

Cetacean research in the southern African subregion: a review of previous studies and current knowledge

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Cetacean research, in terms of the number of papers, and areas for which data are available, has expanded considerably in the southern African subregion in the past decade, especially in the South-West Indian Ocean. We review cetacean research within this subregion from the 1800s to the present to provide an overview of findings, investigate trends and identify knowledge gaps. Data are presented separately for large whales (those subject to commercial whaling) and smaller cetaceans, and are separated by era and ocean basin. Over 550 peer-reviewed papers and books were identified relating to research on cetaceans within the subregion. More than half (284) have been produced since 1990 and 193 relate specifically to South African waters. The most-studied species are those that are most accessible due to their coastal distributions (southern right whale *Eubalaena australis*: 45 papers, humpback whale *Megaptera novaeangliae*: 31 papers, killer whales *Orcinus orca*: 27 papers, Indo-Pacific bottlenose dolphin *Tursiops aduncus*: 30 papers, Indo-Pacific humpback dolphin *Sousa chinensis* (*plumbea* form): 25 papers) and/or were hunted commercially (sperm whale *Physeter macrocephalus*: 25 papers). Identified conservation concerns vary throughout the subregion, but include bycatch and directed hunts, oil and gas development, ecotourism activities, shifts in prey resources, and noise and chemical pollution. The inshore stocks of Bryde's whales *Balaenoptera edeni*, the Indo-Pacific humpback dolphin and the Atlantic humpback dolphin *S. teuszii* were identified as the populations of highest conservation concern, although there are considerable knowledge gaps relating to deep-water species and almost no data (even on species occurrence) are available for several areas and countries.

Keywords: Atlantic Ocean, dolphin, Indian Ocean, Southern Ocean, whale, whaling

Introduction

Cetacean research in the southern African subregion, the 'study area' of this paper, is a relatively small but active field that has produced key insights into several aspects of cetacean biology. The geographical limits of the study area are defined, following Best (2007), as extending between the equator and the Antarctic ice edge, and from the central Atlantic at 20° W to the central Indian Ocean at 80° E (Figure 1). Research on cetaceans in the subregion has increased steadily since the 1960s, although different areas of the subregion have experienced different timing and considerably different levels of research output. The majority

of work prior to 2000 occurred in South African waters, but in the past decade both the output and geographic spread of research has increased throughout the subregion.

The environmental and oceanographic conditions within the subregion are diverse (e.g. Ansorge and Lutjeharms 2007) and well suited for investigating globally important questions such as speciation (Perrin 2007) and adaptation to climate change. The waters of the subregion encompass tropical, temperate and polar systems, including nutrient-rich upwelling systems (particularly the Benguela ecosystem), strong-flowing western boundary currents, subtropical, subantarctic



Figure 1: The southern African subregion, ranging from the equator to the ice edge between 20° W and 80° E. The horizontal grey line shows 40° S. Dashed grey lines show separation of the west and east coasts of South Africa at 20° E, and north and south coasts of Mozambique at Beira (20° S)

and polar fronts, and mixed coastal waters (Ansorge and Lutjeharms 2007). The high diversity of marine life occurring in the subregion can largely be attributed to the varying oceanic conditions and different marine habitats (Findlay et al. 1992, Ansorge and Lutjeharms 2007, Perrin 2007).

Estimating the exact number of cetacean species present in the subregion is complicated by taxonomic uncertainties and the lack of information on the exact range of many species. Best (2007) listed 51 species or subspecies, or 59% of the 86 recognised species of cetaceans worldwide, that occur in the subregion (www.iwcoffice.org/conservation/cetacea.htm). A full list of common and scientific names of cetacean species considered in this manuscript is provided in Table 1; only common names are used in the text hereafter. A breakdown of species occurrence by area suggests that the waters around South Africa are the most diverse, although this may be a reflection of relatively high observer effort. In their extensive review of strandings, scientific surveys and opportunistic sightings, Findlay et

al. (1992) listed 28 species of small odontocete within South African and Namibian waters. To this number can be added the sperm whale, and at least seven species of balaenopterids (i.e. a total of 36 cetacean species) known to occur in South African or Namibian waters (Best 2007). Weir (2010a) compiled similar data (including whaling records) from the waters between Angola and the Gulf of Guinea (which extends northwards of the geographic limits set in this review) and listed at least 28 species of cetaceans (seven balaenopterids and 21 odontocetes). Kiszka et al. (2006, 2010a, 2010b) listed 22 and 12 cetacean species from the waters of Mayotte and the Comoros Islands (Mozambique Channel) respectively, based on recent survey data and Hermans and Pistorius (2007) reported on 13 species that have been sighted around Aldabra, Seychelles.

There are multiple conservation threats within the subregion including directed and accidental capture in fisheries (e.g. Cockcroft and Krohn 1994, Amir et al. 2002) and anti-shark nets (Cockcroft 1990, Dudley and Cliff 2010, Meÿer

Table 1: Nomenclature of the cetacean species occurring within the southern African subregion (based on Best 2007, Weir 2010b) and the number of papers referring to these species or groups of species. The list differs from that of Best (2007) in that we have listed the pygmy blue whale separately to the Antarctic blue whale, the common dolphin is listed as one species, and we have included a separate row for papers referring to both species of humpback dolphin

Common name	Scientific name	<1900	1900– 1959	1960– 1970	1971– 1980	1981– 1990	1991– 2000	2001– 2010	2011 or In press	Total
Southern right whale	<i>Eubalaena australis</i>	0	0	3	3	9	12	18	3	48
Pygmy right whale	<i>Caperea marginata</i>	0	0	0	1	0	2	1	1	5
Blue whale	<i>Balaenoptera musculus</i>	0	3	2	0	2	0	8	0	15
Pygmy blue whale	<i>Balaenoptera musculus brevicauda</i>	0	0	3	0	1	1	4	0	9
Fin whale	<i>Balaenoptera physalus</i>	0	3	3	1	1	1	0	0	9
Sei whale	<i>Balaenoptera borealis</i>	0	2	3	4	1	0	1	0	11
Bryde's whale	<i>Balaenoptera brydei</i> ¹	0	2	1	1	2	1	1	1	9
Dwarf minke whale	<i>B. acutorostrata</i> subsp.	0	0	0	0	1	0	0	0	1
Antarctic minke whale	<i>Balaenoptera bonaerensis</i>	0	0	0	2	10	3	3	0	18
Humpback whale	<i>Megaptera novaeangliae</i>	0	2	0	2	1	10	10	4	29
Sperm whale	<i>Physeter macrocephalus</i>	0	3	13	7	6	1	2	0	32
Dwarf sperm whale	<i>Kogia sima</i>	0	0	0	1	0	0	1	0	2
Pygmy sperm whale	<i>Kogia breviceps</i>	0	0	0	1	0	0	1	0	2
Cuvier's beaked whale	<i>Ziphius cavirostris</i>	0	0	1	2	0	0	1	0	4
Arnoux's beaked whale	<i>Berardius arnuxii</i>	0	0	1	0	0	0	0	0	1
Shepherd's beaked whale	<i>Tasmacetus shepherdi</i>	0	0	0	0	0	0	1	0	1
Longman's beaked whale	<i>Indopacetus pacificus</i>	0	0	0	0	0	0	2	0	2
Southern bottlenose whale	<i>Hyperoodon planifrons</i>	0	0	1	0	0	1	0	0	2
Hector's beaked whale	<i>Mesoplodon hectori</i>	0	0	2	0	0	0	0	0	2
True's beaked whale	<i>Mesoplodon mirus</i>	0	0	3	0	5	0	3	0	11
Gervais' beaked whale	<i>Mesoplodon europaeus</i>	0	0	0	0	0	0	0	0	0
Gray's beaked whale	<i>Mesoplodon grayi</i>	0	0	1	0	0	0	0	0	1
Andrew's beaked whale	<i>Mesoplodon bowdoini</i>	0	0	0	0	0	0	0	0	0
Layard's beaked whale	<i>Mesoplodon layardii</i>	0	0	0	0	1	1	0	0	2
Blainville's beaked whale	<i>Mesoplodon densirostris</i>	0	0	0	1	0	0	0	0	1
Ginkgo-toothed beaked whale	<i>Mesoplodon ginkgodens</i>	0	0	0	0	0	0	0	0	0
Killer whale	<i>Orcinus orca</i>	0	0	0	2	9	5	12	3	31
Long-finned pilot whale	<i>Globicephala melas</i>	0	0	0	2	1	0	0	1	4
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	0	0	0	2	0	0	1	0	3
False killer whale	<i>Pseudorca crassidens</i>	0	1	0	0	1	0	0	0	2
Melon-headed whale	<i>Peponocephala electra</i>	0	0	0	0	2	0	0	0	2
Pygmy killer whale	<i>Feresa attenuata</i>	0	0	2	1	0	1	0	0	4
Humpback dolphin (both)	<i>Sousa</i> spp.	0	0	1	0	0	0	0	0	1
Atlantic humpback dolphin	<i>Sousa teuszii</i>	0	0	0	0	0	1	7	1	9
Indo-Pacific humpback dolphin	<i>Sousa chinensis</i> ²	0	0	1	3	1	13	6	0	24
Rough-toothed dolphin	<i>Steno bredanensis</i>	0	0	0	0	0	0	2	0	2
Dusky dolphin	<i>Lagenorhynchus obscurus</i>	0	0	0	1	0	1	7	1	10

Table 1 (cont.)

