INTRODUCTION

WHALES, DOLPHINS AND porpoises all belong to the mammalian order Cetacea. They are the only mammals to spend their entire lives in water and have exchanged a layer of hair for a thick coating of insulating blubber. They have streamlined their body shape by losing all external trace of ears or hind limbs, and are able to propel their body using horizontally flattened tail flukes (their forelimbs having been relegated to paddle-shaped flippers for steering and stability). They are divided into mysticetes, or those with whalebone (horny baleen plates in the upper jaw), and odontocetes, or toothed whales (although dentition may be reduced to a single pair of teeth in the lower jaw).

Worldwide there are just over 80 species of cetaceans. The uncertainty about the exact number is caused by several factors. For even the 'better known' large whale species, of which many tens of thousands of individuals were killed by the whaling industry, only a tiny fraction are represented in museum collections, presumably because of the onerous task of preparing a skull or skeleton of such a large animal and then finding the space to store it. Consequently, no large series of skulls or skeletons exists for any single population of the great whales.

Other cetaceans are oceanic by nature, rarely venturing into inshore waters, and because they are relatively small in size they did not attract the attention of whalers. Such animals may only make themselves known to science when they strand on a coastline, and this has to happen near somebody who is keen enough to record the event and collect some material (and not eat the specimen). As a result, the science of cetacean taxonomy was handicapped for many years by the relative lack of comparative material and its slow rate of accumulation. It has taken the advent of modern genetic techniques to revolutionise the situation: DNA can be extracted from old museum specimens and other existing collections of biological material, and it can also be obtained from living cetaceans at sea through biopsies. Data from a relatively large series of individuals can now be collected in a reasonably short period and placed in an overall phylogenetic relationship.

However, as with so many other advances in science, all this new knowledge has created almost as many questions as it has answered. Consequently, while we might have been satisfied in the past to talk about one species of Bryde's whale worldwide, we now think there might be two or three. Genetics now tells us that there are three species of right whale (when some of us thought there might only be one), yet we battle to tell them apart morphologically. As more and more information accumulates about individual variation within and between populations, it seems inevitable that much of this will lead to the formulation of new cetacean subspecies or even species.

One of the regions of the world where our knowledge about cetacean fauna is weakest is southern Africa, despite the fact that this is a region of high oceanographic productivity and biological diversity that was once the site of the largest whaling ground outside the Southern Ocean. It is also home to about 63% of the world's whale and dolphin species (not to forget the porpoise), and contains one of the key areas for beaked whale diversity in the world. Attributing reasons for this ignorance is clearly beyond the scope of this book, but they can roughly be classified as political and socio-economic.

By displaying the region's rich cetacean fauna and summarising what we know and do not know about it, this book hopes to stimulate interest in this truly fascinating group of animals and encourage the accumulation of more knowledge about them. Only in this way can their conservation be truly assured.

About the book

As with many regional faunal guides, the geographical limits are largely arbitrary. In this case, the subregion is defined as extending from the equator to the edge of Antarctica, and between longitude 20° W and 80° E, or roughly from the middle of the Atlantic Ocean to the middle of the Indian Ocean. While these boundaries may not correspond to key oceanographic features, they have been chosen to be as broad as possible to make the addition of new species to the fauna list for the region less likely, and to cover as many destinations as possible that the sea-going traveller from southern Africa might visit.

For each species, illustrations are provided of the whole animal, including a side view (all species) and a belly or back view where appropriate. If colour varies with age, there is also an illustration of the juvenile. As photographs of whole cetaceans, particularly the larger ones, are difficult to obtain, we have been particularly fortunate to acquire the services of Pieter Folkens, the renowned marine mammal illustrator. Photographs of live animals are included where possible in order to give an impression of the 'jizz' of the species at sea, while the standardised views of the skull are intended to assist in identifying specimens for which no information on external appearance is available.

