Benguela Trophic Functioning
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THE DISTRIBUTION OF SMALL ODONTOCETE CETACEANS OFF THE COASTS OF SOUTH AFRICA AND NAMIBIA

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A total of 2 077 records of approximately 49 000 small cetaceans, including dedicated and incidental sightings and specimens, was analysed to define distribution patterns of the 28 species found within southern African waters. Distribution analyses reveal distinct component patterns, including cosmopolitan (found in all waters) and pelagic cosmopolitan (found in all pelagic waters) components, tropical, subtropical and warm temperate components of the Agulhas Current system, an Agulhas Bank component, a South and East Coast inshore component, and West Coast neritic and pelagic components. While the offshore distribution appears to be determined by water depth, possibly through distribution of the principal prey, longshore distribution appears to be determined by water temperature. The high diversity of small cetacean species found within the relatively small study region results from the wide range of zoogeographic components present. These components arise from the wide range of water temperature resulting from the warm Agulhas Current and the upwelling Benguela system.

Altesaam 2 077 boekstawings van sowat 49 000 klein walvisagtiges, doelgerigte en toevallige waarnemings en eksemplare ingesluit, is ontleed om die verspreidingpatrone van die 28 spesies wat binne Suider-Afrikaanse waters aangetref word, te omskryf. Verspreidingsontledings toon duidelike patrone van komponente, met inbegrip van kosmopolitiese (in alle waters aangetref) en pelagies kosmopolitiese (in alle pelagiese waters) komponente, tropiese, subtropiese en warmgematigde komponente van die Agulhasstroomstelsel, 'n Agulhasbankkomponent, 'n Suidkus- en Ooskus- aanlandige komponent, en Weskus- neritiese en pelagiese komponente. Die aflandige verspreiding word stellig deur waterdiepte bepaal, moontlik deur die verspreiding van die hoofprooi, maar kuslangse verspreiding word skynbaar deur watertemperatuur bepaal. Die groot verskeidenheid van klein walvisspesies wat binne die betreklik klein studiegebied gevind word, is die gevolg van die voorkoms van 'n wye reeks soögeografiese komponente. Hierdie komponente ontstaan uit die groot reeks watertemperature wat deur die warm Agulhasstroom en die Benguela-opwelstelsel teweeggebring word.

Distribution patterns of extant cetaceans have been categorized into four general types, namely trans-equatorial (anti-tropical), circumpolar, endemic and cosmopolitan (Davies 1963, Marcuzzi and Pilleri 1971, Gaskin 1976, Fordyce 1985). Distribution limits have been said to be determined by a number of topographical and oceanographic factors, including sea surface temperature (Sergeant and Fisher 1957, Gaskin 1968, Würsig and Würsig 1980, Au and Perryman 1985, Polacheck 1987, Ross and Cockcroft 1990), water depth (Kenney and Winn 1986, Würsig and Würsig op. cit.), bottom topography (Dohl *et al.* 1986, Hui 1979), area of frontal convergence (Gaskin 1968, 1982, Polacheck op. cit.), thermocline depth (Au *et al.* 1979, Au and Perryman op. cit., Polacheck op. cit.), ocean colour and turbidity (Smith *et al.* 1986) and salinity (Perrin *et al.* 1983).

The 28 species of small cetaceans that have been recorded off the coast of South Africa and Namibia represent a surprisingly high species diversity. There are, in fact, 27 species in the whole North Pacific and 28 species in the entire North Atlantic. Ross (1984) suggests that the great species diversity of small cetaceans off the South-East Coast can be attributed to the complex oceanographic conditions found in the area, including a tropical/subtropical component, a temperate/Subantarctic component, a cosmopolitan component and a mixed water component.

Of these small cetaceans, 18 are delphinids (*Orcinus orca, Pseudorca crassidens, Feresa attenuata, Peponocephala electra, Grampus griseus, Globicephala macrorhynchus, G. melas, Delphinus delphis, Stenella longirostris, S. attenuata, S. coeruleoalba, Steno bredanensis, Lagenodelphis hosei, Lissodelphis peronii, Lagenorhynchus obscurus, Tursiops truncatus* [*truncatus* and *aduncus* forms], *Cephalorhynchus heavisidii* and *Sousa plumbea*). Eight others are ziphiids (*Ziphius cavirostris, Mesoplodon densirostris, M. hectori, M. layardii, M. mirus, M. grayi, Hyperoodon planifrons* and *Berardius arnuxii*), and two are physeterids (*Kogia simus* and *K. breviceps*).

Many records of southern African strandings and sightings have been published (Smithers 1938, 1983, Talbot 1960, Tietz 1963, 1966, Bass 1969, Best 1969, 1970, Ross 1969, 1970, 1979, 1984, Ross and Tietz 1972, Saayman *et al.* 1972, Perrin *et al.* 1973, Ross *et*