Common name	Scientific name	<1900	1900–1959	1960–1970	1971–1980	1981–1990	1991–2000	2001–2010	2011 or In press	Total
Hourglass dolphin	<i>Lagenorhynchus cruciger</i>	0	0	0	0	0	2	0	0	2
Southern right whale dolphin	<i>Lissodelphis peronii</i>	0	0	0	1	2	1	0	0	4
Risso's dolphin	<i>Grampus griseus</i>	0	0	0	0	0	2	0	0	2
Common bottlenose dolphin	<i>Tursiops truncatus</i>	0	0	0	2	3	1	2	0	8
Indo-Pacific bottlenose dolphin	<i>Tursiops aduncus</i>	0	0	1	4	12	10	12	0	39
Pantropical spotted dolphin	<i>Stenella attenuata</i>	0	0	1	0	2	0	1	0	4
Atlantic spotted dolphin	<i>Stenella frontalis</i>	0	0	0	0	0	0	1	0	1
Spinner dolphin	<i>Stenella longirostris</i>	0	0	0	1	0	0	1	0	2
Clymene dolphin	<i>Stenella clymene</i>	0	0	0	0	0	0	1	0	1
Striped dolphin	<i>Stenella coeruleoalba</i>	0	0	0	1	1	1	0	0	3
Common dolphin	<i>Delphinus</i> spp. ³	0	0	0	1	3	2	2	0	8
Fraser's dolphin	<i>Lagenodelphis hosei</i>	0	0	0	1	0	0	1	0	2
Commerson's dolphin	<i>Cephalorhynchus commersonii</i>	0	0	0	0	5	0	1	0	6
Heaviside's dolphin	<i>Cephalorhynchus heavisidii</i>	0	0	0	1	2	1	7	2	13
Spectacled porpoise	<i>Phocoena dioptrica</i>	0	0	0	0	1	1	1	0	3

¹ The taxonomic status of Bryde's whale is confused; recent molecular analysis conclusively separated Bryde's whale into two species (*Balaenoptera edeni* and *B. brydei*) (Wada et al. 2003). Following Best (2007) and Weir (2010b), *B. brydei* is used for this species within the study area based on the lack of records in the subregion of a small form referable to *edeni*

² The taxonomic status of the genus *Sousa* is unresolved. Many workers consider Indo-Pacific humpback dolphins to consist of at least two species: *S. plumbea* (western Indo-Pacific) and *S. chinensis* (eastern Indo-Pacific). *S. chinensis* (*plumbea* form) is used here following Reeves et al. (2008)

³ The taxonomy of *Delphinus* dolphins is unresolved (IWC 2009). The IWC Scientific Committee concluded that until further genetic information becomes available, the various geographical populations should be denoted in less committal terms such as short-beaked and long-beaked forms rather than as short-beaked (*Delphinus delphis*) and long-beaked (*D. capensis*) species (IWC 2009). Consequently, they are referred to here simply as common dolphin (*Delphinus* spp.)

et al. 2011), overfishing of prey species (e.g. Heymans et al. 2004, Roy et al. 2007), habitat loss (e.g. coastal development, pollution and dredging) (Kiszka et al. 2009), disturbance from commercial marine tourism activities (e.g. Christiansen et al. 2010, Stensland and Berggren 2010), shipping and seismic exploration (e.g. Weir 2008a, 2008b). Both human capacity and available financial resources to monitor threats within the subregion are, however, restrictive. This is further compounded by poor coordination and understanding of existing knowledge which is needed in order to optimise research and conservation efforts within the subregion.

Here, we compile a review of past and existing cetacean-focused research within the subregion. This review has several objectives in relation to cetacean research in the southern African subregion: (1) to present a brief historical review of cetacean research; (2) outline the major trends and developments in cetacean research; (3) identify conservation-related gaps in knowledge and priorities for future cetacean research; and (4) provide a resource of relevant publications.

Data sources and methods

In general, there are distinctions between the research conducted on large whales and on smaller cetaceans in the

subregion, in terms of the motivations for working on them and also in terms of study design. For large whales (those that were the targets of the whaling industry comprising most of the baleen whales and the sperm whale), research is separated into (1) a historical era (prior to 1975), marked primarily by data collected during or associated with commercial whaling operations; and (2) a modern era (1975–present), marked largely by the cessation of commercial whaling and the onset of independent field research. For the smaller cetaceans (including the beaked whales, kogid whales, delphinids and the single phocoenid), research is divided into (1) early opportunistic data collection (prior to 1960); and (2) the beginning of dedicated research up until the current era, including ongoing studies (1960–2010). The split at 1960 for smaller cetaceans was chosen to reflect the rapid increase of research output associated with the appointment of full-time cetologists based in South Africa who carried out much of the pioneering work in this part of the subregion. Research outside of South Africa, especially in the South-West Indian Ocean islands, expanded markedly since the late 1990s.

The information presented is purposefully restricted to the primary peer-reviewed research on cetaceans, and does not include grey literature (i.e. theses or unpublished reports) except where deemed to be particularly relevant

in terms of subsequent research in a given area of the subregion. The *Discovery Reports*, for example, may not have been peer-reviewed in the current sense, but include much of the data available from this era, and were therefore included in this review. Data have been compiled from literature searches of various databases, cetacean review papers and the publication records of several key scientists working in the subregion. To investigate trends in research, the literature was separated by area (part of the subregion, country or coast), time period (as above) and by species or group of species (if a particular publication is directed at more than one species). This manuscript is intended as an overview of the main research and trends and thus does not include all qualifying publications. A full list of these papers is available as online supplementary material at <http://dx.doi.org/10.2989/1814232X.2011.637614>. Statistics of identified papers in the text refer to this full list.

For both large whales and small cetaceans, we present information on research activities in the subregion in chronological order, and have divided the subregion into research performed in South Africa, the eastern tropical Atlantic (north of Namibia), South-West Indian Ocean (excluding the South African coast) and the Southern Ocean (regarded here as south of 40° S and including the sub-Antarctic islands). However, it should be noted that there is some overlap of research approaches across the delineated time periods. For example, research arising from data collected during the whaling era continues to be published in recent years.

Furthermore, we have focused this review on research that is primarily aimed at describing cetacean distribution, biology and ecology, and have not included literature pertaining to methodological studies (such as sighting/survey methods), although these are not an insignificant component of research originating in the subregion.

Large whales and the whaling era (pre-1975)

The majority of early information on mysticetes and sperm whales in the southern African subregion originated from whaling activities during both the historic or 'open-boat' (from around 1770–1929) and the 'modern' whaling eras (steam-driven ships using explosive harpoons from 1908 to 1975). The vast majority of catches within the subregion during the open-boat whaling period were made by British, Dutch, French or American 'Yankee' pelagic fleets operating in extensive whaling expeditions across broad oceanic areas. The bulk of the data available from vessel logbooks during this period was for southern right and sperm whales with some data for humpback whales; catches from shore-based stations by open-boat whalers were considerably fewer and predominantly of southern right whales (Best and Ross 1989).

The scientific value of much of the data gathered during the whaling era was only fully appreciated and analysed much later and only 13 papers could be identified arising from historical whaling data for the subregion. Townsend (1935) summarised catch data from a sample of whaling logbooks for the period 1761–1920 and provided the first published information on the distribution and seasonality of southern right, humpback and sperm whales in the subregion. Catch

data from open-boat coastal whaling have provided information on the exploitation, recovery, distribution and seasonality of southern right whales (Best 1970a, Best and Ross 1986, Richards and Du Pasquier 1989, Best 2006). A more complete review of the history of shore-based, open-boat whaling is provided by Best and Ross (1989).

Research arising from modern whaling activities on the African subcontinent was based on two approaches, namely: (1) biological research carried out at stations or on-deck during flensing operations and largely relating to feeding, reproductive, morphometric and anatomical studies; and (2) research carried out in the searching and catching phases of the operation, relating to catch distribution, abundance and migration seasonality, as well as whale marking programmes. Modern shore-based whaling started in Durban, South Africa, in 1908, and stations were opened all around the coast of the subregion from Gabon to Mozambique, targeting mainly humpback whales. Catch statistics from this industry are available from several sources (Tønnessen and Johnsen 1982, Best and Ross 1986, 1989, Best 1994, Findlay 2001). Sightings information from two humpback whale-focused cruises to the Mozambique Channel from 1937 to 1939 and 1949 to 1950 are available from Bermond (1950) and Angot (1951) respectively.

Whaling research in the subregion was episodic prior to the 1960s and resulted mainly from independent visits to whaling stations by European researchers. Olsen's 1912 visit to the Donkergat and Durban whaling stations produced several important findings, including the first description of the external appearance of the Bryde's whale and observations of the life history and migration patterns of humpback whales up both the east and west coasts of Africa (Olsen 1913, 1914). It should be noted that whalers operating in African waters often could not distinguish between sei whales and Bryde's whales and the catches recorded for these species, particularly in the Atlantic, should be viewed with caution (Olsen 1913, Harmer 1928, Ruud 1952, Best 1994, 1996, 2001). Scientists working for the Discovery Investigation Programme briefly visited stations on the west coast (Donkergat in 1926) and east coast (Durban in 1929) of South Africa. Research from this period included insight into the migration patterns and life history of blue whale and fin whale (Mackintosh et al. 1929, Best and Ross 1989) and information on humpback whales (Matthews 1938a), sei whales (Matthews 1938b), as well as the large number of sperm whales taken in Durban (Matthews 1938c). The deployment and recovery of Discovery tags (numbered darts fired into a whale's body during deployment trips and recovered during flensing operations) resulted in many of the first, and in some cases only, observations on the movement patterns and seasonality of sei, humpback, fin, blue and sperm whales (Rayner 1940, Brown 1962, Best and Ross 1989, Branch et al. 2007) in the subregion. Some early descriptions of the anatomy of sperm whales were made from the investigation of foetuses (Beddard 1915).