A word about the skull photographs. Those for which I was responsible were taken with a Nikon D70 camera and an 18–70 mm 1:3.5-4.5G ED lens. Readers should be aware that because of the wide-angle nature of this lens, I was able to capture even the largest blue whale skull from a reasonable distance, but not without incurring some degree of distortion. Many of the large whale skulls were also photographed through a barricade of metal and other supports, and although the repro house has done an admirable job of removing them from the images, those skulls that have been extensively worked in this way have been annotated as 'retouched'. Mainly as the result of the mechanics of handling the mandibles of large whales, they have been photographed from the lingual side in mysticetes, but the labial side in odontocetes. On occasions where the inappropriate mandible has been photographed for the corresponding lateral view of the skull, its image has been reversed (and noted as such).

The distribution maps provided for most species include actual sighting positions as well as a 'best impression' swath of colour to suggest what the range might be. In this way it is hoped that the reader will get a better feel for the reliability of the distribution shown. Strandings have been considered where appropriate but their distribution treated with some circumspection given that it may include animals outside their normal range. The sources of all location data are held by the MRI Whale Unit.

Each species account contains the following components:

- Appearance
- Length:weight relationship
- Skeletal data
- Distribution and migrations
- External commensals and parasites
- Food and feeding behaviour
- Reproduction and growth
- Behaviour and vocalisations
- Conservation status
- References

In compiling these accounts, priority was given to the results of data collected within the subregion, and only if information was deemed inconclusive or incomplete were data from other populations provided.

Nothing is more annoying than trying to figure out the origin of statements made in general texts, so an attempt has been made to cite a source for each statement of significance. To make these citations as unobtrusive as possible they have been indicated by means of superscript numerals. The names of the authors and the dates of publication appear at the end of each species account, and the full details of each source are given in the Bibliography at the end of the book.

Most species accounts contain a citation to 'MRI Whale Unit data'. This refers principally to unpublished data compiled by the Unit, but also includes compilations of published and unpublished data, some (such as the IWC's DESS data set) not originally collected by the Unit.

A word of explanation is needed about the units of measurement that appear in the book. Although metric units have been preferred throughout, occasionally non-metric measures such as nautical miles, imperial tons or even feet have crept in. These are there because the original (usually historical) source used them, and conversion might have been misleading. For instance, large whales taken by the industry were traditionally measured to the nearest foot, and this has been reflected in much of the scientific literature arising therefrom. Converting the results to an accuracy of more than one decimal point of a metre could give a spurious impression of accuracy.

To somewhat leaven the dough of scientific material, boxes containing brief discussions of topics of particular interest that could not be covered in any detail in the species accounts are scattered throughout the text. The choice and content of these may tend to reflect the author's particular areas of interest or bias, and for this he makes no apology.

PETER B. BEST
Cape Town
September 2007

Key to museum acronyms

MNM	Maldives National Museum, Maldives
NHMZD	Natural History Museum, London, England
NMNZ/TMP	Museum of New Zealand, Te Papa Tongarewa, Wellington, New Zealand
PEM	Bayworld, Port Elizabeth, South Africa
QMJM	Queensland Museum, Brisbane, Queensland, Australia
USNM	Smithsonian Institution, Washington DC, United States of America
ZM	Iziko South African Museum, Cape Town, South Africa

MAP OF THE SUBREGION

THE SOUTHERN AFRICAN subregion has been defined for the purposes of this book as the area extending from the equator to the edge of the Antarctic continent, and between the longitudes of 20° W and 80° E.

Shown below is the map of this subregion that is used within the species accounts to indicate distribution, but providing relevant nations, islands, towns, cities and other geographical features. For oceanographic features such as currents and fronts, the reader should consult Figs 2 to 4 on pages 8, 9 and 10. Anglicised versions of names have been used throughout, as these are how they generally appear in the original publications. An attempt has been made to include all localities mentioned in the text, but for reasons of space it may not have been possible to accommodate all of them on the map.

