carpet flatworm
	NEMERTINES (Ribbon worms)	
Polybrachiorhynchidae	*Polybrachiorhynchus dayi*	Ribbon worm
Nemertina	At least six species	Ribbon worms
	ANNELIDS (Segmented worms)	
Ampharetidae	At least one species	None
Amphinomidae	*Eurythoe complanata*	Fire worm
Arenicolidae	*Arenicola loveni*	Bloodworm
Capitellidae	*Notomastus fauvelii*	None
Capitellidae	At least three other species	None
Chaetopteridae	*Chaetopterus* sp.	None

Chaetopteridae	*Mesochaetopterus* sp.	None
Chrysopetalidae	*Bhawania goodei*	None
Cirratulidae	*Caulleriella capensis*	None
Cirratulidae	*Cirriformia* spp.	Thread-gilled worms
Cirratulidae	At least one species	None
Dorvilleidae	*Schistomeringos* sp.	None
Eunicidae	*Eunice aphroditois*	Bobbit worm
Eunicidae	*Lysidice natalensis*	Mussel worm
Eunicidae	*Marphysa haemasoma*	Estuarine wonder-worm
Euphrosinidae	*Euphrosine capensis*	Plump bristleworm
Fabriciidae	*Oriopsis parvula*	None
Fabriciidae	*Pseudofabriciola capensis*	None
Flabelligeridae	*Flabelligera affinis*	None
Flabelligeridae	*Piromis arenosus*	None
Glyceridae	*Glycera tridactyla*	None
Hesionidae	At least three species	None
Lumbrineridae	*Lumbrineris coccinea*	None
Lumbrineridae	*Scoletoma tetraura*	None
Magelonidae	*Magelona* sp.	None
Magelonidae	*Euclymene lumbricoides*	Bamboo worm
Magelonidae	*Johnstonia knysna*	Bamboo worm
Nephtyidae	*Nephtys capensis*	None
Nephtyidae	*Nephtys tulearensis*	None
Nereididae	*Ceratonereis keiskama*	None
Nereididae	*Perinereis falsovariegata*	None
Nereididae	*Perinereis namibia*	None
Nereididae	*Platynereis entshonae*	None
Nereididae	*Pseudonereis podicirra*	Mussel worm
Nereididae	*Simplisetia erythraeensis*	Estuarine nereis
Nereididae	Another four species	None
Oenonidae	*Arabella iricolor*	None
Oenonidae	*Oenone fulgida*	None
Onuphidae	*Diopatra aciculata*	Moonshine worm
Opheliidae	At least one species	None
Orbiniidae	*Naineris laevigata*	None
Orbiniidae	*Orbinia angrapequensis*	Woolly worm
Orbiniidae	*Orbinia monroi*	Woolly worm
Orbiniidae	*Scoloplos* spp.	None
Paraonidae	*Paradoneis lyra capensis*	None
Pectinariidae	*Amphictene capensis*	None
Pectinariidae	*Lagis koreni*	None
Phyllodocidae	At least five species	Paddle worms
Polynoidae	At least three species	Scale worms
Sabellariidae	*Gunnarea gaimardi*	Cape reef worm

Sabellidae	*Branchiomma* spp.	Fanworm
Sabellidae	*Desdemona ?ornata*	None
Sabellidae	*Pseudobranchiomma longa*	Featherduster worm
Sabellidae	*Pseudopotamilla reniformis*	Gregarious fanworm
Sabellidae	*Sabella* sp.	Fanworm
Sabellidae	Several more species present	Fanworms
Serpulidae	*Serpula vermicularis*	Operculate fanworm
Serpulidae	*Spirobranchus kraussii*	Blue coral-worm
Serpulidae	*Spirorbis* spp.	Fanworms
Sigalionidae	At least two species	None
Spionidae	*Aonides oxycephala*	None
Spionidae	*Atherospio* sp. *nov*	None
Spionidae	*Boccardia proboscidea*	None
Spionidae	*Boccardia pseudonatrix*	None
Spionidae	*Dipolydora socialis*	None
Spionidae	*Malacoceros indica*	None
Spionidae	*Paraprionospio pinnata*	None
Spionidae	*Polydora* c.f. *caulleryi*	None
Spionidae	*Polydora* c.f. *nuchalis*	None
Spionidae	*Polydora hoplura*	None
Spionidae	*Prionospio sexoculata*	None
Spionidae	*Pseudopolydora* c.f. *antennata*	None
Spionidae	*Pseudopolydora* c.f. *kempi*	None
Spionidae	At least three other species	None
Syllidae	At least three species	None
Terebellidae	*Loimia medusa*	Tangleworm
Terebellidae	*Nicolea macrobranchia*	Tangleworm
Terebellidae	*Telothelepus capensis*	Tangleworm
Terebellidae	*Terebella plagiostoma*	Tangleworm
Terebellidae	*Terebella pterochaeta*	Tangleworm
Terebellidae	*Thelepus setosus*	Tangleworm
Tubificidae	At least one species	Oligochaete
	SIPUNCULANS (Peanut worms)	
Golfingiidae	*Golfingia capensis*	Peanut worm
Golfingiidae	*Themiste minor*	Peanut worm
Siphonosomatidae	*Siphonosoma dayi*	Peanut worm
	BRYOZOANS	
Beaniidae	*Beania* sp.	Lace bryozoan
Bugulidae	*Bicellariella* sp.	None
Bugulidae	*Bugula neritina*	None
Candidae	*Menipea crispa*	None

Membraniporidae	*Membranipora rustica*	None
Phidolophoridae	*Schizoretepora tessellata*	None
Vesiculariidae	*Amathia* sp.	None
Watersiporidae	*Watersipora subtorquata*	None
	CLADOCERAN CRUSTACEANS	
Sididae	*Penilia avirostris*	None
	COPEPOD CRUSTACEANS	
Acartidae	*Paracartia africana*	None
Acartidae	*Paracartia longipatella*	None
Acartidae	*Acartiella natalensis*	None
Calanidae	*Calanoides carinatus*	None
Centropagidae	*Centropages brachiatus*	None
Clausidiidae	*Clausidium* sp.	None
Clausidiidae	*Saphiriellla stages*	None
Clausocalanidae	*Clausocalanus furcatus*	None
Clausocalanidae	*Clausocalanus laticeps*	None
Corycaeidae	*Corycaeus* sp.	None
Corycaeidae	*Ditrichocorycaeus africana*	None
Corycaeidae	*Ditrichocorycaeus tenuis*	None
Cyclopidae	*Cyclops* sp.	None
Ectinosomatidae	*Micosetellella rosea*	None
Halicyclopidae	*Halcyclops* sp.	None
Harpacticidae	At least two species	None
Miracidae	*Amphiascus* sp.	None
Oithonidae	*Dioithona oculata*	None
Oithonidae	*Oithona brevirostris brevirostris*	None
Oithonidae	*Oithona nana*	None
Oithonidae	*Oithona similis*	None
Oncaeidae	*Oncaea mediterranea mediterranea*	None
Oncaeidae	*Monothula subtilis*	None
Paracalanidae	*Parcalanus aculeatus*	None
Paracalanidae	*Paracalanus crassirostris*	None
Paracalanidae	*Paracalanus parvus*	None
Pseudodiaptomidae	*Pseudodiaptomus hessei*	None
Pseudodiaptomidae	*Pseudiaptomus nudus*	None
Tachidiidae	*Euterpina acutifrons*	None
	OSTRACOD CRUSTACEANS (Seed-shrimps or mussel shrimps)	
Bairdiidae	*Bairdia* sp.	None
Candonidae	*Aglaiocypris railbridgensis*	None
Candonidae	*Paracypris* sp.	None
Candonidae	*Tasmanocypris westfordensis*	None

Cylindroleberididae	*Cylindroleberis* c.f. *grimaldi*	None
Cytherettidae	*Garciaella knysnaensis*	None
Cytherettidae	*Cyprideis remanei*	None
Cytherettidae	*Perissocytheridea estuaria*	None
Cytherettidae	*Sulcostocythere knysnaensis*	None
Hemicytheridae	*Aurila* sp.	None
Hemicytheridae	*Caudites knysnaensis*	None
Hemicytheridae	*Finmarchinella* sp.	None
Hemicytheridae	*Hemicythere* sp.	None
Hemicytheridae	*Urocythereis* sp.	None
Loxoconchidae	*Loxoconcha megapora*	None
Loxoconchidae	*Loxoconcha parameridionalis*	None
Paradoxostomatidae	*Paradoxostoma auritum*	None
Rutidermatidae	*Rutiderma compressa*	None
Thaerocytheridae	*Bradleya* sp.	None
Trachyleberididae	*Mutilus* sp.	None
Xestoleberididae	*Xestoleberis capensis*	None
Xestoleberididae	*Xestoleberis ramosa*	None
CIRRIPEDE CRUSTACEANS (Barnacles)		
Balanidae	*Amphibalanus amphitrite*	Striped barnacle
Balanidae	*Notomegabalanus algicola*	White dwarf barnacle
Balanidae	*Solidobalanus elizabethae*	Estuarine barnacle
Chthamalidae	*Chthamalus dentatus*	Toothed barnacle
Chthamalidae	*Octomeris angulosa*	Eight-shell barnacle
Tetraclitidae	*Tetraclita serrata*	Volcano barnacle
PERACARIDAN CRUSTACEANS (Amphipods, isopods, tanaids, mysids and others)		
Amaryllidae	*Amaryllis macrophthalma*	None
Ampeliscidae	*Ampelisca spinimana*	None
Ampithoeidae	*Ampithoe africana*	None
Ampithoeidae	*Cymadusa 'filosa'*	Nesting amphipod
Anthuridae	*Cyathura estuaria*	None
Aoridae	*Autonoe hirsutipes*	None
Aoridae	*Grandidierella lignorum*	None
Aoridae	*Lembos hypacanthus*	None
Aoridae	Unidentified species of c.f. *Bemlos*	None
Atylidae	*Nototropis* sp.	None
Bodotriidae	*Iphinoe truncata*	None
Caprellidae	*Caprella equilibra*	Skeleton shrimp
Chiltoniidae	*Afrochiltonia capensis*	None
Cirolanidae	*Cirolana fluviatilis*	Beach louse
Cirolanidae	*Eurydice longicornis*	Beach louse
Cirolanidae	*Exocirolana latipes*	Beach louse
Corallanidae	*Corallana africana*	None

Corophiidae	*Americorophium triaenonyx*	None
Corophiidae	*Monocorophium acherusicum*	None
Cyproideidae	*Cyproidea ornata*	Ornate amphipod
Detonidae	*Deto echinata*	None
Eriopisidae	*Victoriopisa chilkensis*	None
Hyalidae	*Apohyale grandicornis*	Seaweed amphipod
Hyalidae	*Protohyale maroubrae*	None
Hyalidae	*Ptilohyale plumosus*	None
Idoteidae	*Paridotea ungulata*	Green weed louse
Ischyroceridae	*Ericthonius brasiliensis*	None
Ischyroceridae	*Jassa falcata*	None
Ischyroceridae	*Jassa slatteryi*	None
Janiridae	*Ianiropsis palpalis*	None
Leptocheliidae	*Leptochelia* sp.	None
Ligiidae	*Ligia natalensis*	Sea-slater
Limnoriidae	*Limnoria* sp.	Gribble
Lysianassidae	*Lysianassa ceratina*	None
Maeridae	*Ceradocus rubromaculatus*	None
Melitidae	*Melita orgasmos*	None
Melitidae	*Melita zeylanica*	None
Mysidae	*Gastrosaccus brevifissura*	None
Mysidae	*Mesopodopsis africana (wooldridgei?)*	None
Mysidae	*Mysidopsis similis*	None
Mysidae	*Rhopalopthalmus terranatalis*	None
Nebaliidae	*Nebalia capensis*	None
Oedicerotidae	*Perioculodes* sp.	None
Parapseudidae	*Halmyrapseudes cooperi*	None
Podoceridae	*Podocerus cristatus*	None
Pontogeneiidae	*Paramoera capensis*	None
Sphaeromatidae	*Dynamene bidentata*	Horned isopod
Sphaeromatidae	*Exosphaeroma hylecoetes*	None
Sphaeromatidae	*Exosphaeroma planum*	None
Sphaeromatidae	*Exosphaeroma varicolor*	None
Sphaeromatidae	*Exosphaeroma kraussi*	None
Sphaeromatidae	*Exosphaeroma truncatitelson*	None
Sphaeromatidae	*Ischyromene australis*	None
Sphaeromatidae	*Ischyromene huttoni*	None
Sphaeromatidae	*Ischyromene scabricula*	None
Sphaeromatidae	*Paracerceis sculpta*	None
Sphaeromatidae	*Parisocladus stimpsoni*	None
Sphaeromatidae	*Pseudosphaeroma barnardi*	None
Sphaeromatidae	*Sphaeroma terebrans*	None
Stenothoidae	*Stenothoe gallensis*	None
Stenothoidae	*Wallametopa cylindrica*	None

Talitridae	*Eorchestia rectipalma*	Beach hopper
Talitridae	*Orchestia gammarellus*	Beach hopper
Talitridae	*Orchestia inaequalipes*	Beach hopper
Talitridae	*Platorchestia platensis*	Beach hopper
Talitridae	*Talorchestia capensis*	Beach hopper
Tanaididae	*Zeuxoides helleri*	None
Tryphosidae	*Orchomene plicatus*	None
Tylidae	*Tylos capensis*	None
Urothoidae	*Urothoe coxalis*	None
Urothoidae	*Urothoe platypoda*	None
Urothoidae	*Urothoe pulchella*	None
DECAPOD CRUSTACEANS (Shrimps, prawns, crabs, etc.)		
Alpheidae	*Alpheus* sp.	Cracker shrimp
Alpheidae	*Betaeus jucundus*	Commensal shrimp
Alpheidae	*Synalpheus tumidomanus*	Cracker shrimp
Callichiridae	*Kraussillichirus kraussi*	Sandprawn
Camptandriidae	*Danielella edwardsii*	Sandflat crab
Camptandriidae	*Paratylodiplax algoense*	Hairy-eyed crab
Diogenidae	*Diogenes brevirostris*	Sand hermit-crab
Epialtidae	*Acanthonyx dentatus*	Decorator crab
Galatheidae	*Galathea intermedia*	Squat lobster
Grapsidae	*Metopograpsus cannicci*	Estuarine rock crab
Hexapodidae	*Spiroplax spiralis*	Three-legged crab
Hippolytidae	*Hippolyte kraussiana*	Broken-backed shrimp
Hymenosomatidae	*Hymenosoma orbiculare*	Crown crab
Inachidae	*Macropodia falcifera*	Long-legged spider crab
Leucosiidae	*Leucisca squalina*	Nut crab
Ocypodidae	*Ocypode ceratophthalmus*	Horned ghost crab
Ocypodidae	*Ocypode ryderi*	Ghost crab
Ocypodidae	*Austruca occidentalis*	Fiddler crab
Palaemonidae	*Palaemon peringueyi*	Sand shrimp
Portunidae	*Scylla serrata*	Giant mud crab
Sesarmidae	*Cristarma eulimene*	Marsh crab
Sesarmidae	*Parasesarma catenatum*	Marsh crab
Upogebiidae	*Upogebia africana*	Mudprawn
Varunidae	*Cyclograpsus punctatus*	Shore crab
OTHER ARTHROPODS (Insects, spiders and sea-spiders)		
Anyphaenidae	*Amaurobioides africanus*	Chevron shore spider
Chironomidae	At least two species	Midge larvae
Coelopidae	At least two species	Sand fly
Desidae	*Desis formidabilis*	Shore spider
Dolichopodidae	At least one species	Long-legged fly larvae
Neanuridae	*Anurida maritima*	Shore springtail