Analysis of catch data from the eastern tropical Atlantic provided information on the species identity and composition (Budker 1950, 1953, Ruud 1952, Mikhalev et al. 1981a), as well as their seasonality (Budker and Roux 1968, Best 1996, 2001) and aspects of their biology such as size distribution (Budker and Collignon 1952, Budker 1953, Budker and Roux 1968), age determination from baleen plates (Ruud

1952), stomach contents (Budker 1950, 1953, Best 1996, 2001), parasites and scarring (Budker 1950, Best 2001), sex ratios (Budker and Collignon 1952, Budker 1953), and the presence of foetuses and other reproductive data (Budker and Collignon 1952, Budker 1953, Budker and Roux 1968, Best 1996, 2001). Information from Gabon also highlighted a growing awareness of overexploitation of whales, particularly humpback whales, with several workers expressing concern over the unsustainability of whaling activities in this area (Budker 1952, 1953, Budker and Collignon 1952, Budker and Roux 1968).

South African and British scientists worked at the main South African whaling stations at Donkergat and Durban from 1962 onwards and collected large amounts of data, some of which are still being analysed. The high number of catches of sperm whales at both stations allowed for significant early insights into their external characteristics (Best and Gambell 1968a), the reproductive characteristics both of females (Gambell 1966, 1972, Best 1967a, Best 1968a, 1968b) and males (Best 1969a, Gambell 1972), distribution and migration patterns (Best 1969b, Gambell 1967), life history (Best 1970b, Gambell 1972), feeding (Best 1999, Clarke 1980), and the social system (Best 1979, Best et al. 1984a). Other key findings during this period include the description of an inshore and offshore form of the Bryde's whale (Best 1977, 2001) at the same station at which the species was originally described by Olsen (1913), and the first description of the dwarf minke whale (Best 1985). The feeding and seasonal appearance of baleen whales (Bannister and Gambell 1965, Bannister and Baker 1967, Best 1967b), growth and reproduction of sei whales (Best and Gambell 1968b, Best and Lockyer 2002), and the seasonal abundance, feeding, reproduction, age and growth of Antarctic minke whales (Best 1982) were described from animals captured during this period. Material collected at Durban was also invaluable in studies that clarified the rate of lamina formation in the ear plugs of fin (Roe 1967) and sei whales (Lockyer 1974).

Large whale research in the Southern Ocean sector during the whaling era mainly comprised of extensive distributional studies from whaling catch records (Mackintosh et al. 1929, Mackintosh 1942, Ichihara 1966, 1981, Omura 1973), Discovery marks (Brown 1959a) and associated search effort (e.g. Kasuya and Wada 1991). A total of 16 papers could be identified as arising from data collected during these 'modern whaling' operations in the Southern Ocean part of the study area.

Although virtually all cetacean research during this early period was associated with whaling, the recording of sightings of all cetaceans in the region was recognised as valuable by many scientists. For example, large whale sightings from merchant vessels working in the Atlantic Ocean prior to 1956 were collated to provide information on their distribution (Brown 1959b). Records of small cetaceans arising from whaling operations are discussed below.

Large whale research in the post-whaling era (post-1975)

The majority of research on large whales within the subregion since 1975 has taken place in South African waters and in the Southern Ocean. The three most comprehensively studied large whale species are the southern right whale (41

papers since 1975, of which 21 were published since 2000 and several based on historic data), humpback whale (29 papers since 1975, of which 17 were published since 2000) and Antarctic minke whale (14 papers since 1975, although only two since 2000). The vast majority of southern right whale research has been in South African waters, reflecting the species current range within the subregion. Humpback whales have been studied throughout the subregion and Antarctic minke whales have been studied almost exclusively in the Southern Ocean through International Whaling Commission (IWC) survey initiatives. It is clear that research on several of the species that comprised major components of the commercial catch (notably sperm, blue, fin and sei whales) has been negligible since the 1970s, largely reflecting the loss of access to these offshore populations. The majority of publications on large whales prior to 2000 resulted from data collected during whaling operations (Figure 2), and this data continues to be published, reflecting both its sheer volume and value to cetology in general.

South Africa

Between 1975 and 1986, the South African government conducted a series of annual marine mammal cruises to monitor cetaceans within the 200 nautical miles Exclusive Economic Zone (EEZ) of South Africa and Namibia, during which dedicated observations of cetaceans were made (Findlay et al. 1992). The sighting frequencies of large baleen whales were relatively low during these cruises, perhaps reflecting the decimated state of the populations at the time.

A dedicated ship-based survey in January/February 1983 to assess the inshore stock of Bryde's whales that inhabit the shelf waters off South Africa provided the only population estimate to date (582 animals; SE 184) (Best et al. 1984b). Analysis of catch records, and several scientific- and whaling-related cruises (pre and post the end of whaling), have indicated that Bryde's whales in the subregion form at least three stocks ranging between Gabon and Madagascar (Best 2001). A recent study using photo-identification in Plettenberg Bay, on the east coast of South Africa, has provided data on the seasonality of the inshore stock in coastal waters (Penry et al. 2011).

The South African government initiated inshore monitoring of the stocks of southern right whales along the south coast of the country in 1969. Aerial sightings surveys and photographic surveys for right whales have been carried out annually during October since 1969 and 1979 respectively, and the photographic survey series remains unbroken up to 2010 (PB Best, Iziko South African Museum, pers. comm.). Among others, this survey series has provided data on the applicability of photographic identification for monitoring the species (Best 1990a), environmental (Elwen and Best 2004a, 2004b) and social (Elwen and Best 2004c) influences on distribution and long range movement patterns, including to the Tristan da Cunha ground (Best 1988), demography (Best et al. 2001a), population size and trend (Best 1990b, Best et al. 2001a), healing and long-term responses to biopsy and satellite tagging (Best et al. 2005, Best and Mate 2007), and the rate of entanglement in fishing gear (Best et al. 2001b).

Furthermore, boat-based studies of southern right whales have allowed for the collection of tissue samples and

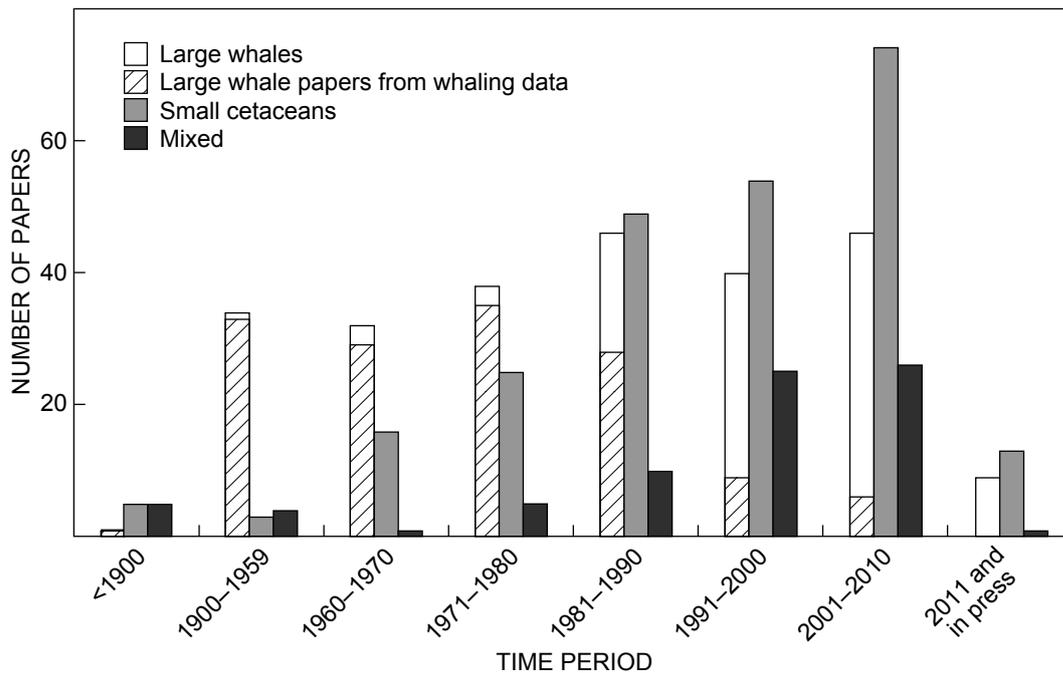


Figure 2: Number of identified papers, books or book chapters relating to research in the southern African subregion during time periods between 1800 and 2011. Manuscripts are divided into those focusing on large whales (hatched portion of bars represents papers resulting directly from whaling data), small cetaceans or papers referring to all or mixed groups of cetaceans (see text for definitions)

behavioural observations. This facilitated investigation into social behaviour (Best et al. 2003), feeding, growth and seasonal movements using stable isotopes (Best and Schell 1996), inheritance of dorsal pigmentation patterns (Schaeff et al. 1999), disease (Mouton et al. 2009), development and structure of the integument (Reeb et al. 2005, 2007), and genetic relationships both locally and internationally (Kaliszewska et al. 2005, Patenaude et al. 2007). Satellite telemetry and photo-identification studies have uncovered broad-scale movement patterns, migration routes and unexpected long-term residencies and feeding areas (Best et al. 1993, Mate et al. 2011), while ultrasound studies of blubber thickness provided a comparison with North Atlantic right whales (Miller et al. 2011). The increasing numbers and expanding range of southern right whales has been investigated in Namibian waters by Roux et al. (2001). The occurrence of a low-latitude summer feeding ground in St Helena Bay, on the west coast of South Africa, has been confirmed by satellite telemetry (Best and Mate 2007, Mate et al. 2011) and analysis of historical catch records (Best 2006) and provides a rare opportunity to investigate diet and feeding of this species outside of Antarctic waters.