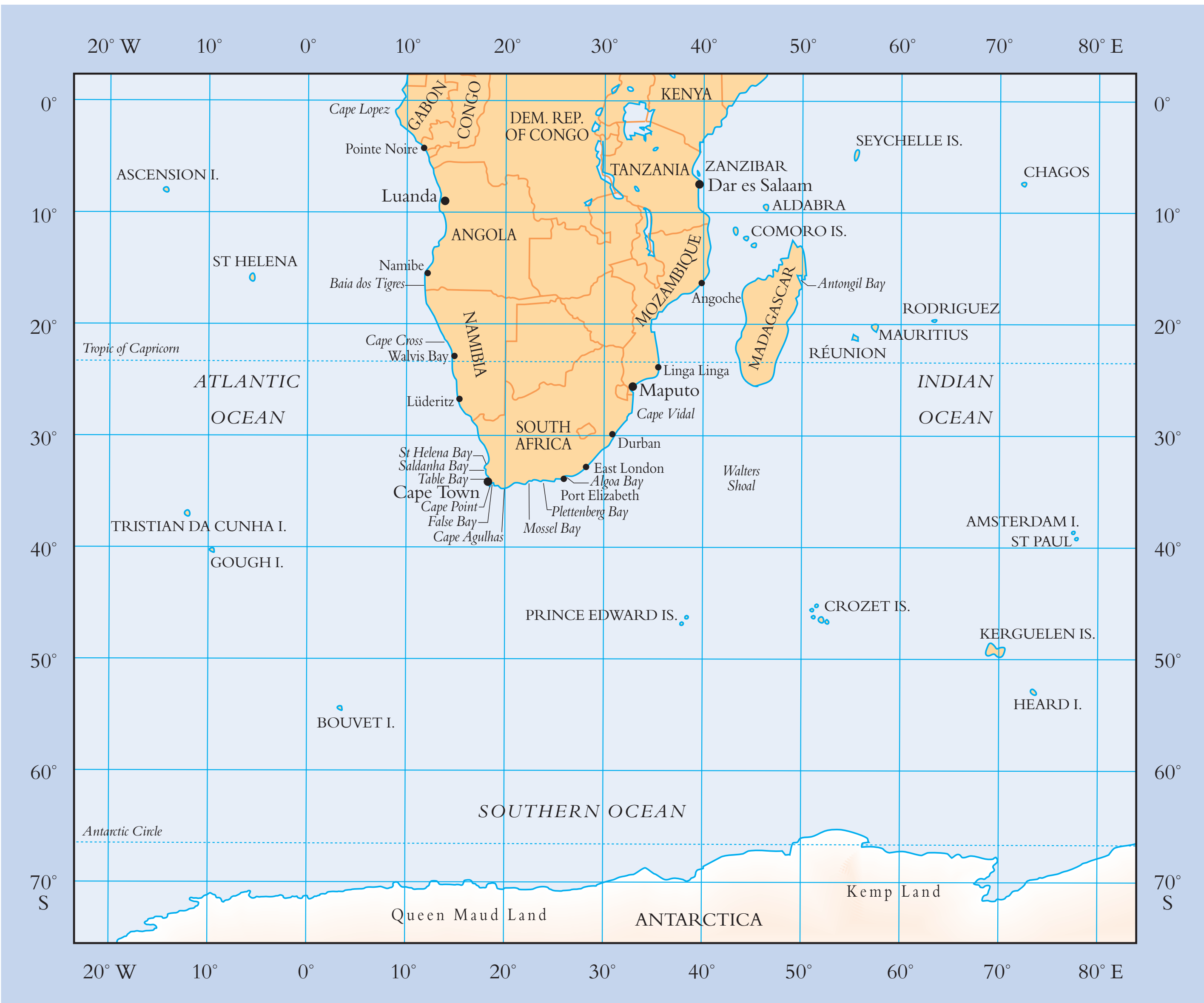

FIG. 1 Map of the southern African subregion as used to depict distribution, showing place names and geographical features.

THE CETACEAN ENVIRONMENT OFF SOUTHERN AFRICA

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THE OCEAN REGION extending from the tropics to Antarctica and including the south-west Indian and the south-east Atlantic oceans encompasses the widest possible variety of circulatory regimes. Many of these may affect cetacean distribution, including currents,[1] fronts,[2] vertical stratification, biological productivity and even faint traces of chemical and physical constituents of sea water that might aid in navigation.