Pycnogona	At least two species	Sea spider
Staphylinidae	At least two species	Staphylinid beetle
	POLYPLACOPHORAN MOLLUSCS (Chitons)	
Acanthochitonidae	*Acanthochitona garnoti*	Spiny chiton
Chaetopleuridae	*Dinoplax gigas*	Giant chiton
Chitonidae	*Rhyssoplax polita*	Tulip chiton
Ischnochitonidae	*Ischnochiton oniscus*	Dwarf chiton
Ischnochitonidae	*Ischnochiton textilis*	Textile chiton
	GASTROPOD MOLLUSCS (Snails, slugs, etc.)	
Aglajidae	*Philinopsis capensis*	None
Aglajidae	*Philinopsis speciosa*	Assassin bubble-shell
Akeridae	*Akera soluta*	Papery bubble shell
Anabathridae	*Afriscrobs ampliorscapus*	None
Aplysiidae	*Aplysia juliana*	Spotted sea hare
Aplysiidae	*Aplysia oculifera*	Spotted sea hare
Aplysiidae	*Aplysia parvula*	Sea hare
Aplysiidae	*Bursatella leachii*	Shaggy sea hare
Assimineidae	*'Assiminea' capensis*	None
Assimineidae	*'Assiminea' globulus*	None
Assimineidae	*'Assiminea' ovata*	None
Buccinidae	*Afrocominella capensis*	Whelk
Buccinidae	*Burnupena catarrhacta*	Flame-patterned burnupena
Buccinidae	*Burnupena cincta*	Ridged burnupena
Buccinidae	*Burnupena lagenaria*	Variable burnupena
Buccinidae	*Burnupena limbosa*	None
Buccinidae	*Burnupena pubescens*	Pubescent burnupena
Caecidae	*Caecum knysnaense*	None
Calyptraeidae	*Crepidula porcellana*	Slipper limpet
Cerithiopsidae	*Cerithiopsis* sp.	None
Chromodorididae	*Goniobranchus* sp.	None
Chromodorididae	*Hypseleotris carnea*	None
Chromodorididae	*Hypselodoris capensis*	Cape dorid
Columbellidae	*Anachis kraussi*	None
Columbellidae	*Mitrella albuginosa*	None
Cornirostridae	*Cornirostra* sp.	None
Coryphellidae	*Fjordia capensis*	None
Cylichnidae	*Cylichna tubulosa*	Barrel shell
Dendrodorididae	*Dendrodoris caesia*	Blue-speckled dorid
Discodorididae	*Jorunna tomentosa*	None
Dorididae	*Doriopsis granosa*	None
Dorididae	*Doriopsis granulosa*	Warty dorid
Dorididae	*Doris ananas*	None
Dorididae	*Doris verrucosa*	None

Dotidae	*Doto* sp.	None
Eatoniellidae	*Eatoniella afronigra*	None
Ellobiidae	*Myosotella myosotis*	Mouse-eared snail
Eubranchidae	At least two species of *Eubranchus*	None
Facelinidae	At least two species of *Cratena*	None
Facelinidae	*Facelina olivacea*	None
Facelinidae	*Favorinus ghanensis*	None
Fissurellidae	*Dendrofissurella scutellum*	Saddle keyhole limpet
Fissurellidae	*Fissurella mutabilis*	Cape keyhole limpet
Goniodorididae	*Ancula* sp.	None
Goniodorididae	*Goniodoris merculiaris*	None
Haliotidae	*Haliotis spadicea*	Green bubble shell
Hermaeidae	*Aplysiopsis sinusmensalis*	None
Hydrobiidae	*'Hydrobia' knysnaensis*	None
Janolidae	*Antiopella capensis*	Cape silvertip nudibranch
Limopontiidae	*Placida* sp.	None
Litiopidae	*Alaba pinnae*	None
Littorinidae	*Afrolittorina africana*	African periwinkle
Littorinidae	*Afrolittorina knysnaensis*	Knysna periwinkle
Littorinidae	*Littoraria scabra*	Estuarine periwinkle
Littorinidae	*Littorina saxatilis*	European winkle
Marginellidae	*Volvarina zonata*	Marginella
Muricidae	*Indothais dubia*	Dogwhelk
Muricidae	*Mancinella capensis*	Whelk
Muricidae	*Nucella dubia*	Dogwhelk
Myrrhinidae	*Godiva quadricolor*	Four-colour sea slug
Nassariidae	*Bullia annulata*	Plough shell
Nassariidae	*Bullia laevissima*	Plough shell
Nassariidae	*Nassarius kraussianus*	Tick shell
Naticidae	*Neverita didyma*	Moon shell
Naticidae	*Tectonatica tecta*	Necklace shell
Neritidae	*Nerita albicilla*	Blotched nerite
Neritidae	*Smaragdia souverbiana*	None
Onchidiidae	At least one species	Airbreathing sea slug
Orbitestellidae	*Orbitestella gemmulata*	None
Oxynoidae	*Oxynoe* sp. *nov*	None
Patellidae	*Cymbula granatina*	Granite limpet
Patellidae	*Cymbula miniata*	Pink-rayed limpet
Patellidae	*Cymbula oculus*	Goat's eye limpet
Patellidae	*Helcion concolor*	Variable limpet
Patellidae	*Helcion pectunculus*	Broad rayed-limpet
Patellidae	*Scutellastra argenvillei*	Argenville's limpet
Patellidae	*Scutellastra barbara*	Bearded limpet
Patellidae	*Scutellastra cochlear*	Pear limpet

Patellidae	*Scutellastra granularis*	Granular limpet
Patellidae	*Scutellastra longicosta*	Long-spined limpet
Phasianellidae	*Tricolia capensis*	Pheasant shell
Phasianellidae	*Tricolia neritina*	Pheasant shell
Philinidae	*Philine aperta*	Sand slug
Plakobranchidae	At least three *Elysia* spp.	None
Pleurobranchidae	*Berthellina granulata*	Lemon pleurobranch
Pleurobranchidae	*Pleurobranchus nigropunctatus*	None
Polyceridae	*Crimora* sp.	None
Polyceridae	*Limacia clavigera*	Orange-clubbed nudibranch
Polyceridae	*Limacia lucida*	None
Polyceridae	*Polycera capensis*	Crowned sea slug
Polyceridae	*Polycera hedgpethi*	None
Polyceridae	*Thecacera pennigera*	None
Potamididae	*Cerithidea decollata*	Truncated mangrove snail
Pyramidellidae	*Polyspirella trachealis*	None
Pyramidellidae	*Pyramidella africana*	None
Retusidae	At least one species	None
Rissoidae	*Alvania argentea*	None
Rissoidae	*Alvania fenestrata*	None
Scyllaeidae	*Notobryon thompsoni*	None
Siphonariidae	*Siphonaria capensis*	Cape false-limpet
Siphonariidae	*Siphonaria compressa*	Eelgrass false-limpet
Siphonariidae	*Siphonaria concinna*	False-limpet
Siphonariidae	*Siphonaria oculus*	False-limpet
Siphonariidae	*Siphonaria serrata*	False-limpet
Thiaridae	*Melanoides tuberculata*	Red-rimmed melania
Tornatinidae	At least one species	None
Tornidae	At least one species	None
Trinchesiidae	*Trinchesia* species complex	None
Tritoniidae	*Marionia* sp.	None
Trochidae	*Gibbula beckeri*	Topshell
Trochidae	*Gibbula capensis*	Topshell
Trochidae	*Gibbula cicer*	Topshell
Trochidae	*Oxystele antoni*	Topshell
Trochidae	*Oxystele impervia*	Beaded topshell
Trochidae	*Oxystele sinensis*	Pink-lipped topshell
Trochidae	*Oxystele tigrina*	Tiger topshell
Turbinidae	*Turbo cidaris*	Turban shell
Turbinidae	*Turbo sarmaticus*	Alikreukel
Turritellidae	*Turritella capensis*	Screw shell
Turritellidae	*Turritella carinata*	Screw shell
Volvatellidae	*Volvatella laguncula*	None

LAMELLIBRANCH MOLLUSCS (Bivalves)		
Anomiidae	*Anomia achaeus*	Saddle oyster
Arcidae	*Barbatia obliquata*	Oblique ark shell
Cardiidae	*Fulvia natalense*	Papery cockle
Carditidae	*Cardita variegata*	False cockle
Cassidae	*Semicassis zeylanica*	Helmet shell
Hiatellidae	*Hiatella arctica*	None
Lasaeidae	*Kellia rotunda*	None
Lasaeidae	*Lasaea turtoni*	Dwarf rusty clam
Limidae	*Limaria rotundata*	File shell
Lucinidae	*Anodontia* sp.	Toothless platter shell
Lucinidae	*Loripes clausus*	Smooth platter shell
Mactridae	*Lutraria* sp.	Otter shell
Mactridae	*Mactra glabrata*	Smooth trough shell
Mytilidae	*Arcuatula capensis*	Estuarine mussel
Mytilidae	*Choromytilus meridionalis*	Black mussel
Mytilidae	*Mytilus galloprovincialis*	Mediterranean mussel
Mytilidae	*Perna perna*	Brown mussel
Nuculidae	*Nucula nucleus*	Nut shell
Ostreidae	*Striostrea margaritacea*	Cape rock oyster
Pholadidae	*Pholas dactylus*	Piddock
Pinnidae	*Atrina squamifera*	Horse mussel
Psammobiidae	*Hiatula capensis*	Sand tellin
Solenidae	*Solen capensis*	Pencil bait
Tellinidae	*Gastrana matadoa*	Ridged tellin

Fishes

Common and scientific names of the 119 fish species recorded in the Knysna Estuary.
Species nomenclature is in accordance with Eschmeyer's Catalog of Fishes (www.calacademy.org).
Fish species that have a strong association with South African estuaries are indicated by *.

FAMILY	SCIENTIFIC NAME	COMMON NAME
	OSTEICHTHYS (Bony fishes)	
Anguillidae	*Anguilla mossambica**	Longfin eel
Ariidae	*Galeichthys feliceps**	White seacatfish
Atherinidae	*Atherina breviceps**	Cape silverside
Blenniidae	*Istiblennius dussumieri*	Streaky rockskipper
Blenniidae	*Omobranchus woodi**	Kappie blenny
Chaetodontidae	*Chaetodon marleyi*	Doublesash butteflyfish
Chanidae	*Chanos chanos**	Milkfish
Carangidae	*Alectis indica*	Indian threadfish
Carangidae	*Caranx heberi*	Blacktip kingfish
Carangidae	*Caranx sexfasciatus**	Bigeye kingfish
Carangidae	*Lichia amia**	Leervis
Carangidae	*Trachurus capensis*	Cape horse mackerel
Centrarchidae	*Lepomis macrochirus*	Bluegill sunfish
Cheilodactylidae	*Cheilodactylus pixi*	Barred fingerfin
Clinidae	*Clinus agilis*	Agile klipfish
Clinidae	*Clinus superciliosus**	Super klipfish
Clupeidae	*Etremeus whiteheadi*	Whitehead's roundherring
Clupeidae	*Gilchristella aestuaria**	Estuarine roundherring
Clupeidae	*Sardinops ocellatus*	South African pilchard
Congridae	*Conger wilsoni*	Cape conger
Coryphaenidae	*Coryphaena hippurus*	Common dolphinfish
Dasyatidae	*Dasyatis chrysonota*	Blue stingray
Dichistiidae	*Dichistius capensis*	Galjoen
Diodontidae	*Diodon hystrix*	Porcupine fish
Eleotridae	*Eleotris fusca**	Dusky sleeper
Elopidae	*Elops machnata**	Skipjack
Engraulidae	*Engraulis capensis*	South African anchovy
Engraulidae	*Stolephorus holodon**	Thorny anchovy
Fistulariidae	*Fistularia commersonii**	Smooth flutemouth
Gobiesocidae	*Apletodon pellegrini*	Chubby clingfish
Gobiesocidae	*Chorisochismus dentex*	Rocksucker
Gobiidae	*Caffrogobius gilchristi**	Prison goby
Gobiidae	*Caffrogobius natalensis**	Baldy
Gobiidae	*Caffrogobius nudiceps**	Barehead goby
Gobiidae	*Croilia mossambica**	Naked goby
Gobiidae	*Glossogobius callidus**	River goby
Gobiidae	*Psammogobius knysnaensis**	Speckled sandgoby

Gobiidae	*Redigobius dewaali**	Checked goby
Haemulidae	*Pomadasys commersonnii**	Spotted grunter
Haemulidae	*Pomadasys olivaceum**	Piggy
Haemulidae	*Pomadasys striatus*	Striped grunter
Hemiramphidae	*Hemiramphus far**	Spotted halfbeak
Hemiramphidae	*Hyporhamphus capensis**	Cape halfbeak
Isonidae	*Iso natalensis*	Surf sprite
Kuhliidae	*Kuhlia mugil**	Barred flagtail
Lobotidae	*Lobotes surinamensis**	Tripletail
Monodactylidae	*Monodactylus argenteus**	Round moony
Monodactylidae	*Monodactylus falciformis**	Oval moony
Mugilidae	*Crenimugil buchanani**	Bluetail mullet
Mugilidae	*Chelon dumerili**	Grooved mullet
Mugilidae	*Chelon richardsonii**	Southern mullet
Mugilidae	*Chelon tricuspidens**	Striped mullet
Mugilidae	*Mugil cephalus**	Flathead mullet
Mugilidae	*Planiliza macrolepis**	Largescale mullet
Mugilidae	*Pseudomyxus capensis**	Freshwater mullet
Ophichthidae	*Ophisurus serpens**	Sand snake-eel
Ostraciidae	*Lactoria cornuta*	Yellow boxfish
Ostraciidae	*Ostracion cubicus*	Smallscale grubfish
Platycephalidae	*Platycephalus indicus**	Bartail flathead
Poeciliidae	*Gambusia affinis*	Mosquitofish
Polynemidae	*Polydactylus sextarius*	Sixfinger threadfin
Pomacentridae	*Chromis dasygenus*	Blue-spotted chromis
Pomatomidae	*Pomatomus saltatrix**	Elf
Priacanthidae	*Priacanthus hamrur*	Moontail bullseye
Regalecidae	*Regalecus glesne*	Oarfish
Sciaenidae	*Argyrosomus japonicus**	Dusky kob
Sciaenidae	*Umbrina robinsoni*	Baardman
Scombropidae	*Scombrops boops*	Gnomefish
Scorpaenidae	*Pterois volitans*	Lionfish
Scyliorhinidae	*Poroderma africanum*	Striped catshark
Serranidae	*Acanthistius sebastoides*	Koester
Serranidae	*Epinephelus andersoni**	Catface rockcod
Serranidae	*Serranus cabrilla*	Comber
Sillaginidae	*Sillago sihama**	Silver sillago
Soleidae	*Heteromycteris capensis*	Cape sole
Soleidae	*Solea turbynei**	Blackhand sole
Soleidae	*Synapturichthys kleinii*	Lace sole
Sparidae	*Acanthopagrus vagus**	Estuarine bream
Sparidae	*Boopsoidea inornata*	Fransmadam
Sparidae	*Cheimerius nufar*	Santer
Sparidae	*Chrysoblephus laticeps*	Roman

Sparidae	*Chrysoblephus lophus*	False red stumpnose
Sparidae	*Cymatoceps nasutus*	Black musselcracker
Sparidae	*Crenidens crenidens*	Karanteen
Sparidae	*Diplodus capensis**	Blacktail
Sparidae	*Diplodus hottentotus**	Zebra
Sparidae	*Lithognathus lithognathus**	White steenbras
Sparidae	*Lithognathus mormyrus**	Sand steenbras
Sparidae	*Rhabdosargus globiceps**	White stumpnose
Sparidae	*Rhabdosargus holubi**	Cape stumpnose
Sparidae	*Rhabdosargus sarba**	Tropical stumpnose
Sparidae	*Sarpa salpa**	Strepie
Sparidae	*Sparodon durbanensis**	White musselcracker
Sparidae	*Spondyliosoma emarginatum**	Steentjie
Sphyraenidae	*Sphyraena jello**	Pickhandle barracuda
Syngnathidae	*Hippocampus capensis**	Knysna seahorse
Syngnathidae	*Syngnathus temmincki**	Longsnout pipefish
Synodontidae	*Trachinocephalus trachinus*	Painted lizardfish
Terapontidae	*Terapon jarbua**	Thornfish
Tetrarogidae	*Coccotropsis gymnoderma*	Smoothskin scorpionfish
Tetraodontidae	*Amblyrhynchotes honckenii**	Evileye blaasop
Tetraodontidae	*Arothron hispidus**	Whitespotted blaasop
Tetraodontidae	*Arothron immaculatus**	Blackedged blaasop
Tetraodontidae	*Lagocephalus lagocephalus*	Oceanic blaasop
Triglidae	*Chelidonichthys kumu*	Bluefin gurnard
	CHONDRICHTHYS (Cartilaginous fishes)	
Carcharinidae	*Carcharhinus leucas**	Zambezi or bull shark
Carcharhinidae	*Triakis megalopterus*	Spotted gully shark
Dasyatidae	*Dasyatis chrysonota*	Blue stingray
Gymnuridae	*Gymnura natalensis**	Backwater butterflyray
Myliobatidae	*Myliobatis aquila*	Eagleray
Myliobatidae	*Pteromylaeus bovinus*	Bullray
Odontaspididae	*Carcharius taurus*	Spotted ragged-tooth shark
Rhincodontidae	*Rhincodon typus*	Whale shark
Rhinobatidae	*Acroteriobatus annulatus**	Lesser guitarfish
Sphyrnidae	*Sphyrna zygaena*	Smooth hammerhead shark
Torpedinidae	*Torpedo fuscomaculata**	Blackspotted electric ray
Triakidae	*Mustelus mustelus*	Smooth hound shark
Triakidae	*Galeorhinus galeus*	Soupfin shark

Birds

Names of the 93 waterbird species recorded at the Knysna Estuary. Common and scientific names follow BirdLife South Africa (2022) and orders (in capitals), families and species ordering follow Donsker et al. (2022). The 30 species with a (V) after their common names were either not recorded on CWAC counts or were recorded on <5% of these counts and can be considered rare vagrants to Knysna Estuary.