Humpback whales have been studied on both the Indian and Atlantic Ocean coasts of South Africa. Initial shore-based monitoring of humpback whales on the west coast of South Africa described a temporary summer residence of whales in what appeared to be a suspended migration (Best et al. 1995, Findlay and Best 1995). Following this, Saldanha Bay was confirmed as a summer feeding ground used by both humpback and southern right whales (Best and Mate 2007, Barendse et al. 2010, 2011). Shore-based monitoring on the east coast at Cape Vidal, South Africa, from 1988

to 1991 and in 2002 (Findlay et al. 2011) was carried out to assess the relative abundance and migration patterns (Findlay and Best 1996a) and also provided data on survey techniques (Findlay and Best 1996b). These surveys laid the groundwork for multiple broader-scale, vessel-based surveys in Mozambican and Madagascan waters.

Eastern tropical Atlantic

Political instability within some countries (Angola and the Democratic Republic of Congo) in the eastern tropical Atlantic part of the subregion during the latter part of the 20th century limited the opportunities for research in this area. During the late 1990s, two short studies investigated the population structure and abundance of humpback whales. Best et al. (1999) carried out brief photo-identification, acoustic and biopsy studies of humpback whales off northern Angola during September 1998. Around the same time (August 1998), Walsh et al. (2000) flew two days of aerial survey transects for humpback whales in the vicinity of Point Gentil in Gabon. They also conducted eight days of boat-based research in this area during 1997, 1998 and 1999, collecting similar data. A long-term study of humpback whales in coastal Gabon was initiated by the Wildlife Conservation Society to investigate the status, distribution and population structure of humpback whales in this area using photo-identification, acoustic and genetic methods (Pomilla and Rosenbaum 2006, Rosenbaum and Collins 2006). During a further study the song structure produced by humpback whales off Gabon and Brazil was analysed and similarities were found, which suggested interaction between whales from different Atlantic breeding populations (Darling and Sousa-Lima 2005).

Between 2004 and 2009, information on the distribution and seasonal occurrence of cetaceans in oceanic waters between Angola and Gabon was collected from platforms of opportunity (geophysical survey vessels), providing the first year-round and multi-year dataset on the occurrence of oceanic large whales, particularly sperm and humpback whales, for the eastern tropical Atlantic (Weir 2007, 2011). While the nature of these surveys prohibits calculations of absolute abundance or in-depth studies on behaviour or biology, they have provided information on spatial distribution, seasonality and group sizes in poorly studied oceanic waters. A dedicated cetacean survey off southern Angola also produced information on the distribution and behaviour of Bryde's whales in coastal areas (Weir 2010b).

South-West Indian Ocean

Subsequent to the last whale marking cruise in the South-West Indian Ocean (Gambell et al. 1975), there was a lull in broad-scale (100s of km) survey effort in this area. However, following the development of the Indian Ocean Sanctuary by the IWC in October 1979, several opportunistic surveys have been undertaken to describe cetacean distribution and relative abundance within the sanctuary (e.g. Keller et al. 1982). The majority of these have taken place since 1990 (Kasuya and Wada 1991, Eyre 1995, 1997, 2000, Tynan 1997, Ballance and Pitman 1998, Ballance et al. 2001). Distribution and seasonality of large baleenopterids in this part of the subregion have been assessed from the logbooks of French tuna fishing vessels operating from the Seychelles between 1982 and 1986 (Robineau 1991).

Following earlier work on the east coast of South Africa at Cape Vidal (Findlay and Best 1996a), multiple broad-scale surveys were carried out using a variety of vessels to assess the absolute abundance and distribution of humpback whales farther north in Mozambican and Madagascan waters (Findlay et al. 1994, in press, Best et al. 1996, 1998). The majority of large whale work in the South-West Indian Ocean has been directed towards humpback whales, probably due to their accessibility to researchers. Localised studies (using small boats in inshore waters) have been carried out in Antongil Bay, Madagascar, between 1996 and 2007 (e.g. Ersts and Rosenbaum 2003) and off the island of Mayotte and surrounding reef banks (eastern Comoros archipelago) (Kiszka et al. 2010b, Ersts et al. in press) to investigate density, group composition, habitat preferences and seasonality. Biopsy samples collected during these surveys have been analysed along with those from the east and west coasts of southern Africa and Gabon to investigate stock structure, relatedness and migration characteristics of humpback whales in the region (Rosenbaum et al. 2009), including individual movements between ocean basins (Pomilla and Rosenbaum 2005).

Research on other species of large whales has included a dedicated survey for sperm whales undertaken off the Amirante Islands (Seychelles) to assess their density and behaviour (Kahn et al. 1993) and the collation of opportunistic records of sperm, fin, blue and humpback whales off Mauritius during the austral winter (Corbett 1994). Recently, the French government has recognised a need for more dedicated research and protection of its overseas EEZ. Therefore, a large-scale aerial survey programme has been

undertaken in the South-West Indian Ocean (covering more than 1 500 000 km²). Preliminary results are already available from the REMMOA surveys (REcensements des Mammifères marins et autre Mégafaune pélagique par Observation Aérienne/Census of marine mammals and other pelagic megafauna by aerial survey) that were set up to run from 2008, working in collaboration with locally based researchers and using a standardised line-transect methods to increase comparability between areas and survey periods (Ridoux et al. 2010). These results have provided new information on the distribution, species composition and abundance of cetaceans in the South-West Indian Ocean, including in the Seychelles EEZ, Mozambique Channel (including Mayotte, Comoros, north-western Madagascar, Juan de Nova, Europa, Bassas da India and south-western Madagascar), Mauritius and La Réunion, and north-eastern Madagascar, including Tromelin (Ridoux et al. 2010).

Southern Ocean

Most large whale research in the Southern Ocean part of the study area has been run under the auspices of the IWC. A series of summer ship-based surveys, the IWC/IDCR (International Decade of Cetacean Research) and IWC/SOWER (Southern Ocean Whale and Ecosystem Research) surveys, have taken place in Antarctic waters (south of 60° S and across different longitudinal bands of the entire Southern Ocean) between 1978/1979 and 2009/2010. These surveys have provided considerable information on the abundance and distribution of the more southerly migrating baleen whale species (particularly Antarctic minke, blue and humpback whales) and sperm whales within the Southern Ocean waters south of 60° S (Kasamatsu et al. 1988, 1990, 1996, 2000, Branch and Butterworth 2001a, 2001b) and have included the first evidence of the recovery of Antarctic blue whales (Branch et al. 2004). The Southern Ocean Cetacean Ecosystem Program (SOCEP) surveys of the Australian government have covered a minor portion of the defined study area (south of 60° S and east of 60° E). However, except for results of acoustic surveys of cetaceans south of 60° S and east of 30° E that were reported by Gedamke and Robinson (2010), no published research from this small sector could be identified.

Smaller cetaceans — research prior to 1960

Early research on small cetaceans in the subregion was largely opportunistic and was associated with particular voyages or events where work consisted largely of collecting and describing specimens and trying to disentangle the various duplicate descriptions made by different taxonomists (Gray 1850, True 1889). This was complicated and slowed by the modes of travel and communication available at the time. A total of 16 publications relating to small cetaceans could be identified prior to 1960.

From the waters around South Africa, specimens of the Layard's beaked whale (Gray 1865), Heaviside's and dusky dolphins (Gray 1828) were collected and described for the first time by European-based biologists. Many other specimens collected during this era were housed in European museums and played a role in the developing taxonomy of the Cetacea (Gray 1850, Flower 1884, 1885, True 1889).

Several species, originally identified elsewhere during this era, were only fully described based on animals collected or stranded in the subregion during more recent decades; for example, Fraser's dolphin (Perrin et al. 1973) and Longman's beaked whales (Dalebout et al. 2003). A mass stranding of false killer whales was documented in Smithers (1938) and the first marine mammal specific guidebook for South Africa was published by Barnard (1954). Observations by biologists along the east coast of South Africa highlighted early indications of bycatch and interactions with fishers (Barnard 1954, Davies 1963).

In the eastern tropical Atlantic, there are almost no published data available on small cetaceans between Gabon and Angola prior to 1960. The capture and scientific description of a pantropical spotted dolphin off Gabon (at 0°15' N, just north of the study area) in 1946 (Fraser 1950) is one of few records. This is in marked contrast to the increase in published information on small cetaceans to the north off Côte d'Ivoire and Senegal during the 1950s (e.g. Cadenat 1959).

Measurements of dolphin swimming speed made in the Indian Ocean were used by J Gray in his seminal paper on the locomotion of dolphins (Gray 1936). Stranding (including mass strandings) and catch records of several odontocete species (e.g. killer whales, false killer whales and Risso's dolphins) were reported from the late 19th century in the South-West Indian Ocean in Zanzibar and along the South African coast (for review see Kruse et al. 1991, Leatherwood and Donovan 1991).

A recent review of odontocetes in the Southern Ocean (Van Waerebeek et al. in press) has noted that in contrast to the larger commercially hunted baleen whale species, research on the smaller cetaceans of the Southern Ocean has historically been very limited. Little or no published work arose from this sector of the study area *per se* prior to 1960, although species records have been analysed to provide distribution patterns of species across the entire Southern Ocean (e.g. Brownell 1974). Cetacean (and pinniped) sightings around Kerguelen and Amsterdam islands were summarised by Flower (1879), Paulian (1953) and Angot (1954).