Along the eastern seaboard of southern Africa the circulation is dominated by the greater Agulhas Current system,[3, 4] the largest western boundary current in the Southern Hemisphere (Fig. 3) (western boundary here meaning the western boundary of the anti-clockwise gyre in the South Indian Ocean). It is a narrow, intense current that extends to the ocean floor and is fed by a complex of sources, perturbations of which dramatically influence its behaviour. Deriving its waters from the tropics and subtropics it is low in nutrients and therefore in biological productivity. The circulation on the western side of the subcontinent is very different. Here the Benguela Current is a wide, shallow movement of water towards the equator, an eastern boundary current[5] (Fig. 2). On its landward side there is an extensive coastal upwelling system, driven by the local winds.[6] This water is cold, rich in nutrients and supports a very productive ecosystem.

Moving south from these subtropical regimes, one enters the Southern Ocean. This ocean region is characterised by zonal fronts, extending roughly along lines of latitude[7] (Fig. 4). The northernmost of these, and the intrinsic border to the Southern Ocean, is the Subtropical Convergence, a region where there is a very large meridional gradient in both temperature and salinity. This front is more intense south of Africa than anywhere else in the world's oceans. Further south other ocean fronts are found, such as the Antarctic Polar Front, but these do not have the same intense gradients. Along and between these fronts the largest current in the world's oceans – the Antarctic Circumpolar Current – carries its waters from west to east. The southern part of the Southern Ocean undergoes marked seasonal changes. A large part is covered by ice in winter, which causes a freshening of the surface layer in summer when this pack ice melts.

The Benguela Current system

The Benguela region encompasses the western coastline, roughly from Cape Town to southern Angola, and is largely characterised by wind-driven coastal upwelling of cool, sub-thermocline water[5] (Fig. 2). The Benguela Current system consists of a coastal branch, modulated by local weather processes, and an offshore oceanic flow, which forms the eastern limb of the South Atlantic subtropical gyre.[5, 8] The atmospheric high pressure cell situated over the south-east Atlantic provides the driving force for the Benguela Current regime.[8] In the south Benguela region, the south-east trade winds are responsible for the offshore transport of near-surface layers, resulting in a belt of coastal upwelling (see below) along the South African and Namibian coasts. The strongest winds are found where the coastline changes orientation from broadly north-westerly to more northerly, at Lüderitz and Cape Frio, and the weakest between Möwe Bay and Walvis Bay, where the coastline is concave.

The coastal upwelling area of the Benguela ecosystem extends between 14° S and 37° S, where its northern boundary has been shown to oscillate in a band between 14° S and 17° S[9, 10] (Fig. 2). There is a well-defined mean flow in the Benguela Current that is mostly confined near the African continent, with typical speeds of 10–30 cm/sec.[5] On its western side, however, flow is more transient and is characterised by large eddies shed from the retroflection of the Agulhas Current (Fig. 3), which are probably responsible for the spatial variations in transport.[11] In the south the current has a width of 200 km, but as it flows northward it widens rapidly to 750 km in the north.[12]

Upwelling regime

Upwelling, the process whereby the surface water is removed offshore by wind action and cold, nutrient-rich water is drawn to the surface, plays an important role in the oceanography and fisheries of the Benguela region. The phenomenon occurs all along the coast of south-western Africa, but is most localised in distinct cells characterised by recurring patches of cold water at the surface (Fig. 2). The area at Lüderitz (27° S to 28° S) presents a permanent and active upwelling cell[5, 13] that divides the Benguela system physically[5] and biologically[14] into two distinct areas, the northern and southern Benguela. Wind stress is greatest here and sea temperatures are lowest.[5, 10] Strong upwelling occurs here for 95% of the year,[10, 15] with a slight maximum in spring and minimum in autumn. It has been suggested that the surface features associated with the upwelling system are largely confined to within 300 km of the coast.[10]

There are high levels of inter-annual variability in the upwelling regions. From sea surface temperature measurements the existence of a weak 8±10-year cycle between alternating cool and warm periods has been found,[16] the cool periods being associated with enhanced cold-water upwelling and vice versa for warm periods. Sea surface temperature may vary 5 °C or more from the long-term mean. Inter-annual variability in sea temperature and salinity,[17] sea level,[18] winds[19] and atmospheric pressure,[20] all occur in the south-east Atlantic, although relatively few long-term studies have been undertaken.