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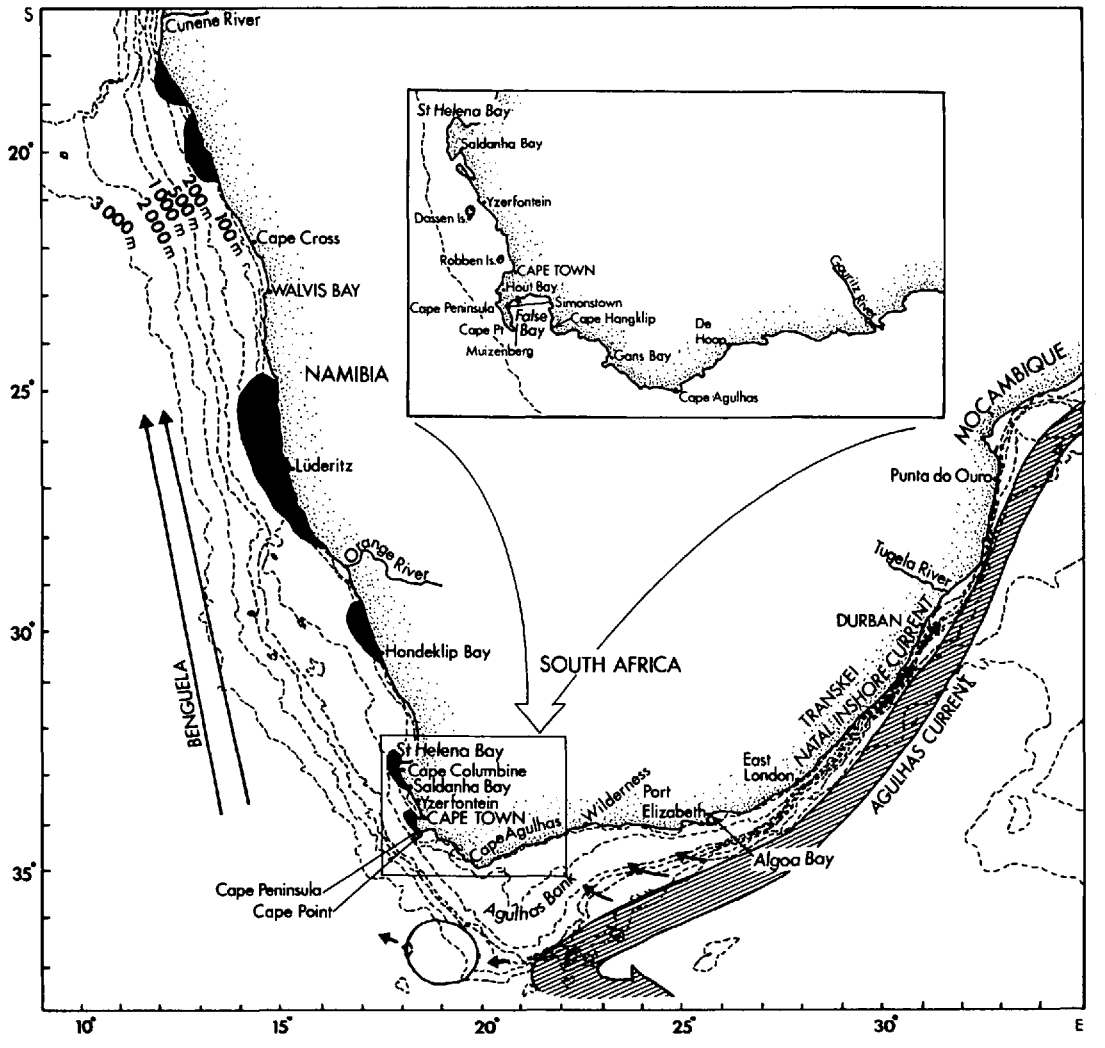

Fig. 1: The bathymetry and the major oceanographic features of the study area. An Agulhas Current Eddy is shown at approximately 37°S, 19°E

al. 1975, 1985, 1987, Van Bree *et al.* 1978, Saayman and Tayler 1979, Best and Shaughnessy 1981, Cruickshank and Brown 1981, Rice and Saayman 1984, 1987, Ross and Cockcroft 1990, Rose and Payne 1991). However, although they provide records of the species in the area in isolation, they do not define the distributions of each species within the region.

THE STUDY AREA

The study area lies between 17 and 38°S and between 9 and 35°E; it includes the coasts of Namibia and South Africa and the surrounding oceans to a depth of more than 3 000 m. The topography of the region is shown in Figure 1. The eastern continental shelf is narrow (5–7 km wide) north of the Tugela River mouth, widens at the Tugela River mouth, but narrows again to about 10 km to the south, off the coast of Transkei. South of the subcontinent the shelf widens to form the Agulhas Bank, and the South Coast from Cape Recife to Cape Point is characterized by rocky capes and shallow (<50 m deep) sandy bays. The West Coast continental shelf is broader than that of the East Coast and its width ranges from 40 km (off the Cape Peninsula) to 180 km (off the Orange River). The width of the shelf plays an important role in the

formation of upwelling cells (Shannon 1985). Offshore, the Walvis Ridge (running in a south-westerly direction to the west of the study area) forms a barrier between the Angola and Cape basins, restricting northward and southward movement of water deeper than 3 000 m.

There are two major oceanographic systems within the study area (Fig. 1). For reference purposes, they are outlined briefly in the following subsections.

Agulhas Current

This is an Indian Ocean western boundary current, formed from the Moçambique and East Madagascar currents. It flows strongly in a south-west direction and dominates East Coast waters, which can be subdivided into three zones (Pearce 1977):

(i) inshore cooler coastal water, the outer boundary of which Pearce (1977) found to correspond to a water depth of 500 m off Durban;
(ii) the Agulhas Current core, where the velocity exceeds 1 $m \cdot s^{-1}$;
(iii) the eastern boundary zone east of the 1 $m \cdot s^{-1}$ isotach.

South of the continent (in the region of 34°50′S, 27°E) the Agulhas Current veers away from the coast to follow the shelf-edge (Darbyshire 1972, Lutjeharms and Van Ballegooyen 1984). There, shear-edge features are formed and plumes of warm Agulhas water may occasionally disperse over large areas of the Agulhas Bank (Catzel and Lutjeharms 1987). South of Cape Agulhas, the current retroflects eastwards as the Agulhas Return Current. Eddies are sometimes shed at this retroflection, and a few of them move around the Cape Peninsula (Lutjeharms 1981), contributing substantial volumes of water to the Benguela system (Shannon 1985). The Agulhas Return Current flows eastwards to the south of the study area and, between the Agulhas Return Current and the Agulhas Current inshore of it, warm subtropical surface water is found to a depth of about 500 m.