Small cetacean research 1960–2011

Dedicated research on delphinids in southern Africa began at the Port Elizabeth Museum and Oceanarium during the 1960s, following the opening of a captive dolphin facility in 1961. Much of the pioneering work done here is discussed in more detail in the Indian Ocean section below and in Best (2007). The majority of small cetacean research after 1960 took place in South African waters but, as with large whale research, has expanded throughout the subregion in the past decade. The vast majority of studies on small cetaceans have been in coastal waters. We could identify a total of 220 papers produced during this period relating to small cetaceans, of which 134 have been published since 1990.

The valuable contribution of museums to cetacean research — through their role in the collection and study of stranded specimens — became more obvious during this period. The attendance of strandings and collection of specimens rapidly increased the number of species known to occur in South African waters. Species records and samples

collected by South African museums during this period have been included in several broad-scale studies spanning South African and Namibian waters (i.e. both Atlantic and Indian oceans). Findlay et al. (1992) summarised the spatial and seasonal distribution patterns of all small odontocete cetaceans in this part of the subregion using a collated dataset of strandings, sightings and multiple surveys from a wide range of historic sources up until the end of 1986. Sekiguchi et al. (1992a) described the diet of 20 odontocete species based on analysis of the stomach contents of animals caught as bycatch, stranded or collected in South African and Namibian waters between 1966 and 1990.

Stranded animals from both the Atlantic and Indian Ocean coasts of South Africa have also been used to examine the morphology and diet of several species. For example, the baleen morphology and the anatomy of the laryngeal apparatus of the pygmy right whale (Sekiguchi et al. 1992b, Reeb and Best 1999) and the diet of Layard's beaked and southern bottlenose whales (Sekiguchi et al. 1993, 1996) have been described.

South Africa has the only two facilities holding captive dolphins in the subregion, at Port Elizabeth (1961–2010) and Durban (captive dolphins since 1976). Although a great potential resource of information, only 10 papers could be identified originating from work on captive dolphins.

Atlantic Ocean

We could identify only nine papers published prior to 1990 relating to delphinids or small cetaceans in the Atlantic Ocean specifically, although there were a further 20 papers that had wider relevance (mainly referring to records from South Africa as a whole). Within South African waters, occasional research studies were conducted on inshore species such as Heaviside's dolphins and dusky dolphins. These included: the establishment of the rate of growth layer deposition in dusky dolphin teeth using tetracycline marking (Best 1976); the first acoustic recording (Watkins et al. 1977); the first comprehensive description of the external appearance and observations of the movements and behaviour of Heaviside's dolphins (Rice and Saayman 1984); and inclusion of both species in broader-scale studies of exploitation and live capture fisheries (Best and Ross 1977, 1984).

More recent ecological studies on Heaviside's dolphin since 1999 have provided an initial population estimate at the southern limit of their range (Elwen et al. 2009a) and insights into genetic population structure (van Vuuren et al. 2002), ranging patterns using photographic mark-recapture and satellite telemetry (Elwen et al. 2006) and fine-scale habitat use (Elwen et al. 2009b, 2010). The echolocation signals of the species have recently been described (Morisaka et al. 2011) and long-term monitoring using moored acoustic click detectors is being developed in Namibian waters (Leeney et al. 2011).

The dusky dolphin remains poorly studied in the subregion (Best and Meyer 2010), although data and samples from local animals have been included in broad-scale morphological, taxonomic and genetic studies (Van Waerebeek et al. 1995, Cassens et al. 2003, 2005, Harlin-Cognato et al. 2007). Best and Meyer (2010) summarised data on opportunistic sightings, diet and life-history parameters from stranded

animals or bycatch. Grahl-Nielsen et al. (2010) compared the fatty acid composition of dusky dolphin blubber and that of their prey and Bernasconi et al. (2011) described acoustic observations of underwater feeding behaviour by dusky dolphins in Namibia.

Very little dedicated field research on small cetaceans has taken place in Namibian waters, although Findlay et al. (1992) provide distribution records based on sightings and strandings and Griffin and Coetzee (2005) provide a species list of small cetaceans recorded in Namibian waters. Opportunistic observations of killer whales preying upon and toying with seabirds at Mercury Island (Williams et al. 1990), and of southern right whale dolphins, have been recorded offshore (Rose and Payne 1991). An incomplete PhD study in Namibia provided baseline data on the population of common bottlenose dolphins known to occur in the vicinity of Walvis Bay (F Praetsch, see Best 2007).

Published information on the smaller cetaceans occurring between Angola and the equator first became available during the 1980s and 1990s. However, information remained sparse and what exists mainly concerns opportunistic records rather than dedicated research surveys. These include at-sea sightings of cetaceans in the eastern tropical Atlantic between 1976 and 1978 (Tormosov et al. 1980), killer whales observed by whaling fleets between 1961 and 1979 (Mikhalev et al. 1981b) and striped dolphins sighted off Angola during 1974 (Wilson et al. 1987). Occasional stranding records from this period have also appeared in the literature and in several cases have extended the known distribution range for the respective species within the southern African subregion. An Antarctic minke whale stranded in southern Angola has, for example, extended the known distribution of this species (Best 2007, Weir 2010a). Van Bree and Purves (1972) discussed common dolphin taxonomy based on skulls from Angola and Gabon and proposed sympatric short- and long-beaked species in Gabonese waters. Opportunistic notes on the distribution and group sizes of common dolphins off Gabon were recorded during the humpback whale surveys carried out by Walsh et al. (2000). The only dedicated small cetacean survey during this period appears to be a study on the pantropical spotted dolphin around St Helena between April and June 1983, during which information on taxonomy, distribution, seasonality and behaviour was collected (Perrin 1985, Perrin and Perrin 1986).

During the late 1990s, the paucity of information from the eastern tropical Atlantic was becoming a source of concern to conservation bodies such as the International Union for the Conservation of Nature (IUCN), resulting in a published review of existing subtropical/tropical dolphin and porpoise records off the west coast of Africa by Jefferson et al. (1997). Very few of these records originated south of the equator, emphasising the lack of research activities in this part of the subregion.

The past decade has seen increasing research focus on smaller cetacean species in the waters between Angola and Gabon, with the publication of an updated review of cetacean occurrence in the waters between Côte d'Ivoire and Angola (Weir 2010a) and some new information presented at the 2010 meeting of the IWC's Sub-Committee on Small Cetaceans, which focused on north-western African and eastern tropical Atlantic waters (IWC 2010).

A short, dedicated survey was carried out around the island of St Helena during the winter of 2003, which examined the distribution and behaviour of the odontocete community (MacLeod and Bennett 2007). The increased number of studies from platforms of opportunity in oceanic waters have provided new records of occurrence of some odontocete species in Angolan and Gabonese waters (Weir 2006a, 2006b, 2010a, Weir et al. 2008, de Boer 2010), as well as information on cetacean community composition, distribution, seasonality (Weir 2007, 2011, de Boer 2010) and behaviour of some species, particularly in relation to the emission of airgun sounds (Weir 2008a, 2008b).

In a review of the status of the Atlantic humpback dolphin, a species endemic to the nearshore tropical and subtropical waters along the Atlantic seaboard of Africa, Van Waerebeek et al. (2004) found only a few stranding and opportunistic sighting records for its occurrence between Gabon and Angola. Since then, dedicated surveys by boat and along the beach have been carried out for the species in Gabon and the Republic of the Congo, producing preliminary data on their distribution and possible threats within this part of the subregion (Collins et al. 2004, 2010). A dedicated survey for Atlantic humpback dolphins was carried out at the southern limit of their range off southern Angola during 2008, representing the first attempt to gather fine-scale, systematic information on the abundance, distribution and behaviour of this species using photo-identification methods (Weir 2009). The study also provided the first description of the whistles of Atlantic humpback dolphins (Weir 2010c), as well as information on the coastal occurrence of common bottlenose dolphins (Weir 2010b).

South-West Indian Ocean

South African researchers based at the Port Elizabeth Museum and Aquarium led much of the early cetacean research that was conducted in the Indian Ocean (1960s–1980s). The combination of field researchers, a museum with an active collection of stranded specimens, and an aquarium in which various dolphin species (mainly Indo-Pacific bottlenose) were kept, proved highly productive. Also noteworthy were the pioneering approaches used by G Saayman and C Tayler to study dolphins, particularly the feasibility of studying wild cetaceans by observation alone (Saayman and Tayler 1973, 1979). A comparison between the social systems of cetaceans and primates was conducted in this period (Tayler and Saayman 1972) and potential signature whistles of Indo-Pacific bottlenose dolphins were recorded (Tietz and Tayler 1964). Further research by members of the Port Elizabeth Museum included novel species observations in South African waters of True's beaked whales (Ross 1969), Hector's beaked whales (Ross 1970) and Cuvier's beaked whales (Ross and Tietz 1972), and of several other species summarised in Ross et al. (1985). Taxonomical research included early work on the differentiation of forms of bottlenose dolphins (Ross 1977, Ross and Cockcroft 1990). Further, early observations of the movement and distribution of Heaviside's dolphins (Rice and Saayman 1984), killer whales (Rice and Saayman 1987) and bottlenose dolphins (Ross et al. 1987, 1989) in South African waters were described. Ecological observations of humpback and bottlenose dolphins (Saayman and Tayler 1973, 1979)

and various oceanic species (Saayman et al. 1972) were documented, and behavioural patterns of wild and captive bottlenose dolphins were published (Tietz and Tayler 1964, Saayman et al. 1973, Cockcroft and Ross 1990).