FAMILY	SCIENTIFIC NAME	COMMON NAME
	ANSERIFORMES	
Anatidae	*Plectropterus gambensis*	Spur-winged goose
	Alopochen aegyptiaca	Egyptian goose
	Tadorna cana	South African shelduck
	Spatula hottentota	Blue-billed teal
	Spatula smithii	Cape shoveler
	Anas sparsa	African black duck (V)
	Anas undulata	Yellow-billed duck
	Anas platyrhynchos	Mallard
	Anas capensis	Cape teal
	Anas erythrorhyncha	Red-billed teal
	Netta erythrophthalma	Southern pochard (V)
	GRUIFORMES	
Rallidae	*Rallus caerulescens*	African rail
	Gallinula chloropus	Common moorhen
	Fulica cristata	Red-knobbed coot
	Porphyrio madagascariensis	African swamphen (V)
	Zapornia flavirostra	Black crake
	PODICIPEDIFORMES	
Podicipedidae	*Tachybaptus ruficollis*	Little grebe
	Podiceps cristatus	Great crested grebe
	PHOENICOPTERIFORMES	
Phoenicopteridae	*Phoenicopterus roseus*	Greater flamingo (V)
	CHARADRIIFORMES	
Burinidae	*Burhinus vermiculatus*	Water thick-knee
Haematopodidae	*Haematopus moquini*	African oystercatcher
Recurvirostridae	*Himantopus himantopus*	Black-winged stilt
	Recurvirostra avosetta	Pied avocet
Charadriidae	*Vanellus armatus*	Blacksmith lapwing
	Pluvialis squatarola	Grey plover
	Charadrius hiaticula	Common ringed plover
	Charadrius pecuarius	Kittlitz’s plover
	Charadrius tricollaris	Three-banded plover
	Charadrius marginatus	White-fronted plover

	Charadrius mongolus	Lesser sand plover (V)
	Charadrius leschenaultia	Greater sand plover (V)
Jacanidae	*Actophilornis africanus*	African jacana (V)
Scolopacidae	*Numenius phaeopus*	Eurasian whimbrel
	Numenius arquata	Eurasian curlew
	Limosa lapponica	Bar-tailed godwit (V)
	Arenaria interpres	Ruddy turnstone
	Calidris canutus	Red knot (V)
	Calidris pugnax	Ruff
	Calidris ferruginea	Curlew sandpiper
	Calidris alba	Sanderling (V)
	Gallinago nigripennis	African snipe (V)
	Calidris minuta	Little stint
	Calidris melanotos	Pectoral sandpiper (V)
	Actitis hypoleucos	Common sandpiper
	Xenus cinereus	Terek sandpiper (V)
	Tringa flavipes	Lesser yellowlegs (V)
	Tringa tetanus	Common redshank (V)
	Tringa stagnatilis	Marsh sandpiper
	Tringa glareola	Wood sandpiper
	Tringa erythropus	Spotted redshank (V)
	Tringa nebularia	Common greenshank
Laridae	*Chroicocephalus cirrocephalus*	Grey-headed gull
	Larus dominicanus	Kelp gull
	Hydropogne caspia	Caspian tern
	Thalasseus bergii	Swift tern
	Thalasseus sandvicensis	Sandwich tern
	Sterna hirundo	Common tern
	Chlidonias leucopterus	White-winged tern (V)
	PHAETHONTIFORMES	
Phaethontidae	*Phaethon aethereus*	Red-billed tropicbird (V)
	Phaethon rubricauda	Red-tailed tropicbird (V)
	CICONIIFORMES	
Ciconiidae	*Mycteria ibis*	Yellow-billed stork (V)
	Ciconia nigra	Black stork (V)
	SILURIFORMES	
Fregatidae	*Fregata minor*	Great frigatebird (V)
Sulidae	*Morus capensis*	Cape gannet (V)
Anhingidae	*Anhinga rufa*	African darter
Phalacrocoracidae	*Microcarbo africanus*	Reed cormorant
	Phalacrocorax capensis	Cape cormorant
	Phalacrocorax lucidus	White-breasted cormorant

	PELECANIFORMES	
Threskiornithidae	*Threskiornis aethiopicus*	African sacred ibis
	Bostrychia hagedash	Hadeda ibis
	Plegadis falcinellus	Glossy ibis
	Platalea alba	African spoonbill
Ardeidae	*Nycticorax nycticorax*	Black-crowned night heron
	Ardeola ralloides	Squacco heron (V)
	Bubulcus ibis	Western cattle egret
	Ardea cinerea	Grey heron
	Ardea melanocephala	Black-headed heron
	Ardea goliath	Goliath heron (V)
	Ardea purpurea	Purple heron
	Ardea intermedia	Yellow-billed egret (V)
	Egretta ardesiaca	Black heron (V)
	Egretta garzetta	Little egret
Scopidae	*Scopus umbretta*	Hamerkop
	ACCIPITRIFORMES	
Pandionidae	*Pandion haliaetus*	Western osprey
Accipitridae	*Circus ranivorus*	African marsh harrier (V)
	Haliaeetus vocifer	African fish eagle
	STRIGIFORMES	
Strigidae	*Asio capensis*	Marsh owl (V)
	CORACIIFORMES	
Alcedinidae	*Alcedo semitorquata*	Half-collared kingfisher
	Corythornis cristatus	Malachite kingfisher
	Megaceryle maxima	Giant kingfisher
	Ceryle rudis	Pied kingfisher
	PASSERIFORMES	
Motacillidae	*Motacilla aguimp*	African pied wagtail (V)
	Motacilla capensis	Cape wagtail

Mammals

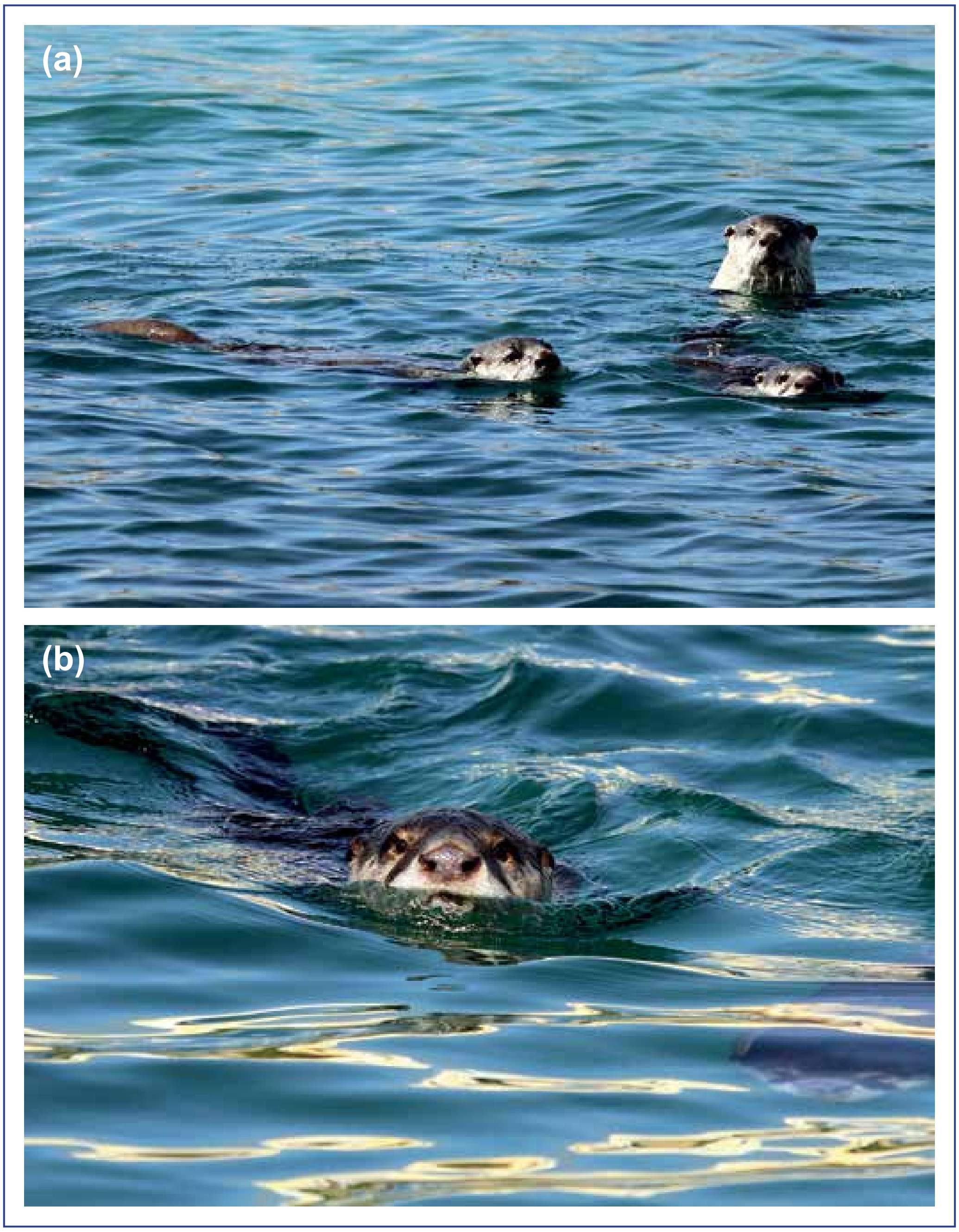
Mammals that have been recorded in the Knysna Estuary intertidal or subtidal zone.
* The hippopotamus would naturally occur in the estuary if this species had not been locally extirpated by hunters with firearms almost three centuries ago.

FAMILY	SCIENTIFIC NAME	COMMON NAME
ARTIODACTYLA (Whales and dolphins)		
Balaenidae	*Eubalaena australis*	Southern right whale
Delphinidae	*Tursiops truncatus*	Bottlenose dolphin
Hippopotamidae	*Hippopotamus amphibius**	Hippopotamus
CARNIVORA (Carnivores)		
Herpestidae	*Atilax paludinosus*	Water mongoose
Mustelidae	*Aonyx capensis*	African clawless otter
Otaridae	*Arctocephalus pusillus*	Cape fur seal
RODENTIA (Rodents)		
Muridae	*Otomys irroratus*	Southern African vlei rat
PRIMATES (Lemurs, lorises, tarsiers, monkeys, apes and humans)		
Hominidae	*Homo sapiens*	Humans

Humans have occupied the Garden Route for more than 100 000 years and their fossilised footprints and stone tools are to be found along the present-day coast in the vicinity of Knysna (Photograph: © Shaen Adey).

Appendix 2

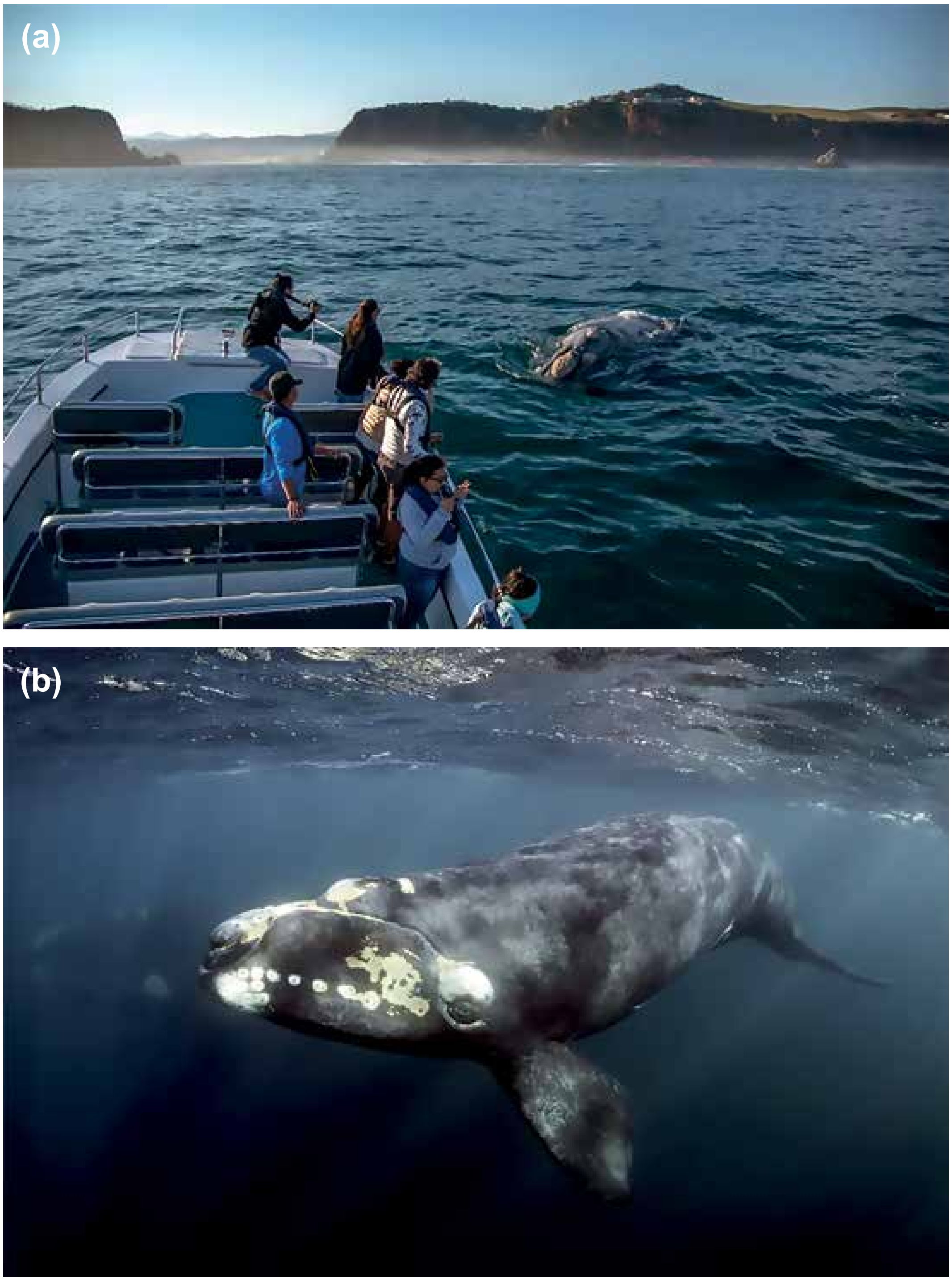
Some Iconic Rarely Seen Knysna Species



(a) The African clawless otter *Aonyx capensis* is a rarely seen resident of the Knysna Estuary, but has been reported in and around Green Hole. Upper photo (a) shows an otter family becoming aware of the photographer. Lower photo (b) shows an adult otter coming to investigate (Photographs: © D. Dankwerts).