Benguela system

The hydrology of the West Coast is dominated by seasonal wind-induced upwelling. The area is further subdivided into northern and southern regions at about 31°S, based on the seasonality of prevalent winds and upwelling. The oceanography of the southern West Coast is regulated by the summer south-easterly winds, which give rise to upwelling and well-defined fronts between the upwelled water inshore and South Atlantic Surface Water offshore (Andrews and Hutchings 1980). Winter conditions see a relaxation of upwelling and the collapse of the frontal system. There are two main upwelling cells within this southern region, off the Cape Peninsula and off Cape Columbine. The Cape Peninsula upwelling cell and its associated oceanic front over the shelf-break are semi-permanent features during summer (Andrews and Hutchings op. cit.).

In the northern region, off Namibia and north-western South Africa, upwelling is less seasonal. In spring/summer, the upwelling maximum is as far north as 25°S, but in late winter/spring it is even farther north. According to Shannon (1985), there are two major cells of upwelling in the northern Benguela:

(i) The Namaqua upwelling area off Hondeklip Bay. This is a cool wedge-shaped zone extending northwards from Hondeklip Bay to the Orange Bight. Shannon (1985) noted that the continental shelf is narrow south of Hondeklip Bay, which enhances the probability of upwelling there.
(ii) The Lüderitz upwelling region. This is the most consistent upwelling cell of the Benguela system, and it stretches from the Orange River mouth to Lüderitz.

Offshore of the upwelling systems, the Benguela flows parallel to the coast in a generally north or north-westerly direction. Nelson and Hutchings (1983) describe it as an ill-defined movement of water which forms the eastern boundary of the South Atlantic gyre.

MATERIALS AND METHODS

Database

Published and unpublished records of cetacean sightings, strandings and actual specimens from within the study area, up to the end of June 1986, were reviewed to define distribution patterns. To facilitate analyses, the data were organized in data-retrieval files according to their source, as outlined in the following subsections.

DEDICATED SCIENTIFIC SURVEYS

On such surveys, an associated measure of effort was recorded, so that densities of animals could be calculated. Effort is usually defined as the distance steamed or flown during times of active searching. In general, there was no associated measure of the width of the effective search path, so measures of density are in reality "encounter rates" and, as such, reflect relative rather than absolute densities. The surveys include flights by specially chartered aircraft and cruises by government research ships or specially chartered vessels. Ships' search tracks and aircraft flight paths (shown

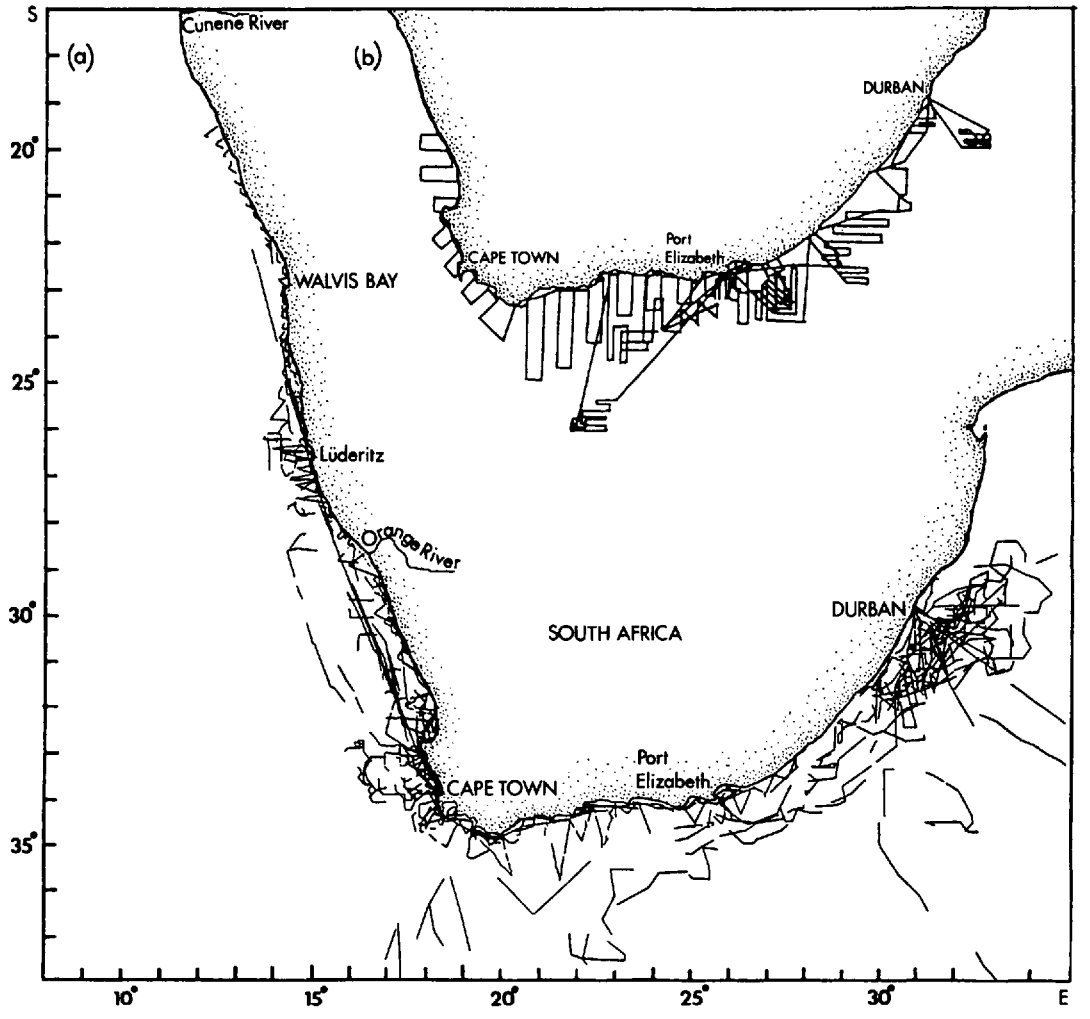

Fig. 2: The distribution of (a) scientific cruise and (b) aerial search effort analysed

on Figure 2) are representative of search effort in that only periods of active searching are plotted. Scientists experienced in marine mammal identification were present on all such flights and cruises, which included:

(i) Eleven marine mammal cruises of the Sea Fisheries Research Institute between 1975 and 1986;
(ii) seven Indian Ocean whale-marking cruises between 1968 and 1975 (Gambell 1968, IOS 1969, 1971, 1972, 1973, 1975, Gambell *et al.* 1975);
(iii) one West Coast whale-marking cruise in 1963;
(iv) three "predator" cruises under the auspices of the Benguela Ecology Programme between 1983 and 1985;
(v) one joint Japan/South Africa cruise for Bryde's whales (inshore stock) in 1983 (Best *et al.* 1984);
(vi) three East Coast dolphin-census flights carried out by the Port Elizabeth Museum in 1980 and 1984;
(vii) one South Coast aerial census for Bryde's whales in 1982;
(viii) one whale-marking aerial spotter flight in 1975.

All cetacean sightings were recorded. The sighting positions were entered on the database to the nearest one minute of latitude and longitude (the navigation technology used did not warrant greater precision). Each record was given field entries which described

both the type (primary — seen during periods of searching effort; secondary — seen outside periods of search effort) and the status (whether species identity and/or number was confirmed). When an estimated range of school sizes was recorded by the observer, the number entered into the database was the mean of the range, rounded upwards to the nearest integer where necessary. In total, some 25 000 nautical miles were searched during scientific cruises and a further 8 000 miles during flights. In all, 747 sightings totalling approximately 26 000 cetaceans, were made during such surveys.

INCIDENTAL SIGHTINGS

These sightings were made from various platforms (land, ship or aircraft), and were reported to the Sea Fisheries Research Institute or the Mammal Research Institute by casual observers, or were extracted from published literature. No information on associated searching effort was available, so the sightings could only be analysed on a qualitative basis. Incidental sightings were only included in the database when it was certain that the identification was correct (i.e. where clear photographs were supplied or when the observer was known to have had sufficient experience in cetacean identification). Records of live captures of small cetaceans for oceanaria were included as incidental sightings (the number observed in the school was entered and not the number caught), as were a number of published sightings (e.g. Cruickshank and Brown 1981, Saayman *et al.* 1972 — original data supplied by D. Bower). Some 408 incidental sightings of approximately 18 000 animals have been placed in the database.

Although useful in supplementing the data on the distribution of certain species (i.e. killer whales off Cape Point and southern right whale dolphins off Lüderitz), incidental sightings show a definite bias towards more densely populated areas and areas of high utilization by observers.

SPECIMENS

Some 1 344 records (of 2 029 specimens) from four sources were reviewed for inclusion in a distributional database. The provenances of these records include strandings and both commercial and scientific catches. The sources are listed below.

(i) *Specimen records* held by the authors (PBB — most between the Cunene River and Mossel Bay; GJBR and VGC — most between Mossel Bay and Punta do Ouro).

(ii) *Published records* — The literature was searched for additional historical records of strandings as far back as they could be verified accurately.

(iii) *Museum specimens* — Additional records of cetacean specimens collected off southern Africa and held in both local and foreign museums were included in the database where an accurate locality and date of provenance could be determined.

(iv) *Unattended strandings* — These are records of strandings that were reported, but not visited, and for which skeletal material was not available. Often the identification was verified from photographs.

Certain areas of the southern African coast are relatively unpopulated and little visited (particularly the West Coast), and there is a noticeable lack of stranding records from such areas. By contrast, there is a high incidence of strandings in the vicinity of populated areas. Correction for this bias is difficult, because there is a further seasonal effect due to coastal utilization by holidaymakers during summer, and few quantitative data on beach utilization are available. However, qualitative interpretation of this information is possible. The source files are held by the Whale Unit of the Mammal Research Institute.

The bathymetry of southern Africa was digitized from South African Navy charts (1 : 600 000) and included the coast and the 50, 100, 200, 500, 1 000, 2 000 and 3 000 m isobaths. Application programs written in Fortran and Pascal allowed for: plotting of contour maps, cruise and flight tracks and associated sightings, incidental sightings and specimen localities; calculation of the depth interval over which the sighting occurred; calculation of the distance searched on a dedicated cruise or flight per five-minute cell; calculation of the relative densities of animals sighted per five-minute cell as a function of distance searched. (Only primary ["on effort"] sightings were used in the calculation of relative densities.)

For depth analysis of dedicated scientific sightings, the study area was divided into four areas on the basis of plotted cetacean distributions. Area 1 was west of the subcontinent and north of 32°S, Area 2 took in waters west of 19°E and south of 32°S, Area 3 lay south of the subcontinent between 19 and 27°E, and Area 4 was east of 27°E. Relative densities were calculated by depth interval (0–50, 50–100, 100–200, 200–500, 500–1 000, 1 000–2 000, 2 000–3 000 and >3 000 m). Seasonal distributions of search effort by depth are shown on Figure 3. Densities were calculated by summing the number of animals observed in all of the five-minute cells falling within a particular interval, and dividing the result by the distance searched in all five-minute cells within that particular interval. Densities were calculated separately for summer (October–