In 1952, protective anti-shark gillnets (shark nets) were first deployed along the Durban coastline in KwaZulu-Natal to protect bathers. The nets have been responsible for considerable mortality in several cetacean species (Best and Ross 1977, Cockcroft 1990, Peddemors 1993a) and growing concern over the level of bycatch motivated the next period of dedicated research on small cetaceans in South Africa. The large number of animals caught in the nets provided considerable opportunities for research. Scientists from the Port Elizabeth Museum and the KwaZulu-Natal Sharks Board (formerly Natal Sharks Board) published data based on delphinids retrieved from the nets, including a comparison of milk composition between bottlenose, common and humpback dolphins (Peddemors et al. 1989) and analyses of the diets of common dolphins (Young and Cockcroft 1994), Risso's dolphins (Cockcroft et al. 1993) and Indo-Pacific humpback dolphins (Barros and Cockcroft 1991). Several studies during the late 1980s and early 1990s investigated pollutant levels of all cetaceans that were found stranded or caught as bycatch along the east coast of South Africa (Cockcroft and Ross 1991a), including specific studies on bottlenose and common dolphins (Cockcroft et al. 1989a, Cockcroft et al. 1990). Indo-Pacific humpback dolphins have been shown to have the highest pollutant levels of any marine mammal in South Africa (de Kock et al. 1994, Cockcroft 1999).

The Indo-Pacific bottlenose dolphin is the most frequently entangled species in the shark nets (Cockcroft 1990, Cockcroft and Ross 1991b) and research on this species in South Africa has included investigations into the reasons for entanglement (Cockcroft 1992, 1994), distributional patterns (Ross et al. 1987, Cockcroft 1990, Cockcroft and Ross 1991b), abundance (Ross et al. 1989), alongshore genetic variation (Goodwin et al. 1996), natural predation (Cockcroft et al. 1989b) and appropriate survey techniques for monitoring the population (Cockcroft et al. 1992, Peddemors 1993b). A more in-depth review of delphinid research in South Africa is provided by Peddemors (1993a, 1999).

Subsequent research revealed the existence of at least two stocks of Indo-Pacific bottlenose dolphins along the South African coast (Goodwin et al. 1996, Natoli et al. 2007): a small resident stock along the KwaZulu-Natal coastline (described above) and a much larger population along the South-East Coast. Photo-identification data collected in the vicinity of Port Elizabeth in the early 1990s have recently been used to estimate the number of animals in this larger population (Reisinger and Karczmarski 2010). Shore-based tracking of bottlenose dolphins that were recorded as part of a humpback whale study at Cape Vidal in the early 1990s has recently been published (Photopoulou et al. 2011). Some recent data on the distribution of bottlenose dolphins along the east coast of South Africa are available as part of several broad ecological studies investigating the KwaZulu-Natal 'sardine run' and its associated predators (O'Donoghue et al. 2010a, 2010b).

The population(s) of common bottlenose dolphins that occur on the shelf and offshore throughout the subregion

(Ross 1984, Findlay et al. 1992, Best 2007) have not been the focus of any directed field studies and there are no data available on population size or movements. Some samples from animals stranded and caught between Walvis Bay and Durban have been included in a global comparison of inshore and offshore forms of bottlenose dolphins (Hoelzel et al. 1998).

The Indo-Pacific humpback dolphin has been studied in several parts of the subregion since 1990. A four-year study of these dolphins during the early 1990s in Algoa Bay on the south-east coast of South Africa produced data on daily movements and ranging behaviour, abundance, habitat use and group dynamics (Karczmarski and Cockcroft 1999, Karczmarski et al. 1998, 1999a, 2000a, 2000b). Building on these earlier studies in South Africa, research on this species has expanded considerably throughout the subregion during the past 10–15 years. Population-level data, including ranging behaviour, abundance, habitat use and group dynamics, are available for Richards Bay, South Africa (Keith et al. 2002, Atkins et al. 2004), Maputo Bay, Mozambique (Guissamulo and Cockcroft 2004), and Zanzibar, Tanzania (Stensland et al. 2006).

Much of the research carried out in the South-West Indian Ocean (outside of South Africa) prior to 2000 largely consisted of summaries of opportunistic sightings (Leatherwood et al. 1982, Kruse et al. 1991, Leatherwood and Donovan 1991) and species lists for particular islands or areas including Mauritius (Corbett 1994) and the Seychelles (Racey and Nicoll 1984). Limited dedicated field studies have been performed in the South-West Indian Ocean. Species lists for many parts in this area have only been produced during the past decade. These are available for East Africa (Berggren 2009) and the islands of Madagascar (Rosenbaum 2003), Zanzibar (Berggren 2009, Amir et al. 2005a), the Comoros (Kiszka et al. 2010b), Mayotte (Kiszka et al. 2007, 2010a), Réunion (Dulau et al. 2007) and Aldabra (Hermans and Pistorius 2007). We could identify 38 and 12 papers referring to small cetaceans or mixed species research on the Indian Ocean coast of South Africa and the South-West Indian Ocean outside of South Africa respectively between 1991 and 2000. Since 2001, trends have reversed with only 14 papers from the former and 38 from the latter part of the subregion, indicating the rapidly increase of research outside of South Africa.

A growing recognition of the impact of bycatch as well as directed catches of dolphins in artisanal fisheries throughout the South-West Indian Ocean (Cockcroft and Krohn 1994, Rakotonarina et al. 1994, Guissamulo and Cockcroft 1997) has raised conservation concerns, particularly for inshore species. In Mozambique, data are available from monitoring of coastal dolphins and dugongs *Dugong dugon* in Maputo and Bazaruto bays (Guissamulo and Cockcroft 1997, 2004). In 1998, a reconnaissance trip was conducted off Zanzibar to assess the presence and occurrence of cetaceans, particularly Indo-Pacific humpback and bottlenose dolphins, in relation to high levels of bycatch (Stensland et al. 1998). This dedicated research and capacity-building programme focused on assessments of conservation status of delphinids, particularly that of Indo-Pacific bottlenose dolphins (Berggren et al. 2007, Amir 2010). Data are available on various parameters including levels of bycatch (Amir et al. 2002) and feeding ecology based on animals taken as bycatch (Amir

et al. 2005b), growth and reproduction (Amir 2010), the occurrence and distribution of species around Zanzibar (Amir et al. 2005a), population size and behaviour (Stensland et al. 2006), behavioural changes in response to tourism vessels (Englund and Berggren 2002, Christiansen et al. 2010, Stensland and Berggren 2010), phylogenetic placement and population structure (Särnblad et al. 2010), and pollutants in the blubber of Indo-Pacific bottlenose and spinner dolphins (Mwevuraa et al. 2010).

Level of bycatch in artisanal fisheries are available for several areas: Zanzibar, Tanzania (Amir et al. 2002), south-western Madagascar (Razafindrakoto et al. 2004) and Mayotte (Kiszka et al. 2008, Pusineri and Quillard 2009). Around Mayotte, a dedicated research programme on delphinids has been developed during the past decade, focusing on habitat preferences, community and genetic population structure, social behaviour, mixed-species associations, and ecological niche segregation (Gross et al. 2009, Kiszka 2010, Kiszka et al. 2010a). A study to evaluate the behavioural reactions of small dolphins to remote biopsy sampling was undertaken (Kiszka et al. 2010c). The health status of small cetaceans and the presence of lobomycosis-like disease was described for the first time in the Indian Ocean, especially around Mayotte (Kiszka et al. 2009). Pollutant levels were investigated across a wide range of sites in the South-West Indian Ocean (Mwevuraa et al. 2010, Jauniaux et al. 2011).

Southern Ocean

Cetacean research in the Southern Ocean sector of the study area has been facilitated by the research bases on French and South African territorial possessions (islands) in the sub-Antarctic. This includes opportunistic observations and dedicated studies at the islands themselves, and observations from the ships servicing the islands.

The population of Commerson's dolphin that occurs at the Kerguelen Islands has recently been described as a subspecies by Robineau et al. (2007). This population has been relatively well studied, especially during a productive period during the 1980s. Information is available on external anatomy and pigmentation (Robineau 1984), several aspects of the skeletal structure and growth (De Buffr enil and Robineau 1984, Robineau and De Buffr enil 1985), genital tract (Collet and Robineau 1988), reproductive habits (De Buffr enil et al. 1989), distributional patterns (Robineau 1985), organochloride pollutant levels (Abarnou et al. 1986), and the adaptive significance of morphological characteristics (Robineau 1986). The acoustic signals produced by Commerson's dolphin have also been studied (Dziedic and De Buffr enil 1989). A vagrant sighting has been reported on the Agulhas Bank in South African waters (de Bruyn et al. 2006).

Killer whales have been studied at the Possession Islands in the Crozet archipelago, including descriptions of social behaviour and foraging strategies (Guinet 1991a, 1992) such as the intentional stranding technique used to catch seals on land and the teaching of this behaviour to their young (Guinet 1991b, Guinet and Bouvier 1995, Guinet et al. 2000). The initiation of photo-identification studies and biopsy sampling in the Crozet archipelago has generated data on population

dynamics (Poncelet et al. 2010, Tixier et al. 2010a) and the level of persistent organic pollutants in their blubber (Noel et al. 2009). Farther to the west, on Marion Island, observations of killer whales have generated data on their distribution, movements, seasonal abundance (Condy et al. 1978), social structure (Tosh et al. 2008), diet and abundance (Pistorius et al. 2002, Reisinger et al. 2011a, 2011b), as well as the potential impact of killer whale predation on seal and penguin populations on the island (Reisinger et al. 2011c). Data are also available on the seasonality of killer whale occurrence at Amsterdam Island (Roux 1986) and of interactions with longline operations in open waters (Roche et al. 2007, Tixier et al. 2010b).