(a) Water mongoose *Atilax paludinosus*, a rarely seen resident of the Knysna Estuary (Photograph: © Flickr). This secretive predator consumes mainly invertebrates such as crabs but is also known to feed on fish.
(b) The water mongoose frequents shallow marginal areas of the upper Knysna Estuary and river where refuge is readily available in the form of reeds or sedges (Photograph: © Colin Ralston).

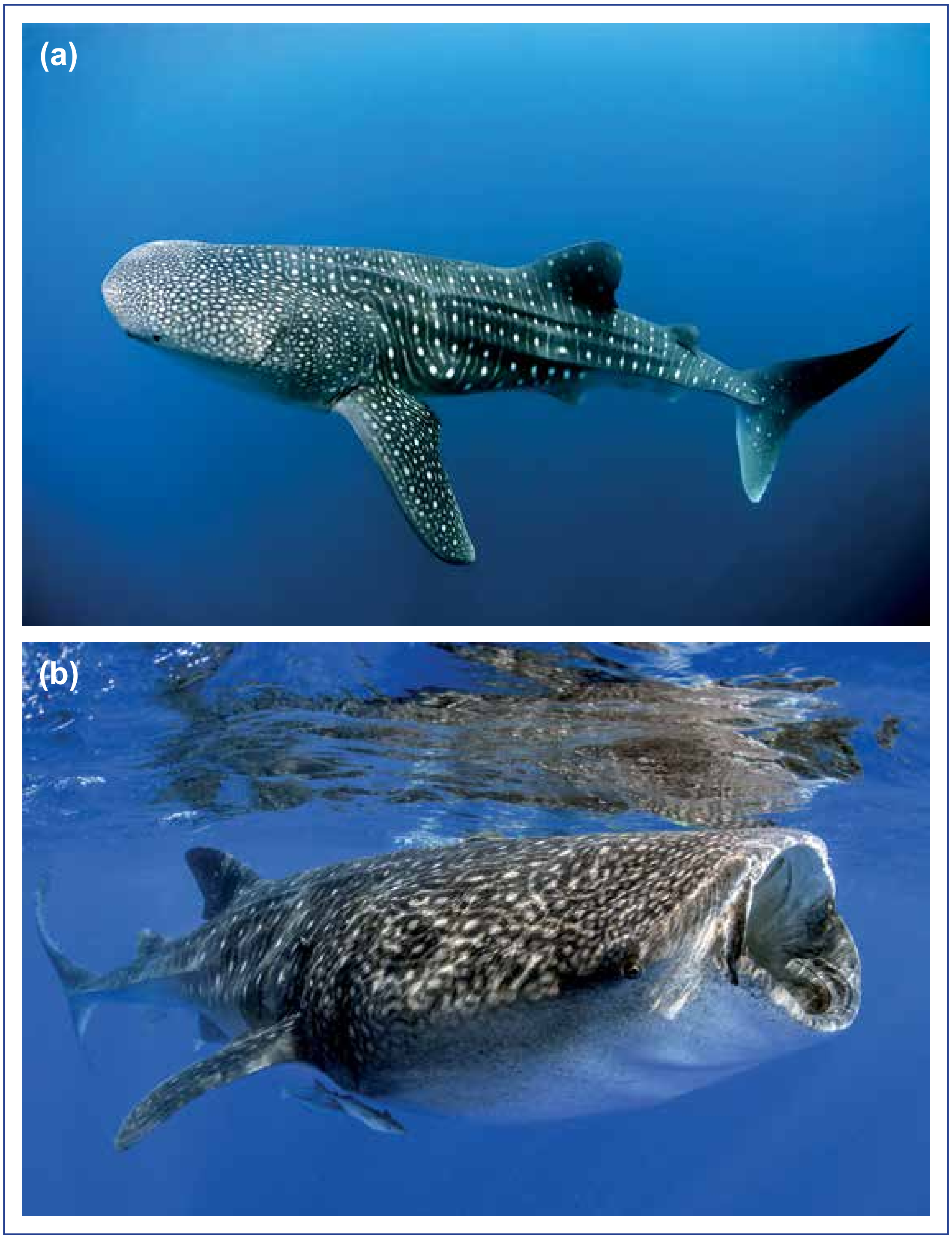
(a) The Cape fur seal *Arctocephalus pusillus* is a known visitor to the Knysna Estuary, mostly in the vicinity of Leisure Isle where it hunts for fish in shallow waters (Photograph: © Alan Whitfield). (b) When this species captures a fish in its jaws, it often thrashes the prey around so forcefully that the abdominal contents of the fish fly off in all directions and are collected by scavenging gulls (Photograph: © Steven Benjamin).



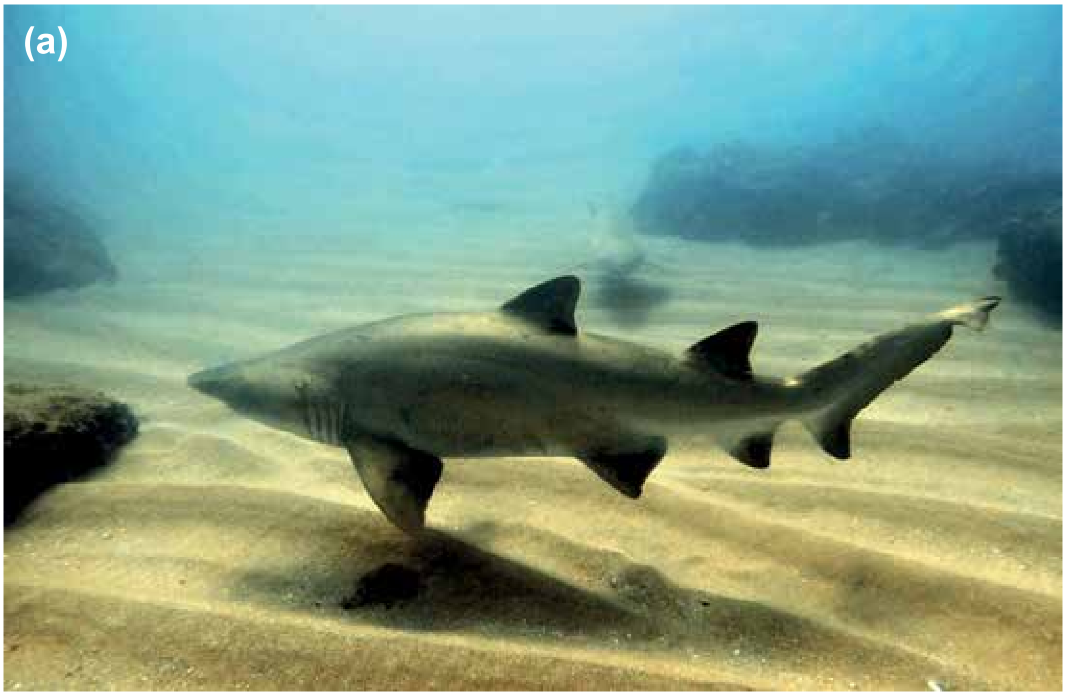
(a) The southern right whale *Eubalaena australis* is commonly seen off the Eastern and Western Cape coasts during winter and spring, but these large mammals rarely enter the Knysna Estuary (Photograph: © Ocean Odyssey).
(b) An underwater view of a southern right whale showing the white calluses that develop mainly on the head region of these creatures (Photograph: © Earth.com).

(a) Orca (*Orcinus orca*) have not been recorded entering the Knysna Estuary but have been sighted in the vicinity of The Heads. This photo shows part of an orca pod that arrived off Knysna in October 2021 (Photograph: © Ocean Odyssey).
(b) Male orcas can attain 8 m in length and females up to 4 tonnes in weight (Photograph: © Nicolai Georgiou).

(a) The common bottlenose dolphin *Tursiops truncatus* is frequently seen along the southern Cape coast (Photograph: © Wikimedia).
(b) Large pods of bottlenose dolphin often gather in nearshore waters but only small pods sometimes enter the Knysna Estuary (Photograph: © Ocean Odyssey).

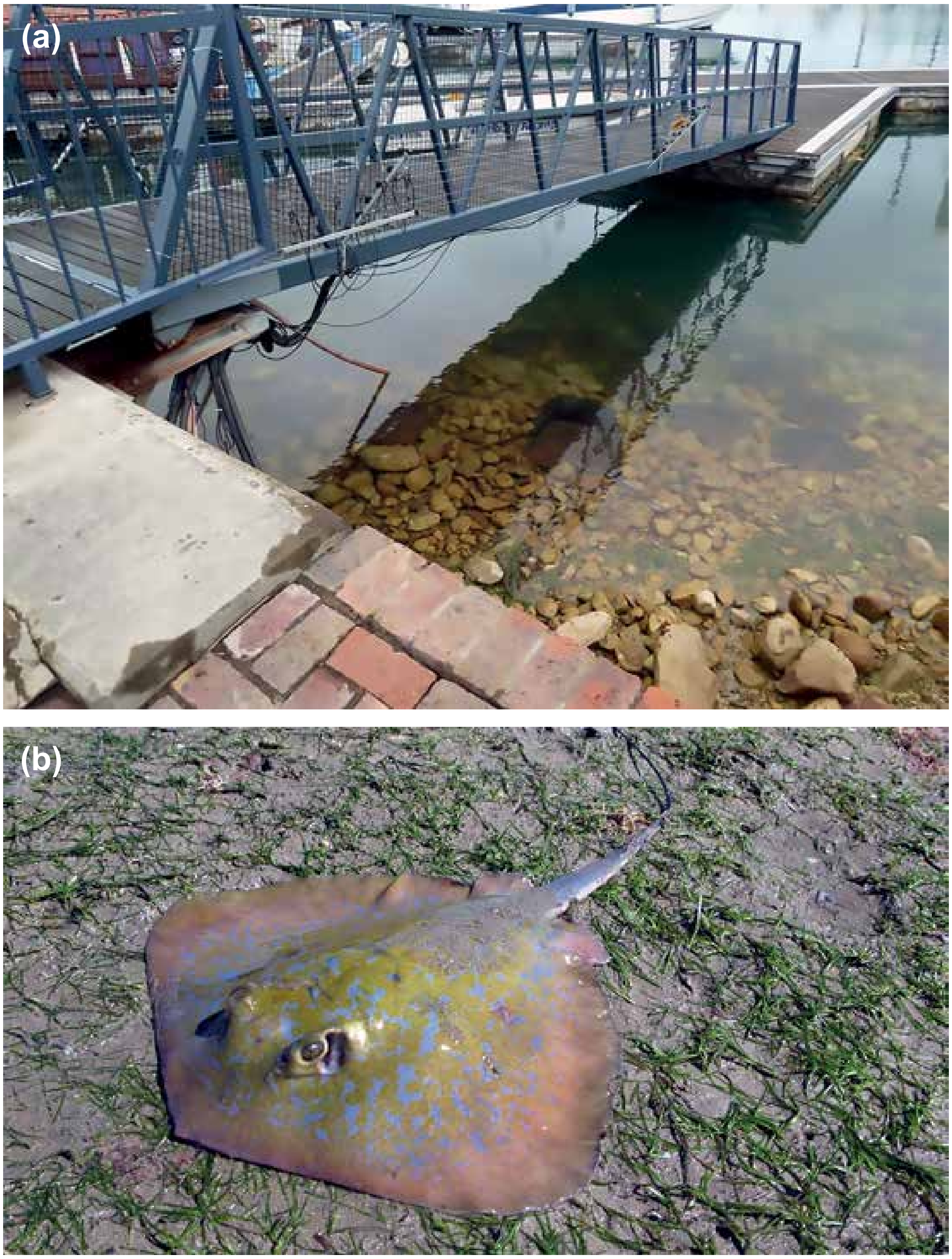


(a) The whale shark *Rhincodon typus* is a shark not a whale and a single individual strayed into the Knysna Estuary in March 2017. They are the largest fish species in the world, with adults weighing up to 20 tonnes (Photograph: © 99images).
(b) The enormous mouth is ideal for filtering large volumes of water containing planktonic and nektonic marine organisms (Photograph: © Andy Murch).

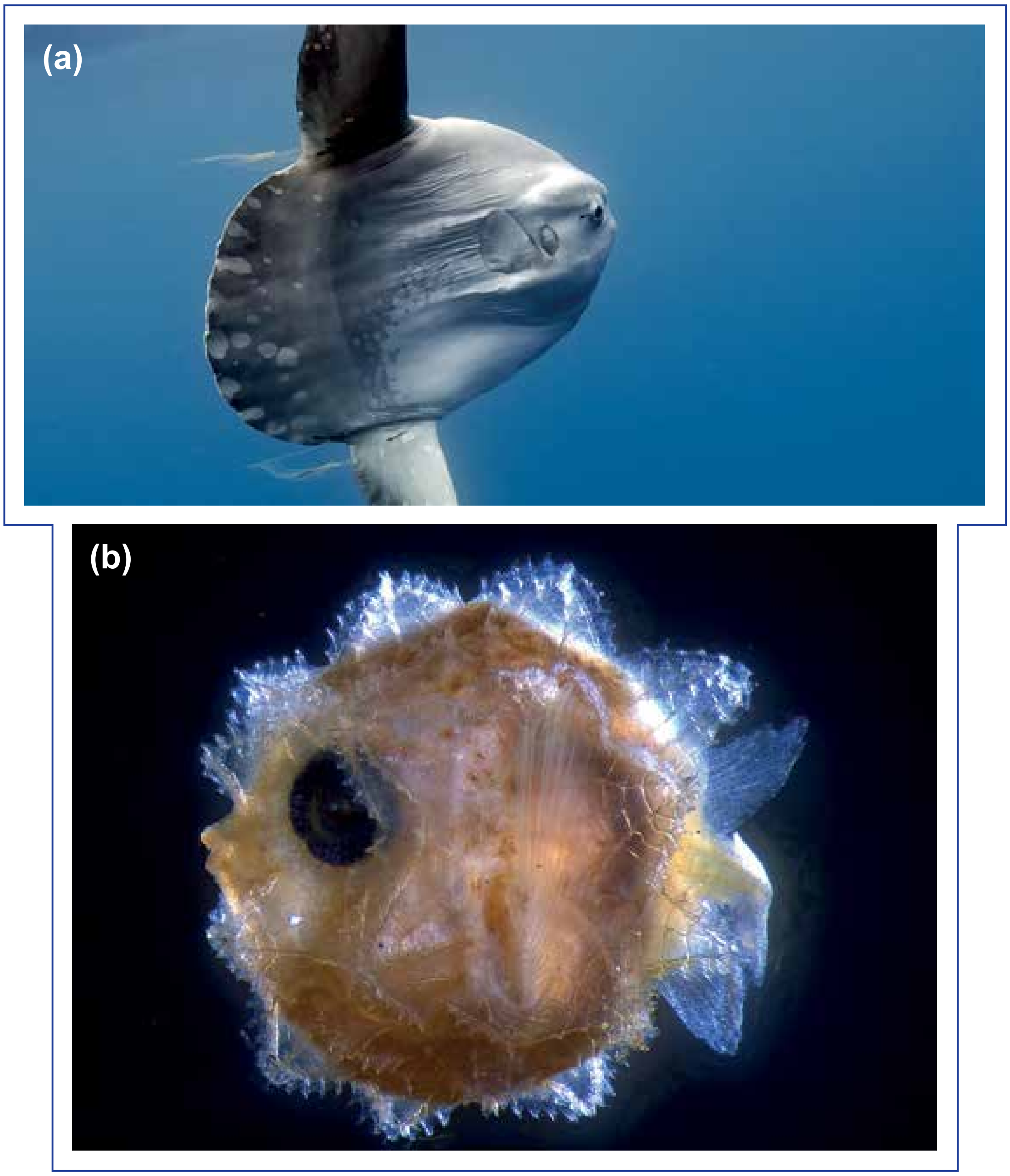


(a) The spotted ragged-tooth shark *Carcharias taurus* is an infrequent visitor to the Knysna Estuary and is sometimes caught by anglers who are using live mullet as bait (Photograph: © sharklife.co.za).
(b) In January 2016, this photograph of the tips of the first dorsal and caudal fin of a small ragged-tooth shark was taken in a Thesen Island canal, with the species known to occur as far up the estuary as the White Bridge (Photograph: © Megan Smart).