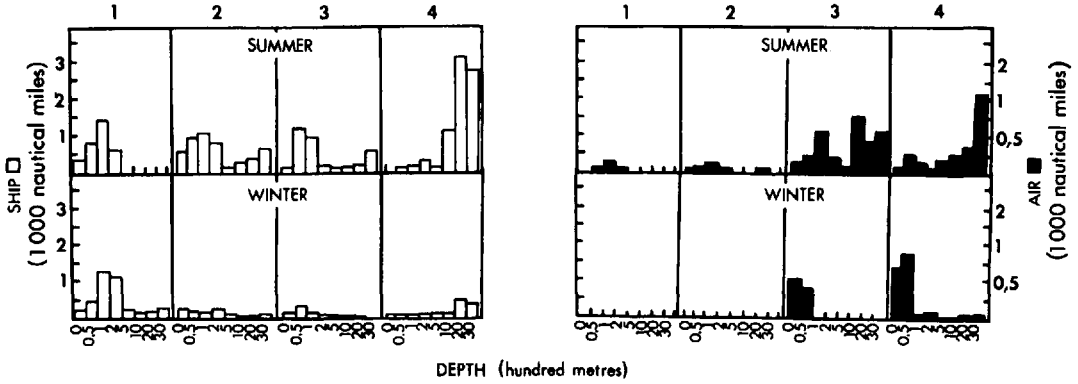

Fig. 3: Seasonal distribution of shipboard and aerial search effort, by depth interval in each area

March) and winter (April–September) in each of the four Areas.

Depth intervals were also calculated for incidental sightings.

In discussing the depth distribution of the animals, the term "pelagic" has been used to describe animals occurring off the continental shelf (water depth >500 m), and "neritic" has been used to describe those occurring over the continental shelf (water depth <200 m). Waters between 200 and 500 m deep are herein referred to as continental shelf-edge waters.

RESULTS

Physeteridae

THE GENUS *KOGIA*

Nishiwaki (1967) noted that *Kogia* species are widely distributed in tropical and temperate oceans. Both the pygmy sperm whale *Kogia breviceps* and the dwarf sperm whale *K. simus* are found off southern Africa (Ross 1979). Handley (1966) stated that *K. breviceps* is confined to the warmer waters of the world and most frequently strands on the coasts of South Africa, south-eastern Australia, New Zealand and the south-eastern U.S.A., and that *K. simus* has been recorded from the coasts of South Africa, India, Ceylon, Japan, Hawaii, South Australia and the east coast of the U.S.A. Off southern Africa, Ross (1984) recorded *K. breviceps* from Cape Cross (Namibia) to Natal and *K. simus* from Saldanha Bay to East London.

Owing to the difficulty of identifying sightings of kogiids to species level at sea, one incidental sighting of a *Kogia* at 30°36′S, 31°08′E in August 1971 was recorded as "*Kogia* species". Specimen records of 71 *Kogia simus*, 94 *Kogia breviceps* and 17 unidentified kogiids were reviewed in this study. Certain specimens were too decomposed to be identified to species level and were recorded as unidentified kogiids.

The distribution of the 17 unidentified kogiids is plotted in Figure 4a. In this Figure and indeed in all species distribution Figures, the localities of sightings and strandings of more than one individual are plotted as single events. Therefore, the number of specimens or sightings presented in the text may not tally with the number of localities presented in the figures. The distribution of the specimen records of *K. breviceps* (Fig. 4b) shows the species to be found along the entire coastline from 22°S on the West Coast to 29°50′S on the East Coast. The distribution of the records of *K. simus* (Fig. 5a) suggests that the distribution of this species is limited to the South Coast between Cape Columbine and approximately 28°E. Ross *et al.* (1985) suggest that the one record of *K. simus* from the northern coast of Natal is a stray, possibly linked to a warm water event in 1982. The large discontinuities in the distribution of strandings of *K. breviceps* on both East and West coasts presumably reflect the distribution of reporter effort.

Ross (1979) concluded that *K. simus* is associated with the shelf-edge of the Agulhas Bank, and that *K. breviceps* is a pelagic species. He later suggested (Ross 1984) that both species live in the open ocean, but that immatures utilize the continental shelf or slope as a "nursery" area. Despite the prevalence of strandings of both species, there is only one incidental sighting of *Kogia*, and definition of the offshore distribution patterns is impossible without further sighting records. The paucity of sightings could presumably be a result of one or more of the following factors: small sizes of schools (most strandings are of single ani-