Longshore fronts and cold filaments

Well-developed longshore thermal fronts exist between 18° S and 34° S. These fronts demarcate the seaward boundary of upwelled water. South of Lüderitz, a single front is usually well defined, and although spatially and temporally variable, coincides approximately with the edge of the continental shelf.[5] Further north, the surface definition of the front is more diffuse and multiple fronts are evident on occasion. Upwelling filaments are characteristic of these offshore fronts and exist as westward surface streamers of cold water typically 50 km wide and extending beyond the normal offshore extent of the upwelling cell.[21] These fronts have a typical lifespan from a few days to weeks, and are generally perpendicular to the coast. Although the influence of the upwelling regime may be between 150 and 200 km wide on average, the filamentous mixing area may extend up to 625 km offshore.[10, 21] Upwelling filaments tend to be highly-convoluted, eddy-shedding regions, and show extensive seaward penetrations at major upwelling cells such as Cape Frio and Lüderitz/Walvis Bay.[5, 10]

Poleward undercurrent

The most significant discovery during the past two and a half decades has been of a poleward undercurrent to the Benguela system[5] lying 100−150 km offshore at a depth of 200−400 m. On the shelf the undercurrent can be found at 50−100 m, and between Cape Point and Cape Cross (Namibia) it exhibits a seasonal trend in strength and occurrence. South of 33° S, where the shelf is narrow, the flow is not seasonally dependent, and average net poleward flow of only 5 km/day has been observed.[6] In contrast, north of 33° S, where the shelf broadens, the flow is variable over periods of weeks, alternating between the equator and the poles. This poleward undercurrent may provide clues to the occurrence of oxygen-depleted shelf water, which may be advected southwards from the tropical south-east Atlantic along the edge of the shelf.[22]

While the coastal upwelling area of the Benguela ecosystem shares many of the generic characteristics of other eastern boundary currents, it is unique in that it is bordered at both northern and southern ends by warm water systems, the Angola Current and the Agulhas Current respectively.[5] These borders are known to be highly dynamic with prominent 'pulsing' implications for the local ecosystem.

Angola Current system

The westward flow in the 15–20° S latitudinal band forms the confluence of the Benguela Current and the southerly flank of a large clockwise gyre west of Angola. The poleward Angola Current is a fast (40–50 cm/sec.), narrow and stable flow of warm (more than 24 °C), saline water that reaches a depth of 250−300 m and meanders laterally and vertically over both the continental shelf and the slope of the Angolan coast.[23–26] This water mass gradually becomes colder and less saline as it travels further south.[26] In addition, the Angola Current displays a degree of seasonality, retreating north-westwards in winter and spring to be replaced by slightly cooler waters (20−26 °C). This periodic south-east advance and north-west retreat of the Angola Current seems to be linked to the intensity of upwelling off the Namibian coast.[27, 28]

Another prominent feature associated with this Current is a regionally fixed, cyclonic gyre known as the Angola Dome lying at approximately 12° S, 4−5° E.[26] The Angola Dome is characterised by a decrease in salinity, compared to the surrounding water, that may result from the entrainment and vertical mixing of low-salinity Congo River water from the surface layer. The Angola Dome is less prominent during winter months,[29] and its width and extension depend on the intensity of the south-easterly trade winds.[30]

Angola-Benguela front

The Angola-Benguela frontal zone is the convergence between the south-flowing, warm Angola Current and the north-flowing, cold Benguela Current.[9] This frontal region also demarcates the water of the warm, nutrient-poor Angola Current and the cold, nutrient-rich Benguela upwelling regime, creating a transition zone between the tropical ecosystem in the north and the upwelling-driven ecosystem in the south.[26] This front is a permanent feature at the sea surface, maintained throughout the year in a narrow latitudinal band between 14° S and 6° S, with a general west to east orientation at the coast.[27] It is characterised by an average sea surface temperature of 23.6 °C in the northern region and 20.6 °C in the southern boundary at 16° S. Salinity data suggest the front may extend to a depth of 200 m, but it is particularly marked at the surface by a temperature gradient reaching 4 °C per 1° of latitude.[9] It is termed a frontal zone because often two or three parallel fronts can be observed.[6] The front fluctuates seasonally in latitude, seaward extent, temperature and strength, being furthest south in summer and early autumn and furthest north in winter and early spring. This migration has been associated with the seasonal movement of the Intertropical Convergence Zone in the equatorial Atlantic (a region where the north-east and south-east trade winds converge, forming an often continuous band of clouds).[31]