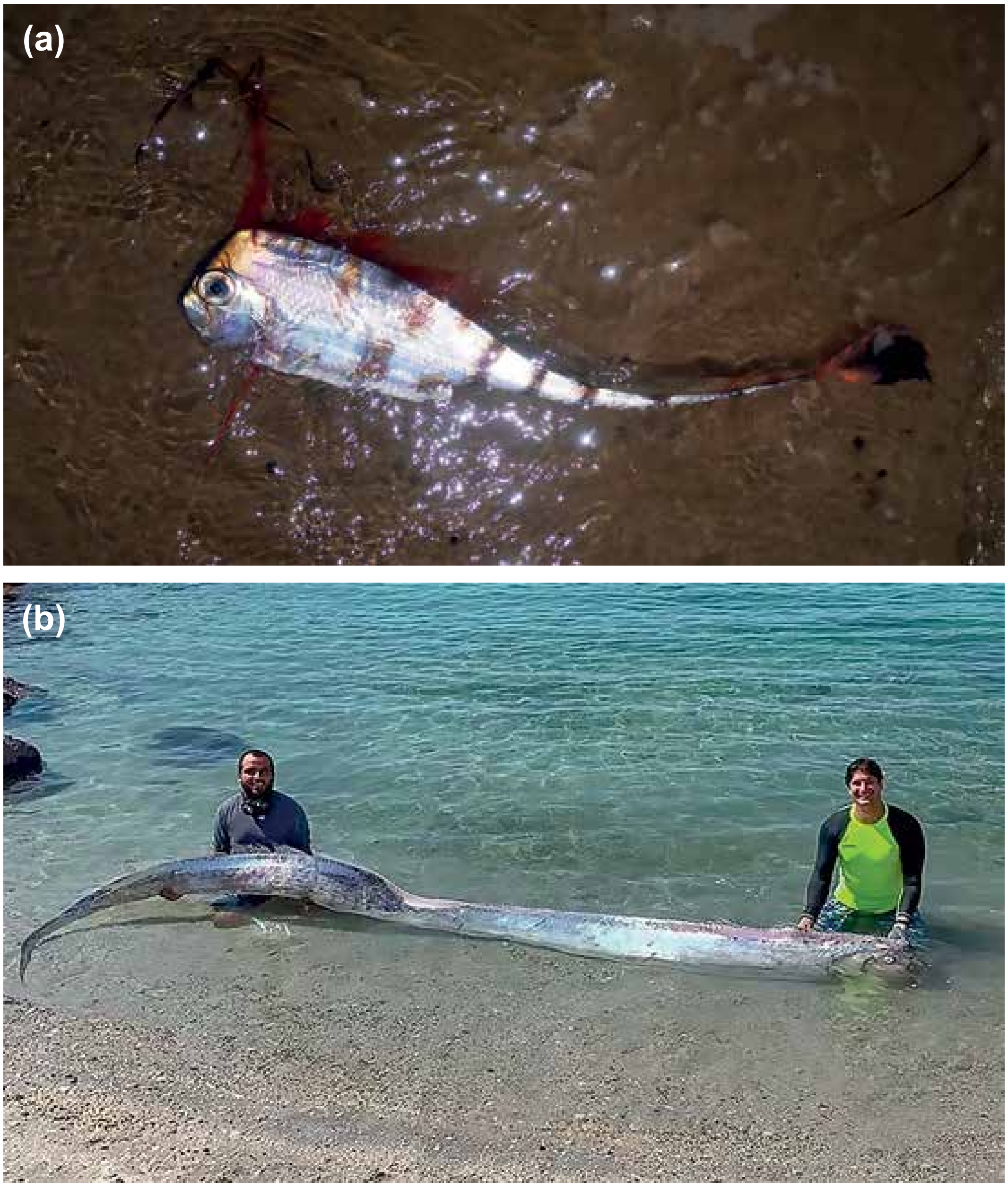
(a) The Zambezi shark *Carcharinus leucas* is a tropical/subtropical species that extends into the warm temperate waters of the Western Cape but is rarely recorded in the Knysna Estuary (Photograph: © Flickr).
(b) A large female Zambezi shark being tagged by scientists prior to release in the nearby Breede Estuary (Photograph: © Alison Towner).



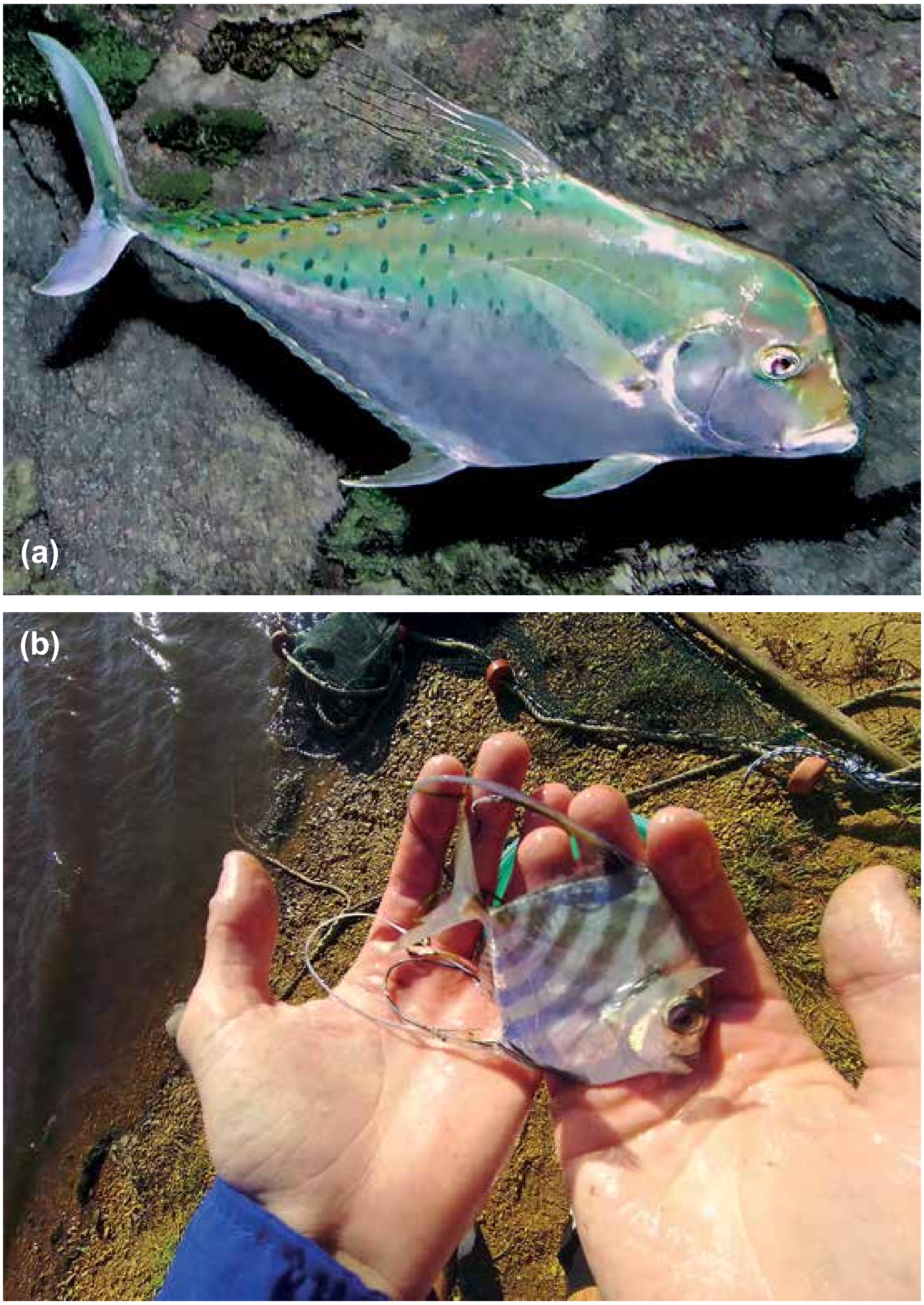
(a) A gathering of blue stingrays (*Dasyatis chrysonota*) at the Knysna Waterfront (Photograph: © Gabi Miebach).
(b) A single blue stingray captured in the Knysna Estuary that is about to be released (Photograph: © Kyle Smith). These stingrays enter shallow coastal waters during spring/summer to pup and mate, and some occupy certain estuaries such as Knysna during this period. Mature females have a 9 month gestation period and give birth to 1-7 young per annum.



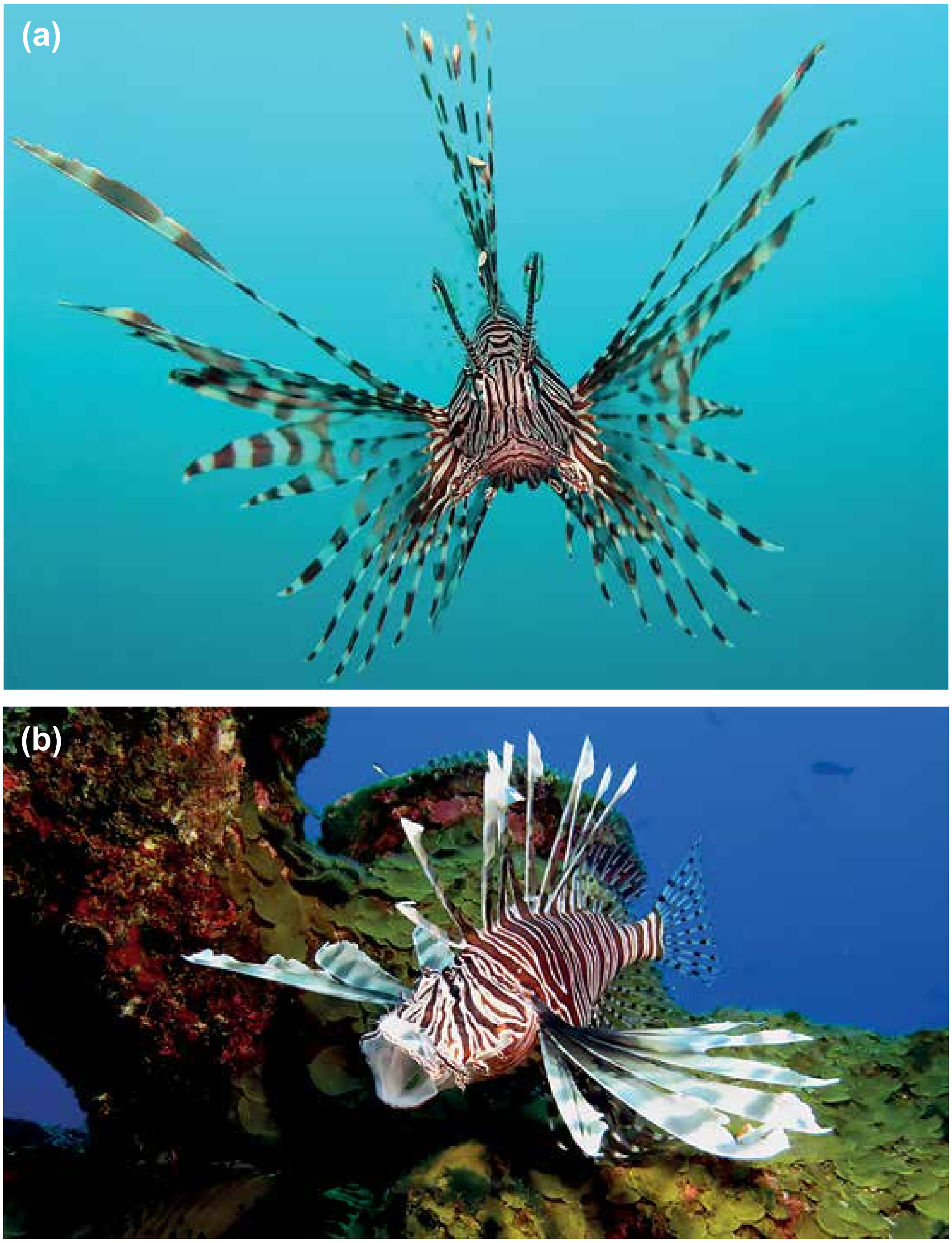
(a) Adult sunfish *Mola mola* can attain 2 tonnes in weight and 2 m in length (a), with individual females producing up to 300 million eggs per spawning season (Photograph: © Daniel Botelho).
Sunfish have been filmed on Dalgleish Bank off Knysna but have not been recorded entering the estuary.
(b) Only a small proportion of the millions of eggs from each female are fertilised during a spawning event.
This 2 cm long sunfish larva looks very different to the juvenile or adult life stages (Photograph: © Kerryn Parkinson).



(a) A juvenile oarfish *Regalecus glesne* entered the Knysna Estuary in November 2019 (Photograph: © Kobus & Kevin Oosthuysen). Note the very different shape and coloration when compared to the adult below.
(b) An adult oarfish may attain a length of 8 m (Photograph: © P. Thomas) and is normally found in deep offshore waters where it maintains a vertical position whilst feeding on small invertebrates and fishes in the upper part of the water column.

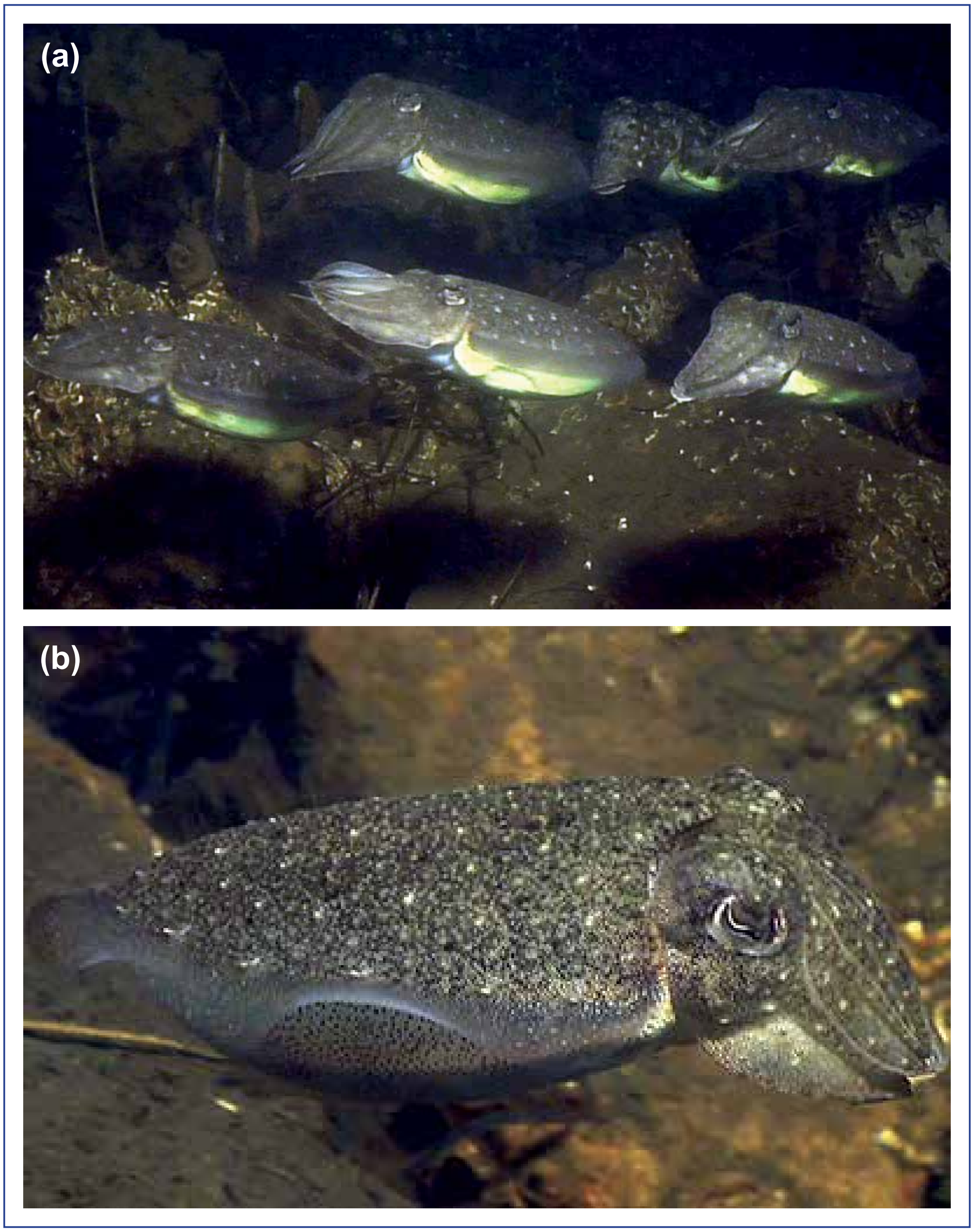


(a) An adult Indian threadfish *Alectis indica* is a mainly marine species associated with reefs in tropical and subtropical waters (Photograph: © Guiseppe Mazza).
(b) However, juveniles of this species have been captured during seine netting operations in the Knysna Estuary and have a different coloration, body shape and fin ray lengths to the adults (Photograph: © Xolani Nadani).