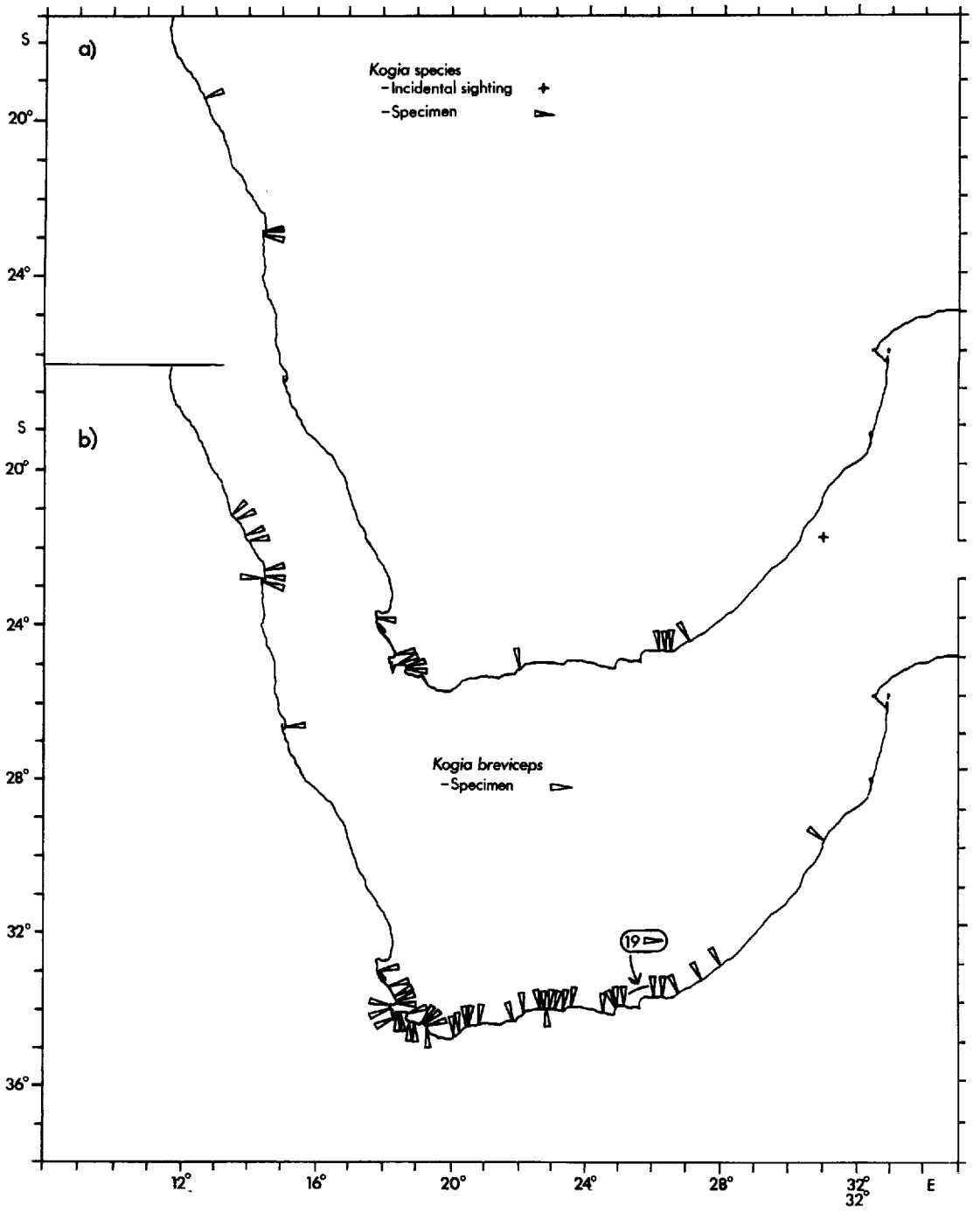

Fig. 4: Localities of (a) incidental sightings and specimens of unidentified *Kogia* species and (b) specimens of *Kogia breviceps*. In this and all following distribution maps, localities of specimens often refer to stranding events, so that the numbers of localities and specimens need not necessarily tally