Temperatures associated with the front exhibit a similar pattern of seasonal change. At the coast, the front is least defined in winter, a period coinciding with the coolest water off Namibia and the stronger northward flow of Benguela water. It is most clearly developed during summer and autumn, when the warm-flowing southward Angola Current is at its maximum and coastal upwelling is at its weakest. On average, the front reaches its southernmost position in near-coastal zones and penetrates seawards up to distances of about 250 km, although traces of it can be found up to 1 000 km offshore. The maximum seaward extent is in spring and summer.[9, 27]

Benguela Niños

At times an extreme southward migration of the Angola-Benguela front results in large intrusions of warm, saline tropical water.[5, 17, 32] These intermittent anomalous warm events obstruct coastal upwelling by depressing the thermocline and stabilising the water column.[33] Extremely warm, nutrient-poor waters replace the cold, nutrient-rich upwelling water, with drastic consequences for productivity in the northern Benguela ecosystem. Thus, well-known warm years (1934, 1963, 1984 and 1995) are characterised by a reduction of upwelling in the northern Benguela and increased rainfall over the Namibian hinterland.[5] From a number of similarities between the 1963 and 1984 events and El Niño-Southern Oscillation events in the Pacific, the term 'Benguela Niño' has been suggested to describe them.[34] Similarities included apparent connections to anomalous atmospheric conditions in the tropical Atlantic in terms of relaxed westerlies along the equator, poleward propagation of tropical water along the Namibian coast, suppression of phytoplankton production, displacement of fish stocks, and a reduction in fish catches.[32] Long-term sea level records have shown that anomalously high sea levels correspond to these years of strong positive anomalies in sea temperature along the entire south-west African coast.[18] Furthermore, it has been suggested that Benguela Niño signals propagate polewards from the equatorial Atlantic similar to El Niño events, although not as intensely.[34]

Seasonality

The large-scale atmospheric weather systems over the south Atlantic display a seasonal pattern of northward and southward migration, and the effect of this seasonal cycle together with changes in insolation is manifested in the upper layer of the ocean.[5] Off the Namibian coastline there is a distinct seasonal cycle in surface and upper layer temperature, with a maximum in March and a minimum in August/September, the overall range in sea surface temperature being about 4–6 °C.[5] In the southern Benguela the upwelling season coincides with the period of maximum insolation, and accordingly the range in seasonal average temperature is only 1–2 °C. At the boundaries of the upwelling system, the water column becomes strongly stratified during the austral summer, particularly so over the eastern Agulhas Bank and off Angola, north of the Angola–Benguela front.

In the south, the boundary at the Agulhas retroflection likewise displays apparent seasonality, being furthest south in autumn. The Agulhas retroflection area is one of the global 'hot spots' in terms of variability of temperature and water movements.

Agulhas Current system

The Agulhas Current system can be thought of as extending from the Comoro Islands in the northern mouth of the Mozambique Channel (Fig. 3) to the Subtropical Convergence in the south.[35] The longitudinal borders are more difficult to define. The sources of the system include the whole South Indian Ocean and the throughflow between the Indonesian archipelago, whereas its outflow goes both into the South Atlantic Ocean and towards Australia in the South Indian Ocean. The behaviour of this system is also greatly affected by the underlying bottom topography.