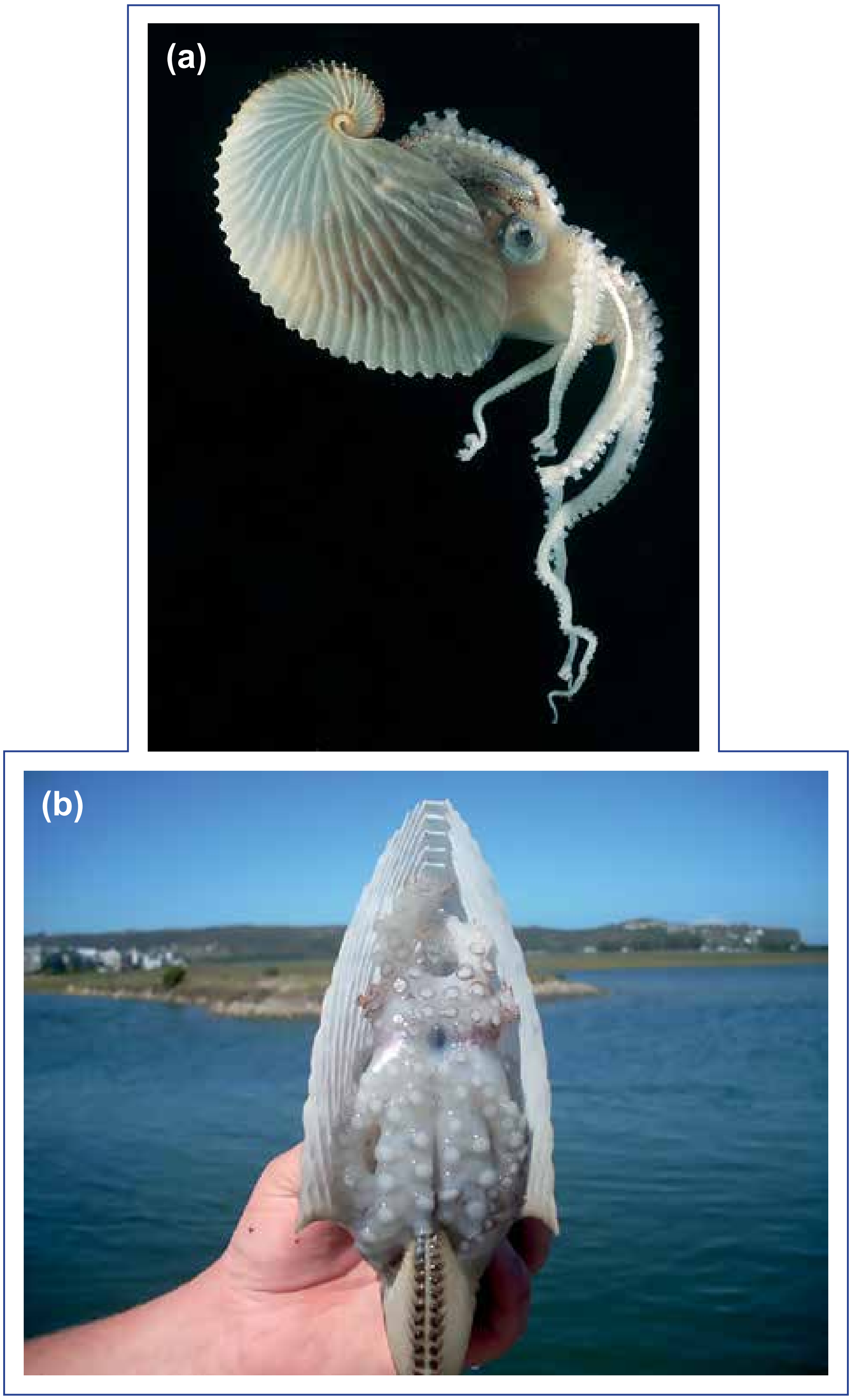


(a) The lionfish *Pterois volitans* is a tropical species that sometimes 'strays' into the Knysna Estuary during summer (Photograph: © Wikipedia).
(b) This slow swimming ambush predator has an extremely large mouth for its size and can swallow relatively big fish and invertebrates (Photograph: © NOAA).

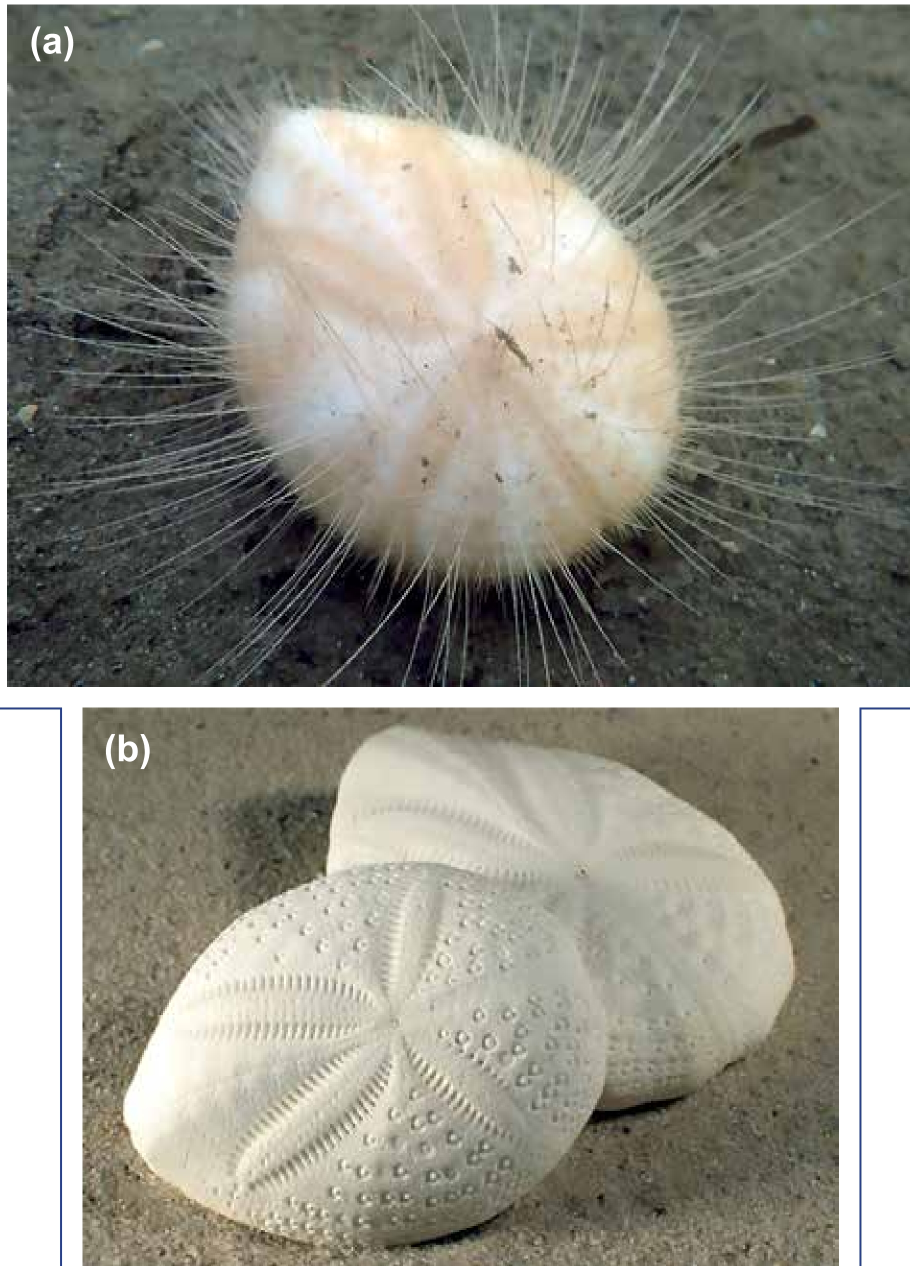
(a) The endemic Knysna seahorse *Hippocampus capensis* is the only known member of the seahorse family to be restricted to estuaries, in this case the Knysna, Swartvlei and Keurbooms systems of the southern Cape (Photograph: © Brian Gratwicke).
(b) This seahorse has the ability to change colour according to the prevailing background (Photograph: © David Harasti).



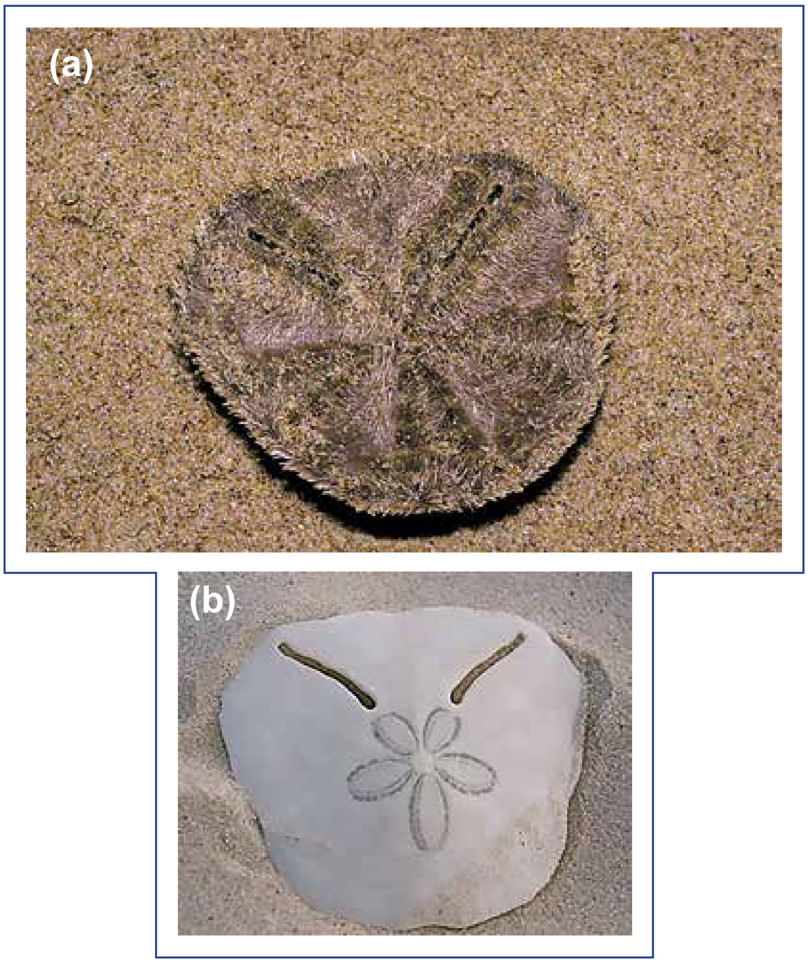
(a) A group of common cuttlefish *Sepia vermiculata* in the Knysna Estuary. This species seldom enters estuaries due to salinity fluctuations, but the Knysna system has near marine conditions and is therefore an ideal environment for cuttlefish.
(b) *Sepia vermiculata*, like the Knysna seahorse, can change colour to blend in with the surroundings (Photographs: © earth-touch.com).



(a) The greater argonaut (*Argonauta argo*) is a pelagic oceanic octopus species, usually solitary, and has been recorded entering the Knysna Estuary (Photograph: © George Branch).
(b) The female argonaut secretes a special case, clearly visible in this picture, which acts as an egg repository. The males, however, lack the dorsal tentacles used by the females to create their eggcases (Photograph: © SANParks).

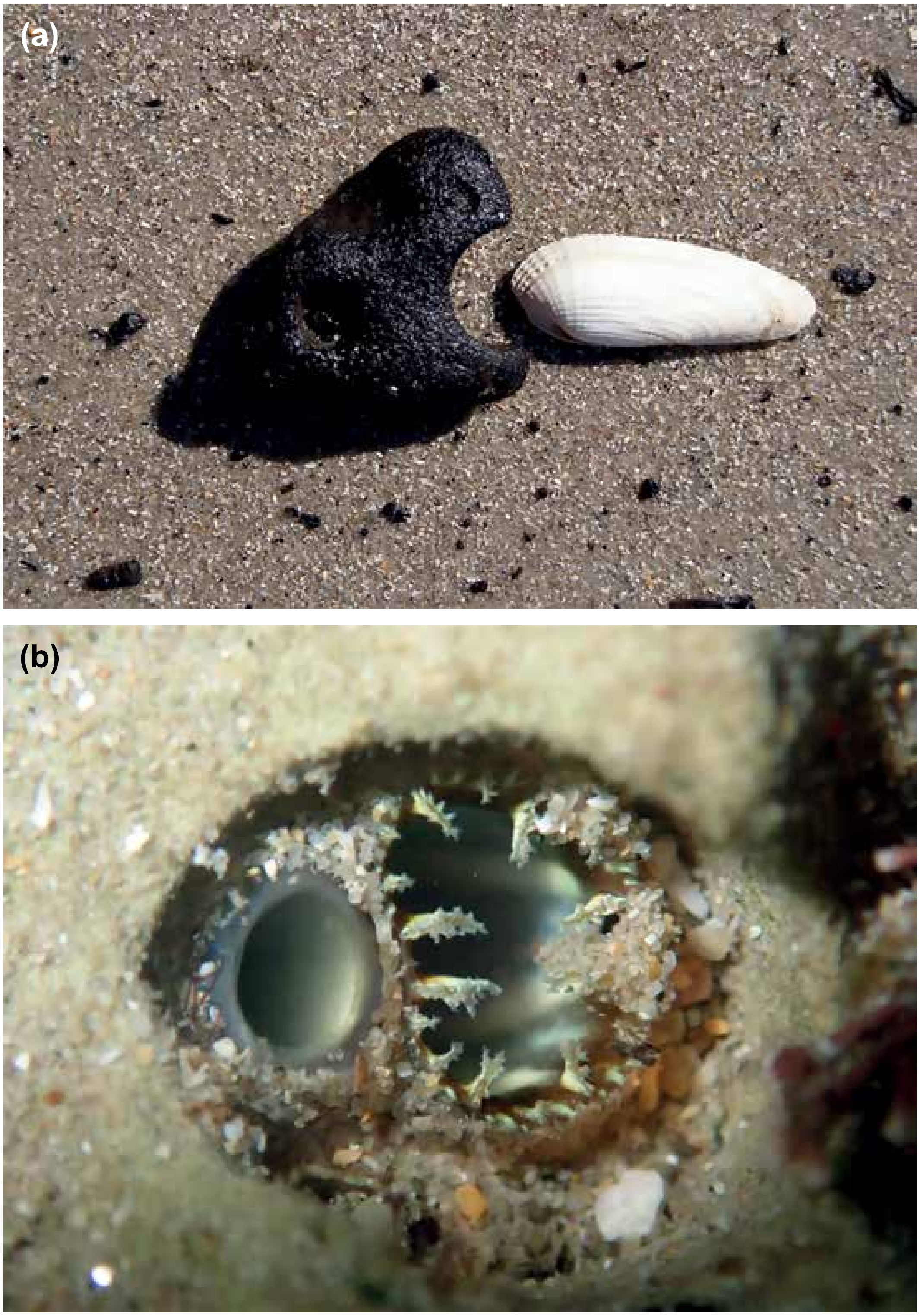


a) The longspine heart urchin *Maretia planulata* in the Knysna Estuary
(Photograph: © Louw Claassens).
The mouth is on the underside of the animal and the anus is located in the rear.
(b) Dorsal and underside views of the skeletons of *M. planulata* showing the typical radial symmetry
of this echinoderm (Photograph: © Unknown).
Fossils of this genus have been recovered from Eocene marine strata up to 40 million years of age.