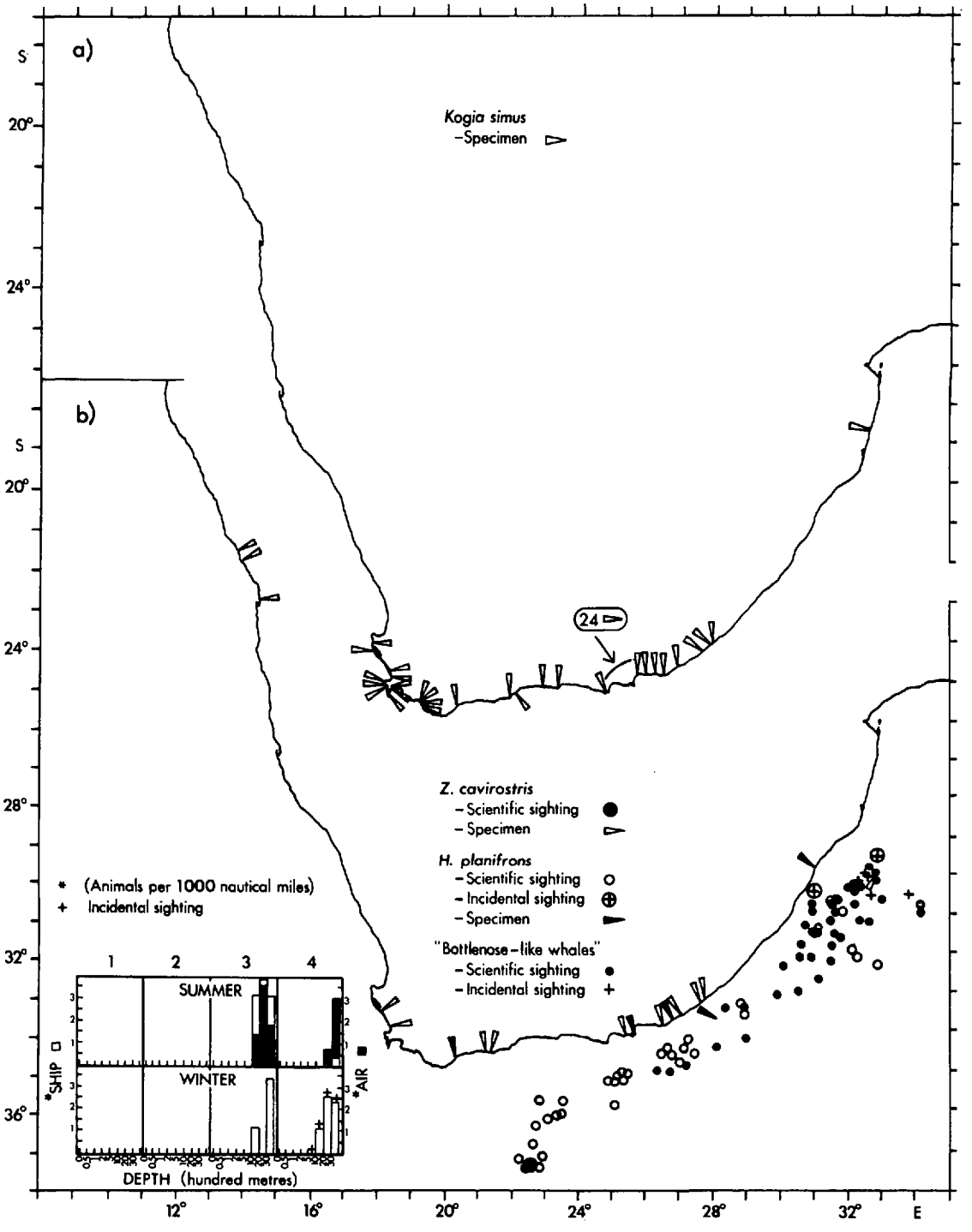

Fig. 5: Localities of (a) specimens of *Kogia simus* and (b) scientific and incidental sightings and specimens of *Ziphius cavirostris*, *Hyperoodon planifrons* and "bottlenose-like whales". The inset shows densities of individuals of *Hyperoodon planifrons* and "bottlenose-like whales" sighted during scientific cruises and flights and the occurrence of incidental sightings, by depth interval in each area

mals), small body size, a preferred deep-water habitat and possibly the diving behaviour of the species. Furthermore, kogiids are comparatively slow-moving, inconspicuous at the surface and do not provide good sighting cues (Caldwell and Caldwell 1989).

Ziphiidae

The *Ziphiidae* are poorly known because of their preference for deep water and the difficulty of spotting and identifying them at sea. Therefore, their distribution patterns are largely derived from stranding records. Ross *et al.* (in prep.) review the distributions and seasonal occurrence of beaked whales in the southern hemisphere and note that the majority of records are strandings.

CUVIER'S BEAKED WHALE *ZIPHIUS CAVIROSTRIS*

Nishiwaki (1967) suggests that this is a temperate species, whereas Ross (1984) states that it is widely distributed in tropical and temperate waters. Moore (1963) noted that *Z. cavirostris* appears to have a worldwide distribution, but questioned its occurrence off South Africa because the origin of the one specimen recorded from the Cape of Good Hope prior to those of Ross and Tietz (1972) was subject to controversy. Ross *et al.* (in prep.) note that, in the southern hemisphere, the species is distributed from the equator southwards and state that there are no records south of the Antarctic Convergence. However, Kasamatsu *et al.* (1988) report two sightings of Cuvier's beaked whale south of the Antarctic Convergence.

Only one *Z. cavirostris* has been sighted off the coast of southern Africa, at 37°28′S, 22°39′E during a scientific cruise in January 1975 (Fig. 5b). The water depth at the sighting was more than 3 000 m. Nishiwaki and Oguro (1972) state that *Z. cavirostris* occurs in waters of depths of >1 000 m. Two specimens (one found dead floating off Durban and one taken off Durban at 29°50′S, 32°49′E, both in water depths >1 000 m), provide further evidence of the deep-water preference of the species.

The distribution of 14 *Z. cavirostris* specimens is plotted on Figure 5b, and it would appear that this species has a cosmopolitan pelagic distribution in southern African waters.

SOUTHERN BOTTLENOSE WHALE *HYPEROODON PLANIFRONS*

The distribution of the genus *Hyperoodon* is antitropical, *H. planifrons* occurring in the southern hemisphere and *H. ampullatus* in the North Atlantic Ocean. Brownell (1974) states that *H. planifrons* is widespread in all southern oceans, being found off the coasts of Argentina, the Falklands, Chile, New Zealand and South Africa, and off Antarctica south of both Indian and Pacific oceans. Tietz (1966) records a stranding of *H. planifrons* at Humewood (33°58′S, 25°38′E) and states that the record conforms with McCann's (1961) conclusion that the species is restricted to the southern hemisphere south of 20°S. Ross (1984) suggests that *H. planifrons* is rarely found north of latitude 30°S and notes further that the species appears to have a summer seasonal occurrence in southern African waters. Ross *et al.* (in prep.) give the species' range as 30°S to Antarctic waters, with regular occurrence in southern African waters. It should be noted, however, that the locality of the type specimen is at approximately 20°S (Flower 1882). Miyashita and Balcomb (in press) found a beaked whale similar to *Hyperoodon* in the central and western Pacific between the equator and 34°N in July, August and September. The relationship of these animals to *H. planifrons* is unknown.

In all, 47 sightings of a total of 161 *H. planifrons* were made on scientific cruises and flights (Fig. 5b). Of these, 23 sightings were during cruises and 24 during flights. All sightings were made during December, January or February and in waters more than 1 000 m deep (Fig. 5b). Group size ranged between 1 and 15, with a mean of 4,62 (±*SD* 2,74). Two incidental sightings were made off the East Coast during March 1973 (Fig. 5b), and there are five stranding records of the species from the East and South coasts. The few records of strandings (as compared to the abundance of sighting records) further reflect the pelagic distribution of the species.

Ross (1984) notes the apparent summer seasonality of the species in southern African waters and that there are insufficient records from elsewhere to determine any migration patterns. Lichter (1986) states that there is a similar possible seasonality in the South-West Atlantic, but notes two winter records there. Gianuca and Castello (1976) state that *H. planifrons* appeared to have been abundant in Subantarctic and Antarctic waters in summer in the late 1800s and early 1900s, but Ross (1984) suggests that this observation may be a reflection of the inaccessibility of the region to man at other times of the year. Ross *et al.* (in prep.) suggest that there is indeed little latitudinal change in the seasonal distribution of the species and that the apparent seasonality arises from the movement of animals offshore during winter. Nemoto *et al.* (1980) found the skin diatom *Cocconeis ceticola* on a specimen of *H. planifrons* from southern African waters, and Sekiguchi *et al.* (in press) record the presence of beaks from Antarctic squid in the stomachs of animals from South African waters, providing evidence of movement from Antarctic or Subantarctic waters.