Due to the inaccessibility of this part of the subregion and the fact that dedicated observations are seldom made from South African vessels in the Southern Ocean, small cetaceans in open waters have been poorly studied here. Van Waerebeek et al. (in press) note that circumpolar abundance estimates of small odontocetes have been calculated from the IDCR/SOWER datasets from south of 60° S (Kasamatsu et al. 1996, Branch and Butterworth 2001a), although these are generally for broader Southern Ocean areas than the subregion specifically. Papers arising from this research are largely global Southern Ocean reviews that include records from the study area (e.g. Sekiguchi et al. 2006, Van Waerebeek et al. in press).

Synthesis of cetacean research in the southern African subregion

The southern African subregion has a long history of productive and internationally relevant cetacean research conducted by both locally based and visiting scientists. We identified a total of over 562 papers, books or book chapters pertaining to research in this subregion, of which over half (284) have been published since 1990 (Figure 2). Notably, the number of published studies on large whales has remained fairly stable since 1980, and the major source of data has shifted away from whaling in recent years (Figure 2), whereas the number of manuscripts focusing on small cetaceans has increased consistently and has outnumbered those on large whales since the 1980s.

The high number of cetacean species in the subregion provides considerable potential for research. However, even such basic information as the occurrence and distribution of many species in the subregion remain poorly documented. There are furthermore clear biases towards certain focal species in terms of the research activities that have been carried out to date. Such biases largely reflect the low number of scientists working in the field as well as accessibility to study animals, the high cost of studying cetaceans, the extent of available resources, and the political state of the respective countries within the subregion. The conservation status of many species is poorly understood, with very limited population abundance studies having been carried out in the subregion.

The vast majority of cetacean research in the low- and mid-latitudes of the study area prior to 2000 was conducted in South African waters (Table 2, Figures 3, 4). Work on small cetaceans has decreased on the east coast and

increased on the west coast of South Africa and off Namibia (Figure 3). This latter pattern reflects the highly productive period during the 1980s and early 1990s when considerable effort was expended investigating issues of bycatch surrounding the anti-shark nets on the KwaZulu-Natal coast.

Research output in the Southern Ocean has remained fairly steady over the past three decades. A considerable amount of research on large whales in the Southern Ocean originates from IWC initiatives and is available in documents associated with meetings of the scientific committee thereof, but is not available in the peer-reviewed literature. The majority of the small cetacean research in the Southern Ocean originates from the sub-Antarctic islands, and pertains mostly to Commerson's dolphins and killer whales. Due to the inaccessibility of the Southern Ocean and its islands, the majority of research is associated with government-sponsored or -supported expeditions.

The number of publications and research projects in the South-West Indian Ocean and eastern tropical Atlantic has increased markedly since 2000 (Table 1, Figures 3, 4). Research is being undertaken on many of the islands in the South-West Indian Ocean, although the continental waters, especially northern Mozambique and Kenya, remain poorly studied (Table 2). The Atlantic coast north of South Africa remains poorly studied, especially with regard to large whales (Figures 3, 4). Consequently, while expanding markedly during the past decade, cetacean research in Namibia and the eastern tropical Atlantic remains relatively sparse and is driven by a small number of interested individuals rather than by government resources. This is also the case throughout much of the southern African subregion, highlighting the importance of individual efforts in resource-limited areas.

A further consequence of research being driven by individuals or small groups is that much of the data collected subsequent to the end of commercial whaling are extremely irregular, both temporally and spatially, with few studies of more than 10 years in duration. Long-term studies of keystone species are of great value to ecological research and allow for the investigation of environmental changes and adaptations at a variety of temporal scales. Longer-term studies include: (1) annual southern right whale photo-identification surveys that have been carried out off South Africa since 1979; (2) the annual IDCR/SOWER series of Southern Ocean minke whale assessment cruises, which have intermittently surveyed the area south of 60° S across the study area; (3) long-term photo-identification and genetic data on humpback whales are available from a series of separate projects run throughout the subregion since the late 1980s (Findlay et al. 1994, in press, Findlay and Best 1996a, Pomilla and Rosenbaum 2005, Rosenbaum et al. 2009, Barendse et al. 2010); (4) long-term datasets (from 1964) are available for several dolphin species (predominantly Indo-Pacific bottlenose, common and Indo-Pacific humpback dolphins) that form part of the bycatch in the shark nets of eastern South Africa, including necropsies since 1982 (Peddemors 1993a, 1999); and (5) long-term stranding records from the entire South African (and Namibian prior to ~1992) coast of all species are kept by the Iziko: South African Museum in Cape Town (from about Mossel Bay to

Namibia) and the Bayworld Port Elizabeth Museum (from Mossel Bay to Mozambique). Only (1) and (2) above are associated with known or constant effort, without which the values of the long-term datasets may be limited.

There is much spatial variation in terms of research effort dedicated to the respective species occurring within the subregion. In particular, the limited accessibility to offshore species reflects a strong bias towards research on coastal species (Table 1), with most recent effort focused on Indo-Pacific bottlenose and humpback dolphins, killer whales, southern right whales and humpback whales. Most of these species are also easily distinguished individually (for photo-identification), widespread and comparatively easy to work with (accessible and approachable). In contrast, research on cetaceans inhabiting offshore, deep-water areas is very scarce. Access to the deep-water cetacean fauna off South Africa, Namibia and Mozambique has been severely limited since the end of whaling operations and dedicated

Table 2: Breakdown of the number of identified publications (journal articles, book chapters, books) by country or part of the subregion

Area	Number
<i>Continental Africa</i>	
Gabon	13
Democratic Republic of Congo	2
Angola	9
Namibia	13
South Africa (entire coast)	64
South Africa (west coast)	31
South Africa (east coast)	98
Mozambique (entire coast)	3
Mozambique (south coast)	2
Mozambique (north coast)	0
Tanzania	14
Kenya	0
<i>Indian Ocean and Southern Ocean islands</i>	
Comoros (including Mayotte)	10
Madagascar	11
Mauritius, Rodrigues, Réunion	3
Seychelles	3
Other Indian Ocean islands	0
Bouvet	0
Prince Edward Islands	7
Crozet	11
Kerguelen	21
<i>Atlantic islands</i>	
Ascension and St Helena	4
Gough and Tristan	3
<i>Region</i>	
Atlantic Ocean	0
Indian Ocean	17
Southern Ocean — open water	58
Global review	49
Regional review	66
Species review	48
Captive	10
Technical	25
<i>Ocean</i>	
Atlantic	94
Indian	177
Southern	101

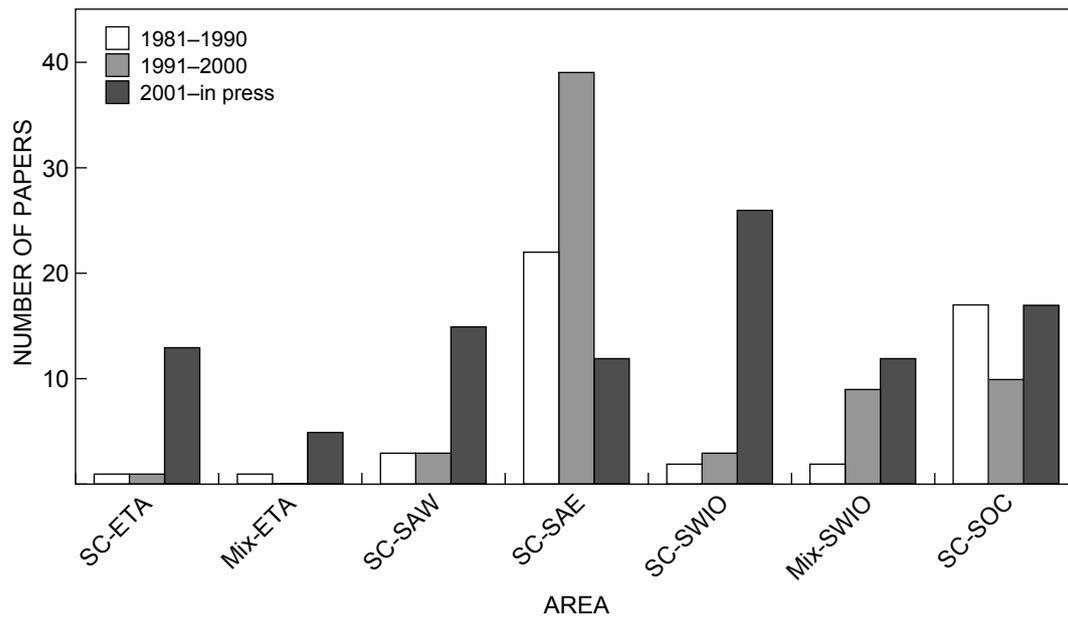


Figure 3: Breakdown by area of the number of identified papers, books or book chapters published between 1981 and 2011 that focus on small cetaceans (SC) or mixed species (e.g. 'cetacean sightings'). The areas include eastern tropical Atlantic (ETA), South African west coast (SAW, including Namibia), South African east coast (SAE), South-West Indian Ocean (SWIO) and islands (outside South Africa) and Southern Ocean (SOC, including sub-Antarctic islands)