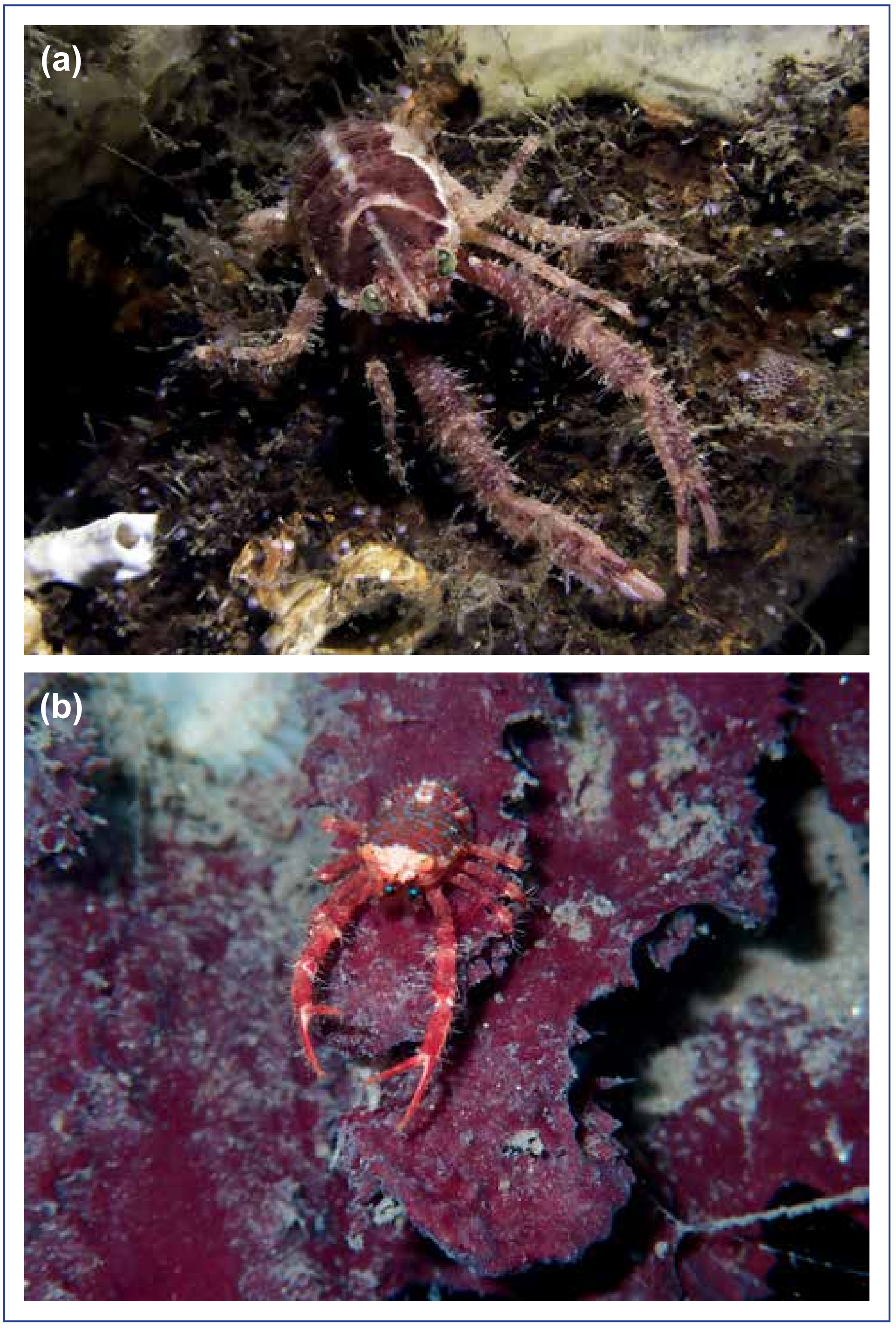
a) A live specimen of the pansy shell *Echinodiscus bisperforatus* is shown in this picture but the common name is a misnomer since no shell is involved (Photograph: © Peggy Heard). Essentially *E. bisperforatus* is a type of flat sea urchin that lives in fine sandy areas of sheltered bays and certain estuaries along the southern Cape coast. In the Knysna Estuary they occur subtidally in the vicinity of Leisure Isle.

(b) When the animal dies and the tissues decompose, the internal skeleton bleaches but remains intact, with the 'five-petal flower' pattern (from which the term 'pansy' is derived) becoming more distinct (Photograph: © geocaching.com).

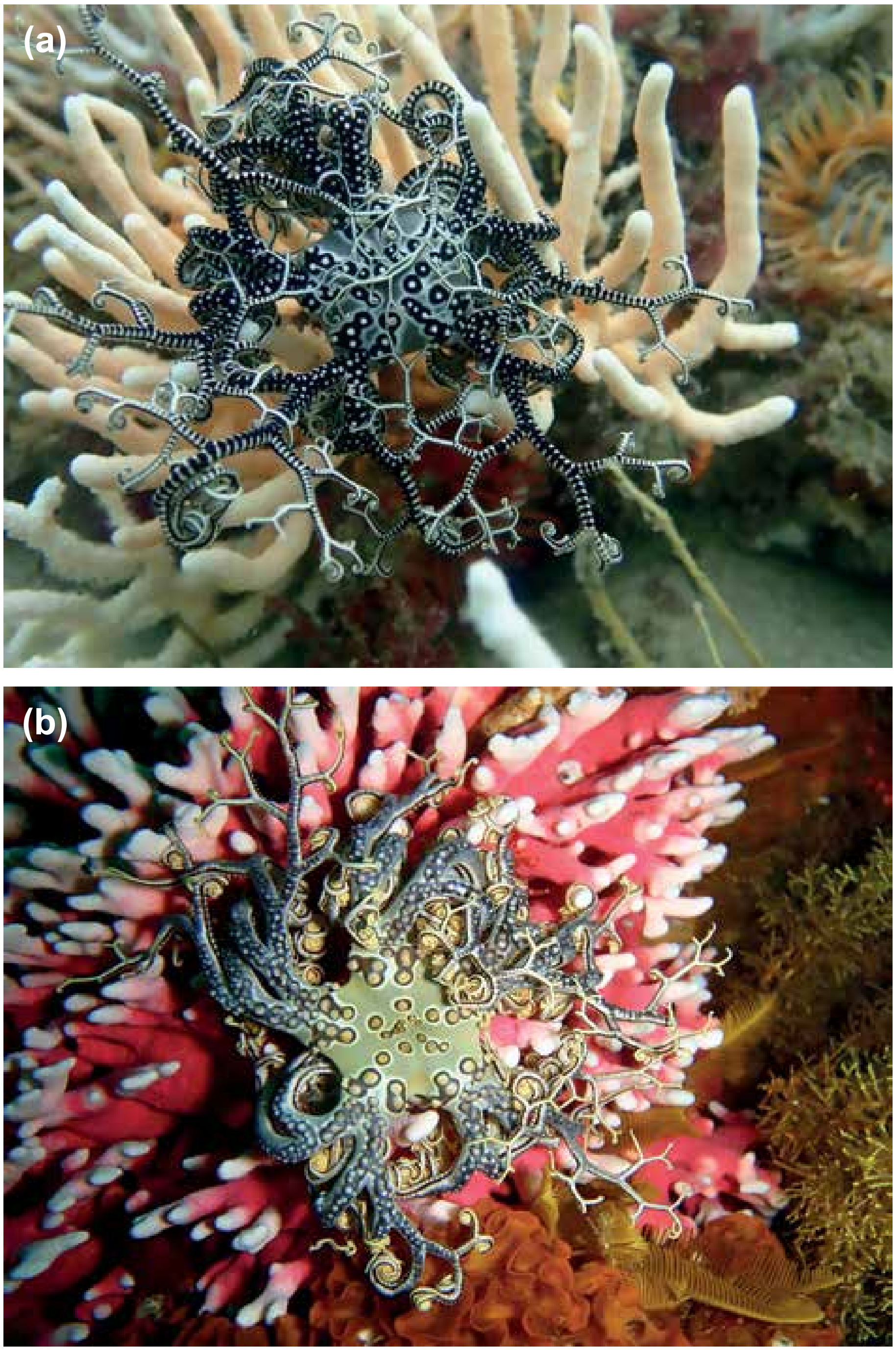


(a) The piddock *Pholas dactylus* is an interesting type of clam that bores into rock or hard intertidal surfaces to create a protective home for itself (Photograph: © beachexplorer.com).
This species can be found embedded in soft shale habitat of the Knysna Estuary western shore near Brenton-on-Lake.
(b) Only the inhalant and exhalent siphons are visible in this Knysna Estuary specimen, with the rest of the piddock embedded in the rock (Photograph: © Louw Claassens).

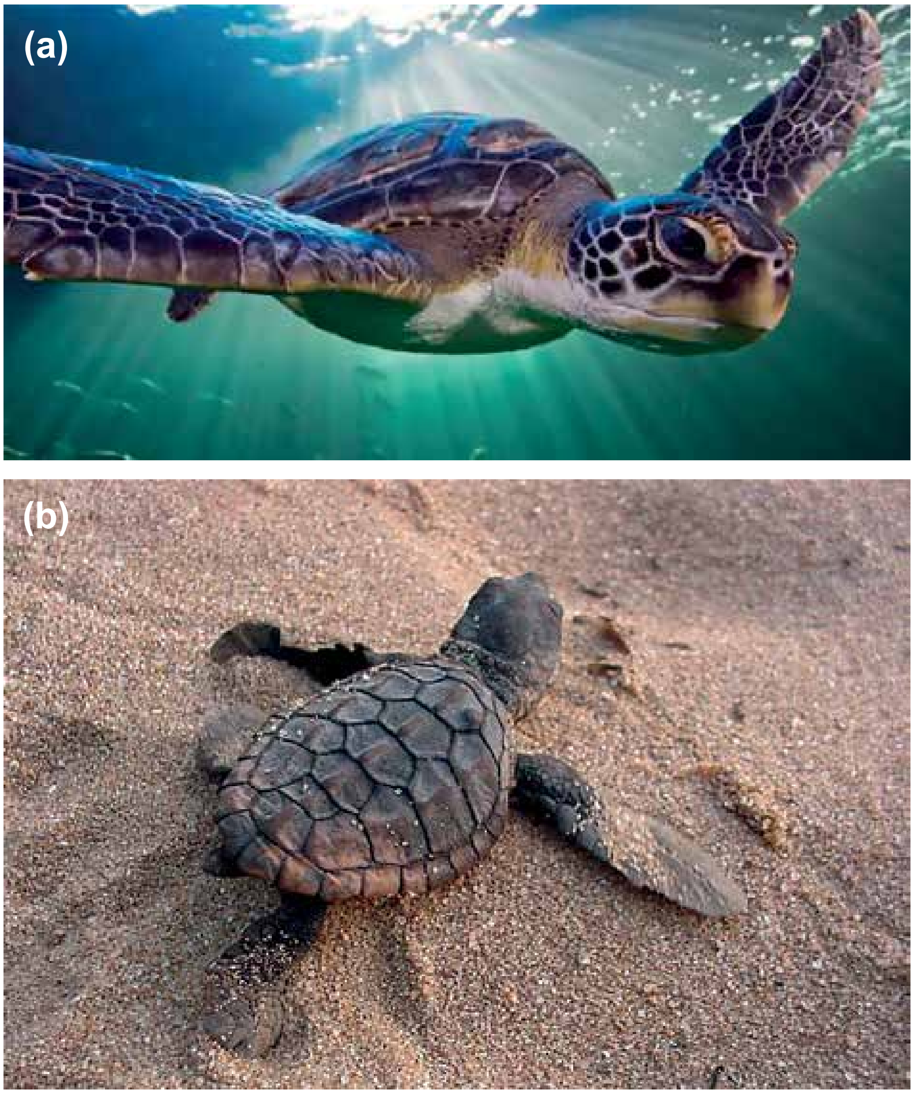
(a) The giant mud crab *Scylla serrata* used to be relatively common in the Knysna Estuary but is now rare due to overexploitation. The species can have a shell width of 30 cm and the pincers in this threat posture are strong enough to crush a finger! (Photograph: © Alan Whitfield).
(b) Isolated burrows belonging to the giant mud crab are sometimes found in the intertidal zone where this animal takes refuge in a small pool at low tide (Photograph: © Janine Adams).



(a) *Galathea intermedia* is a very small squat lobster species, less than 2 cm long as an adult (Photograph: © Jim Anderson).
(b) This Knysna Estuary photograph shows the reddish colouration and neon blue spots on the front of the body, possibly something to do with species recognition (Photograph: © Louw Claassens).