The most obvious element of this bathymetry is the presence of the large land mass of Madagascar. It has a narrow shelf on its eastern side that stabilises the East Madagascar Current flowing along this coastline. Furthermore, the presence of Madagascar prevents the formation of a strong western boundary current in the Mozambique Channel. South of Madagascar there is a very shallow ridge, the Madagascar Ridge, that may play a decisive role in the movement of water in that region. From the coastline of Africa a similar, but deeper ocean ridge, the Mozambique Ridge, extends southwards, running parallel to the Madagascar Ridge. It may inhibit the flow of bottom water, but at lesser depths it may also affect the movement of deep-sea eddies. The edge of the continental shelf of eastern Africa is mostly narrow, allowing the Agulhas Current to flow quite close to the coast. However, at certain places there are offsets in the coast, such as at the Delagoa Bight, and here lee eddies may be formed (Fig. 3). South of Africa the continental shelf widens to form the Agulhas Bank. The Agulhas Current continues to follow the shelf edge, thus moving further offshore as it progresses southward along this wider shelf.[36] One of the final outflows of the Agulhas Current, the Agulhas Return Current, has to negotiate a number of shallower features on its way eastwards. These include the Agulhas Plateau (Fig. 3), which causes this current to carry out wide meanders in the direction of the equator.

The sources of the Agulhas Current proper come from an extensive recirculation in the south-west Indian Ocean, from water originating east of Madagascar, and from water passing through the Mozambique Channel. The circulation in the Mozambique Channel is dominated by eddies that form at the narrows of the channel and move steadily southward. These eddies may extend to great depths and may be anti-cyclonic (anti-clockwise) or cyclonic. The former seem to be stronger and longer lasting. As these eddies move past the shelf edge they may stimulate the formation of lee eddies. These eddies have upwelling at their centres and may thus enhance biological productivity. One such eddy is found in the Delagoa Bight[37] at the mouth of the Mozambique Channel.

To the east of Madagascar the South Equatorial Current carries water from east to west. As it reaches the eastern coast of Madagascar it splits (Fig. 3), one branch going north and the other south. The northern branch is eventually reunited with the rest of the South Equatorial Current and moves past the northern tip of Madagascar. The southern branch rapidly increases in strength until it reaches the southernmost part of Madagascar. Here it may either retroflect and flow eastward (as the South Indian Ocean Countercurrent) or move over the Madagascar Ridge. In this process it may break up into an assortment of eddies[38, 39] that subsequently drift into the Mozambique Channel or towards the Agulhas Current.[40, 41] At the point where the southern branch of the East Madagascar Current leaves the coast there is a well-developed upwelling cell[42] that has been associated with the presence of blue whales in spring.[43]

The Agulhas Current proper becomes fully constituted only somewhere along the north-east coast of South Africa. It is an intense current, about 100 km wide, and some of its surface water moves at speeds of more than 2 m/sec. Its northern part, namely as far downstream as Port Elizabeth (Fig. 3), is extremely stable, meandering less than 15 km to either side.[1] This stability is interrupted at irregular intervals by a singular meander, the Natal Pulse,[44] the lateral dimensions of which grow as it travels downstream. On its inshore side it causes rapid but short-lived changes in the direction of the coastal currents.

The depth of the Agulhas Current at any one location can vary over a period of a few months from the surface to 2 000 m or all the way to the bottom. Its landward border is sharply defined by a sudden increase in speed and temperature if one travels across it in a seaward direction.[45] At a depth of about 1 000 m the current is underlain by a countercurrent[46] that carries water towards the equator and may extend as one continuum into the Mozambique Channel. Between Durban and St Lucia, to the north, there is a wider and partly sheltered shelf region, the Natal Bight, while at St Lucia itself there is an intense upwelling cell[42] that brings nutrient-rich water onto the shelf and may control the whole ecosystem of the Bight.

By contrast the southern Agulhas Current meanders much more widely. Along the eastern side of the Agulhas Bank it develops shear edge eddies[47] and attendant plumes of warm water. The latter may penetrate far onto the Bank. Similar to the situation in the Natal Bight, there is a distinct upwelling cell at Port Alfred[48] where the Agulhas Current leaves the narrow shelf. Here nutrient-rich water is believed to be drawn up onto the shelf and spreads over the whole Agulhas Bank. The circulation on the western side of the Agulhas Bank may be more complicated.

(continued on page 11)