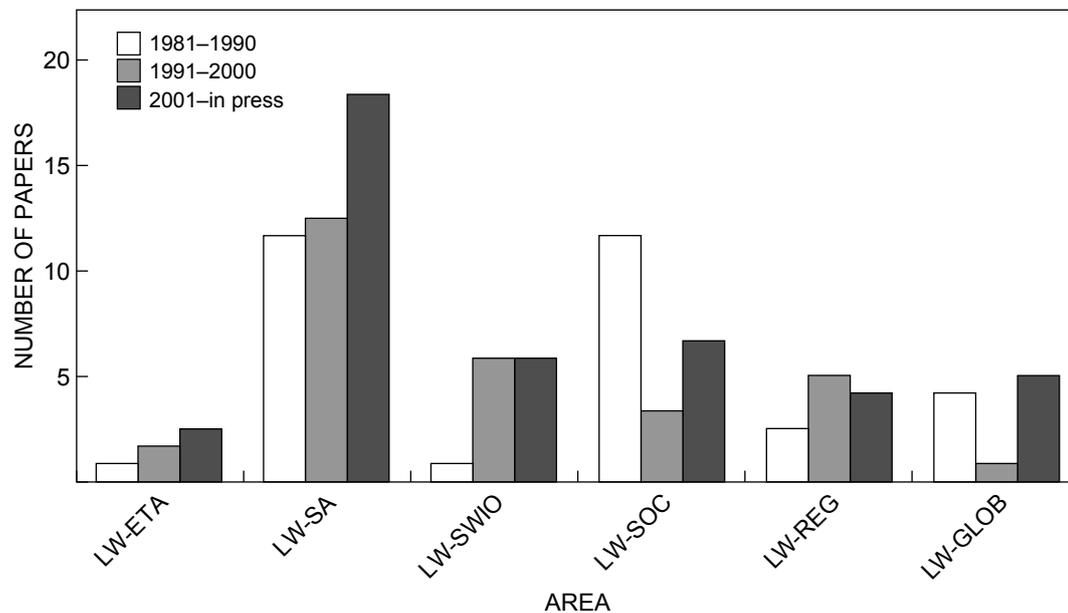


Figure 4: Breakdown by area of the number of identified papers, books or book chapters published between 1981 and 2011 that focus on large whales (LW). The areas include eastern tropical Atlantic (ETA), South Africa (SA both coasts), South-West Indian Ocean (SWIO) and islands (outside South Africa), Southern Ocean (SOC including sub-Antarctic islands) and regional (REG) or global (GLOB) studies

government-supported marine mammal cruises. Oceanic cetacean communities have received some attention in other areas. The steep volcanic islands of the Indian Ocean provide access to deep-water species (e.g. Kiszka et al. 2010a), and the use of platforms of opportunity in the Atlantic

Ocean has provided information on the tropical, deep-water cetacean communities in the eastern tropical Atlantic (e.g. Weir 2007, de Boer 2010). The recent REMMOA surveys (Ridoux et al. 2010) described above are an indication of a positive change.

Suggested priorities for future cetacean research

Identifying research (and conservation) priorities in such a large area as the southern African subregion is a considerable challenge, especially given the lack of basic knowledge about several species and the areas that they inhabit. Knowledge about many of the species in the subregion, especially poorly known oceanic species, is derived almost exclusively from stranded specimens. No published research was found from Kenyan or northern Mozambican waters. The majority of conservation concerns throughout the region reflects global trends and are human-induced, being far higher in coastal and shelf waters. Identified threats include bycatch in artisanal and commercial nets, directed fisheries (Kiszka et al. 2008, Poonian et al. 2008), oil and gas development (Rosenbaum and Collins 2006), tourism activities (Christiansen et al. 2010), noise and chemical pollution (Cockcroft 1999, Jauniaux et al. 2011), shifts in prey resources (Roy et al. 2007), entanglement and ship strikes (Best et al. 2001b), and the overarching impact of climate change. Below we propose some area-specific conservation and research priorities.

South Africa

Although cetaceans in the waters around South Africa are the most comprehensively studied within the subregion, much of the research has been focused on very few species, particularly right whales and humpback whales and Indo-Pacific bottlenose and Indo-Pacific humpback dolphins. Humpback dolphins remain a conservation priority due to their low population sizes coupled with unknown population trends (Karczmarski et al. 1999b), nearshore habitat and high pollution loads (Karczmarski et al. 1998). Little is known about the current abundance or population status of species that exist predominantly on the continental shelf, including the dusky dolphin, common dolphin and Bryde's whale. These species potentially compete with fisheries and levels of bycatch are unknown. Furthermore, several major fish stocks in South Africa have undergone considerable changes in size and distribution in recent years (e.g. Heymans et al. 2004, Roy et al. 2007) with unknown consequences for cetaceans. The inshore stock of Bryde's whale is small (Best et al. 1984b) and non-migratory (Best 2001). Consequently, it may be particularly vulnerable to changes in local food resources that potentially are driven by shifts in fisheries and climate. No published estimates of abundance or trends are available for this population of Bryde's whale since 1982 (Best et al. 1984b, Penry et al. 2011), therefore obtaining a current estimate of population size is important. The degree of recovery of several previously hunted large whale stocks in South African waters, particularly for blue, fin and sei whales, remains unknown. Access to the majority of the abovementioned species requires working in shelf and offshore waters. Access to vessel time and development of broad-scale, repeated surveys to investigate distribution, seasonality and abundance trends of these species should be prioritised. Static acoustic monitoring provides another method with which to investigate patterns of relative abundance, distribution and seasonality (Van Parijs et al. 2002, Marques et al. 2009, Leeney et al. 2011) and techniques to estimate absolute abundance are rapidly developing (Marques et al. 2010).

South-West Indian Ocean

Many gaps have been identified in this part of the subregion, including the need to identify diversity and, as is the case elsewhere, to determine the abundance of oceanic species. The REMMOA project, conducted in late 2009 and early 2010, should provide new information on distribution, absolute abundance, habitat preferences and community structure of cetaceans over a wide area (Ridou et al. 2010).

For management purposes, information on population and demographic structure, abundance and trends of all cetaceans is clearly needed, especially on species affected by bycatch and direct hunting, including the Indo-Pacific bottlenose dolphin, the humpback dolphin and the spinner dolphin. An assessment of the level of bycatch, particularly in gillnets, is needed throughout this part of the subregion. This could potentially be achieved with rapid bycatch assessments that have been successfully developed in other countries, including in the Comoros archipelago and Tanzania (Moore et al. 2010). With the exception of the Indo-Pacific bottlenose dolphins in Zanzibar (Amir et al. 2005b), the feeding ecology of cetaceans in this part of the subregion is poorly understood. This information is critical, particularly for small cetaceans that potentially compete with coastal fisheries. Furthermore, basic information on migration patterns, seasonal abundance and population structure is still lacking for most large whale species, especially Bryde's, fin and blue whales.

A few locations in the South-West Indian Ocean (e.g. Mayotte and La Réunion) allow easy access to deep-water species that are poorly studied both globally and regionally, such as beaked whales and oceanic delphinids (e.g. melon-headed whales and false killer whales; Dulau et al. 2007, Kiszka et al. 2010b). More research needs to be dedicated to those species that interact directly with fisheries (e.g. depredation by false killer whales in the pelagic longline fishery). Capacity-building and the training of local scientists is required, especially to ensure the establishment of longer-term research.

Eastern tropical Atlantic

Cetacean research in the eastern tropical Atlantic part of the subregion is in its infancy and baseline data on the distribution, abundance and seasonality of almost all cetacean species are lacking. Therefore, there is considerable scope for future development of research activities in this area. Priorities for research include establishing year-round bycatch estimates and setting up stranding and sighting monitoring programmes for both coastal and offshore cetaceans. The latter are required particularly for evaluating the importance of this part of the subregion to breeding populations of sperm and humpback whales that seasonally occur here in high numbers (Rosenbaum and Collins 2006, Weir 2007, 2011). The Atlantic humpback dolphin, which is endemic to the eastern tropical Atlantic, is perhaps the greatest research priority in this part of the subregion. Their low population size, coastal distribution and their restricted geographical range (that coincides only with developing countries) are factors that combine to make this species extremely vulnerable to human activities (Van Waerebeek et al. 2004, Van Waerebeek and Perrin 2007, Weir 2009, Weir et al. 2011). Although the Atlantic humpback dolphin is currently listed as Vulnerable in

terms of IUCN Red Data criteria, it has been recommended that its status should be reassessed and potentially changed to a more threatened category, in light of the serious conservation concerns (IWC 2010, Weir et al. 2011). Efforts to identify the distribution, abundance and status of this species are needed. The eastern tropical Atlantic as a whole remains a problematic locality for cetacean research, given the logistical, political and socio-economic factors prevailing in many countries. Capacity-building and the training of local scientists is required to ensure advances are made in cetacean research in this part of the subregion.

Southern Ocean

The future of cetacean research in the African sector of the Southern Ocean remains uncertain following the termination of the SOWER series of cruises by the IWC in 2010. The considerable volume of data that exists following these cruises, including baseline information on the distribution of cetaceans in relation to oceanographic and topographic features, should be seen as an incentive for further research and monitoring in this part of the subregion. Continued monitoring of the trends in Antarctic large cetacean populations in the post-whaling era, especially in the light of assessing possible influences of climate change, would be extremely valuable. The migratory nature of many of these species means that a significant component of such work can be carried out in low-latitude waters.

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