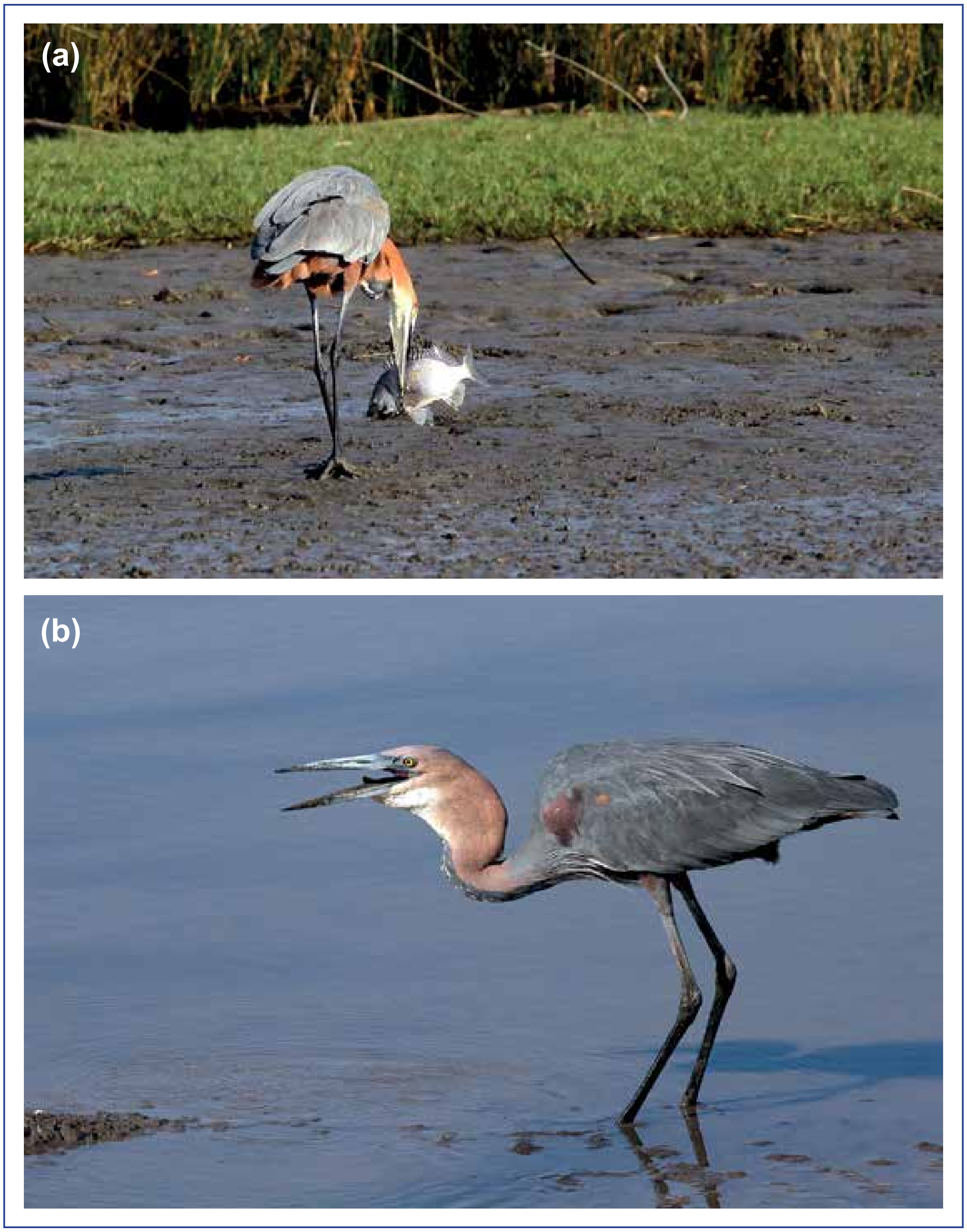


(a) The stunningly beautiful basket star *Astrocladus euryale* occurs in The Heads region of the Knysna Estuary and appears very conspicuous against the background organisms (Photograph: © Louw Claassens).
(b) However, the same species in deeper waters off the Tsitsikamma Coast blends in very well with the more colourful noble coral background (Photograph: © Peter Southwood).



(a) Adult loggerhead turtles *Caretta caretta* move past Knysna en route to coastal feeding areas west of Cape Agulhas, with the occasional individual entering the estuary for a brief visit (Photograph: © linkedin.com).
(b) If certain stormy seas prevail during late summer, then hundreds of early juvenile loggerheads from the breeding beaches in KwaZulu-Natal can be stranded along the beaches of the Cape south coast, including Knysna (Photograph: © Thonga Beach).

(a) A western osprey *Pandion haliaetus* in the process of diving and
(b) capturing a southern mullet *Chelon richardsonii* in the Knysna Estuary (Photographs: © Mike Pienaar).
This non-breeding migrant from the northern hemisphere feeds almost exclusively on fish
and may occasionally be seen on the Knysna Estuary during the summer months.



(a) A goliath heron *Ardea goliath* capturing and (b) swallowing an estuarine bream *Acanthopagrus vagus* (Photographs: ©Tris Wooldridge).
This infrequent visitor to the Knysna Estuary is normally solitary in its behaviour and is the largest of the heron species, reaching a height of 1.5 m.

(a) The giant kingfisher *Megaceryle maxima* is the largest of the kingfishers in Africa and a rare resident of the Knysna Estuary (Photograph: © Tris Wooldridge).
(b) A giant kingfisher capturing its prey by diving into the water from its perch, to which it will return and then swallow the fish head first (Photograph: © Andre Klopper).

(a) The great crested grebe *Podiceps cristatus* is sometimes recorded in the upper reaches of the Knysna Estuary (Photograph: © Elliot Montieth).
(b) A great crested grebe about to swallow a fish it had captured (Photograph: © Bouke Atema).

(a) A small flock of greater flamingos *Phoenicopterus roseus* has been visiting the estuaries and lagoons of the southern Cape during late summer and autumn for several years. Although their preferred habitat during this period has been in the Keurbooms Estuary, Langvlei and Rondevlei, they have also been known to stop-over at the Knysna Estuary (Photograph: © Johan Coetzee).
(b) Two greater flamingos taking off. Notice the pink feather coverts on the wings that are not easily visible when the birds are at rest (Photograph: © Mike Bridgeford).

Glossary

Abiotic: non-living.
Acheulean: archaeological term relating to a period when hand-axe industries were widespread about 1.5 million to 150 000 years ago.
Adaptive co-management: similar to adaptive management but with greater emphasis on shared decision-making and authority.
Algoa Group: geological formations which range in age from 41 million years to 100 000 years ago.
Adaptive governance: flexible and learning-based governance processes involving both state and non-state actors, often at multiple levels, with the aim to adaptively negotiate and coordinate management of social-ecological systems.
Adaptive management: a decision approach for uncertain circumstances, systematically linking learning with implementation.
Alien species: a species not naturally occurring in a defined area but introduced into that area from elsewhere.
Amphipods: bilaterally compressed crustaceans of the order Amphipoda.
Anomura: decapod crustaceans that include burrowing prawns.
Anoxic: devoid of oxygen.
Anthropocene: the epoch in which human activities impacted enough to constitute a distinct geological and ecological change.
Anthropogenic: caused by humans.
Archaeology: The study of the ancient and recent human past through material remains.
Avifauna: bird life.

Bathymetry: depth profile or bottom contours of a water body obtained by measurements from the surface.
Benthic: living on the bottom.
Biodiversity: the variety of plant and animal species in an area.
Biofilm: an assemblage of surface-associated microbial cells that stick to each other within a slimy matrix.
Biogeographic: the geographic distribution of plants, fishes, birds, mammals and other forms of life.
Biomass: the mass of living matter present.
Biotic: living (characteristics).
Bivalves: common name for a large class of molluscs that have a soft body enclosed in a calcareous two-part shell.
Brachyura: true crabs.

Cape Supergroup: a sedimentary succession of Palaeozoic age rock layers in the Cape Fold Belt.
Carnivorous: flesh eating.
Cenozoic: the current geological era, representing the last 66 million years of Earth's history.
Cephalopoda: a class of molluscs, the members of which have distinct heads, e.g. squid and octopus.
Common name: an informal vernacular name for an organism.
Common pool resource: relatively large systems (e.g. groundwater basins, fishing grounds) that face potential overuse and conflict by multiple users.
Community: populations of different organisms living together in a particular environment.
Competition: use or defense of a resource by one individual that reduces the availability of that resource to other individuals.
Copepoda: a subclass of minute crustaceans which usually form part of the zooplankton.
Complex systems: systems that are characterised by unpredictable behaviour because their constituent parts interact in an interdependent and evolving manner.
CPUE: Catch Per Unit of fishing Effort.
Crustaceans: a large group of mostly aquatic invertebrate animals such as shrimps and crabs.

Detritivorous: feeding primarily on detritus.
Detritus: particles of decaying plant and animal material, and associated micro-organisms.
Diatoms: unicellular algae with walls impregnated with silica.

Ecosystem: a natural system of interacting organisms and their environment.
Eelgrass: an underwater flowering plant belonging to the genus *Zostera* (also known as seagrass).
Elasmobranchs: cartilaginous fishes, including all modern sharks and rays.
Embryo: the developing organism either within the egg envelope or hatched, and which is dependent on egg yolk for nourishment.
Endemic: organisms that are limited to a particular geographic region.
Environment: surroundings of an organism, including the plants and animals with which it interacts.
Epifauna: animals found on the surface of any substratum.
Epiphyte: non-parasitic plants which live on the surface of other plants.
Episodic floods: large river floods which occur irregularly.
Estuarine fish species: fishes which breed in estuaries and spend most or all of their life-cycle within the estuarine environment.
Estuary: that part of a river system closest to the sea and where salinities can fluctuate considerably.
Euryhaline: the ability of an organism to tolerate wide-ranging salinities.
Eutrophication: enrichment of water bodies, primarily caused by sewage and runoff from fertilized agricultural land.

Filamentous: thin and thread-like.
Food chain: a continuum of organisms in which each is the food of one or more subsequent members of the chain.
Food web: a system of inter-relating food chains.

Garden Route: section of coast between Humansdorp and Mossel Bay.
Gastropoda: molluscs with a ventral muscular disc adapted for creeping.
Geomorphology: study of the physical features of the earth's surface and their relation to its geological structures.
Gills: the breathing organs of fishes consisting of vascularised filaments attached to the gill arches.
Glacial period: a period when ice sheets were unusually extensive across the Earth's surface.
Gonads: reproductive organs.
Governance: the social context (e.g. rulemaking, assigning of responsibilities) that enables management.

Habitat: the specific environment of an organism.
Halocline: a layer of water exhibiting a steep salinity gradient.
Heads: The rocky headlands on either side of the Knysna Estuary mouth.
Headwaters: The portion of the estuary that is strongly influenced by river flow.
Herbivorous: feeding on plants.
Hermaphrodite: an organism possessing both male and female reproductive organs.
Holocene: period that covers the last 10 000 years.
Hominin: the group consisting of modern humans, extinct human species and all our immediate ancestors.
Hydrography: scientific study of water bodies.

Ichnology: the study of trace fossils.
Ichthyofauna: the assemblage of fishes in a particular area.
Ichthyology: the scientific study of fishes.
Interglacial period: geological interval of warmer global average temperature lasting thousands of years.
Intertidal: between the high-tide and low-tide levels on the shore.
Invertebrates: any animal which lacks a vertebral column or backbone.
Isopoda: dorsoventrally flattened crustaceans.

Jurassic Period: extending from 201 to 145 million years ago.
Juvenile: young organism essentially similar to the adult form.

Lagoon: The section of the Knysna Estuary between the rail bridge and the road bridge.
Larva: a developing organism after hatching from the egg, which has begun to feed itself and is not solely dependent on egg yolk for nourishment.
Littoral: at or near the shore of a water body.
Lower reaches: the lower longitudinal section of an estuary.

Macrophytes: large plants.
Management: the operationalization of a collective vision through resource allocation to implement selected actions and initiatives.
Marine fish species: fishes which breed at sea and spend most or all of their life-cycle in the marine environment.
Marine stragglers: marine fish species which rarely enter estuaries.
Meiofauna: microscopic or semi-microscopic animals that inhabit sediments.
Meroplankton: planktonic larval stages of organisms that are often benthic as adults.
Mesozoic Era: the geological era between 252 and 66 million years ago.
Microalgae: unicellular plants.
Middle reaches: the middle longitudinal section of an estuary.
Microphytobenthos: benthic microalgae.
Microtidal: applied to coastal areas or estuaries in which the tidal range is less than 2 m.
Middle reaches: the middle longitudinal section of an estuary.
Migration: coordinated movement of animals from one place to another.
Mollusca: invertebrates mostly distinguished by the presence of a hard, calcareous external shell.
Morphology: the study of shape or form.
Mucus: a viscous or slimy fluid secreted by the skin of many fishes.

Neap tide: smallest tidal range experienced due to the sun’s gravitational forces acting against those of the moon.
Nutrient: any substance required by organisms for normal growth and maintenance.

Oligotrophic: waters with a limited supply of nutrients and hence a reduced organic production.
Omnivorous: feeding on a wide variety of foods including plants and animals.
Organic matter: carbon compounds derived from plants and animals.
Osteichthyes: class of bony fish.
Otolith: a calcium carbonate structure in the inner ear of bony fishes.

Palaeo-Agulhas Plain: a southern Cape plain, now inundated by the sea, that was occupied by humans and vast herds of herbivores during recent global ice ages.
Palaeozoic: an era which began 570 million years ago and lasted 345 million years.
Palearctic: the large biogeographic realm stretching across all of Eurasia north of the Himalayas.
Parasite: an organism living on or in another and being nourished by it.
Pelagic: organisms living in open water, especially near the surface.
Periphyton: Biotic material found on, or attached to, the submerged parts of aquatic plants.
Phytoplankton: microscopic plants drifting in the plankton.
Piscivorous: feeding primarily on fish.
Planktivorous: feeding primarily on plankton.
Plankton: mainly microscopic floating organisms that drift more or less passively within the water column.
Pleistocene: the geological epoch that lasted from about 2 580 000 to 11 700 years ago.
Polychaeta: a segmented marine worm with bristles.
Postflexion larva: developmental stage of a fish from formation of the caudal fin to attainment of fin rays and scales.
Preflexion larva: developmental stage beginning at hatching and ending with commencement of upward flexion of the notochord.
Prey: animals that are the food of predators.
Primary production: the production of organic matter from inorganic materials by autotrophic organisms such as plants.

Red Data Book: world's most comprehensive inventory of the conservation status of biological species.
Resource: a substance or object required by an organism for normal maintenance, growth and reproduction.

Sea level: level continuous with that of the sea, half-way between high and low tide.
Seine net: a net, hanging from floats and having a central bag and equal-sized wings, that can be pulled through the water and onto the shore.
Semi-diurnal tides: tides with two high and two low waters during a tidal day (24 hours and 50 minutes).
Social-ecological system: referring to combined or intertwined human and nature systems across a range of scales, from a small river basin to the planet.
Southern Cape: the coastline between Cape St Francis in the east and Cape Agulhas in the west.
Species: a particular kind of organism; the fundamental taxonomic unit.
Species diversity: the variety (usually number of taxa) of species in a community or area.
Spring tide: maximum tidal amplitude during the new and full moon periods.
Standard length (SL): the length of a fish from the tip of the snout to the base of the tail.
Stenohaline: species which cannot tolerate a wide range of salinities during their life histories.
Stone Age: prehistoric period (2.6 million to 3 000 years ago) when stone tools were used by humans.
Strategic Adaptive Management (SAM): a brand of adaptive management tailored by SANParks to respond to local challenges arising from interdependent social and ecological systems that interact in unpredictable ways.
Stratification: a word used to describe a layered water body.
Substratum: a bottom surface of a habitat.
Subtidal: below the lowest level on the shore reached by the tides.
Supratidal: above the level on the shore reached by the tides.

Table Mountain Sandstone: predominantly quartzitic sandstone laid down between 510 and 400 million years ago.
Taxon: any taxonomic unit (e.g. family, genus, species).
Thermocline: a relatively narrow layer of water with a steep temperature gradient across it.
Tidal prism: the difference between the volume of water (in an estuary) at high tide and that at low tide.
Trace fossil: a fossil record of biological activity but not the preserved remains of the plant or animal itself.
Trophic group: a group of consumers that feed at a similar trophic level.
Turbid: descriptive of water which is muddy or murky due to the presence of suspended particles.

Ungulate: a hoofed mammal.
Upper reaches: the upper longitudinal section of an estuary.
Upwelling: a process whereby deeper, cold waters, rise to the surface as a result of the combined effects of wind, ocean currents and the Earth's rotation.

Warm-temperate region: the coastal area and estuaries between the Mbhashe Estuary and Cape Point.
Water column: the body of water between the bottom and surface.

Zoobenthos: bottom-dwelling animals.
Zooplankton: minute animals drifting in the water column.

Biological Names Index

B

C

This is a place where the river meets the sea
Where the past meets the present
And amber waters from ancient forests come up against the flood of the tide
This is a place where The Heads stand guard above surging swells
And silver shoals fold and unfold aquatic secrets to interested anglers
Where the shrill call of a whimbrel echoes across the mudflats
And the crack of pistol shrimps herald low tide
Where a fish eagle soars high above the languid lagoon
And sends out a message that is transmitted unchanged across Africa
For evening has arrived as the sun plunges towards the silver sea
And if you remain absolutely still and listen to your past
You may even hear an old elephant bull splashing through the shallows
And our hominin ancestors laughing as they collect intertidal seafood from Coney Glen
This is a paradise of forests, ferns and the tides of life—a place called Knysna

Alan Whitfield—2020
(Photograph: © Gemsbok: Dreamstime.com)

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