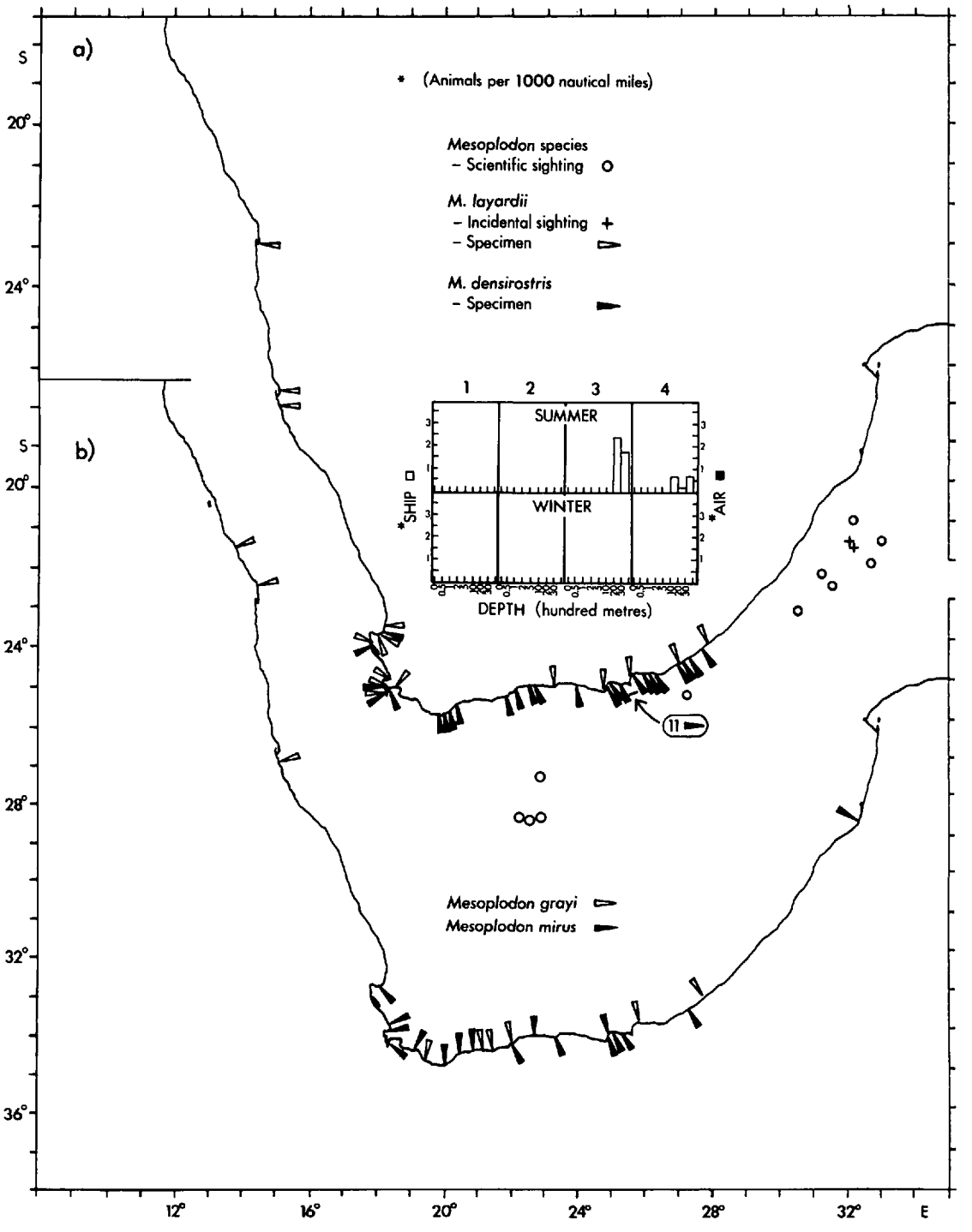

Fig. 6: Localities of (a) scientific and incidental sightings and specimens of unidentified *Mesoplodon* species, *M. layardii* and *M. densirostris* and (b) specimens of *Mesoplodon mirus* and *M. grayi*. The inset shows densities of individuals of unidentified *Mesoplodon* species sighted during scientific cruises and flights, by depth interval in each area

"BOTTLENOSE-LIKE WHALES"

The term "bottlenose-like" was frequently used by East Coast whaling crews and spotter aircraft personnel to describe any large unidentified beaked whale. Although the majority of these records probably can be ascribed to *H. planifrons*, they have been considered separately as "bottlenose-like whales".

A total of 47 sightings of 182 "bottlenose-like whales" was made on scientific cruises. All were made in summer (December — 3; January — 9; February — 35) and in waters deeper than 1 000 m (Fig. 5b). Group size ranged between 1 and 10 with a mean of 3,89 (±*SD* 2,41). Six incidental sightings of a total of 26 animals were made in March or April and group size of these sightings ranged between 2 and 10 with a mean of 4,33 (±*SD* 2,94). "Bottlenose-like whales" show a similar distribution pattern to that of bottlenose whales and appear to be strongly associated with the Agulhas Current (Fig. 5b).

Bottlenose whales of the southern African subregion appear to be confined to temperate and subtropical waters of the Agulhas Current. The marked summer seasonality suggests that the species moves out of the region during winter, but too few data are available to determine the winter destination of the species.

ARNOUX'S BEAKED WHALE *BERARDIUS ARNUXII*

The genus *Berardius* has an antitropical distribution pattern (Brownell 1974), the southern hemisphere species *B. arnuxii* being recorded from strandings from New Zealand, Australia, South Africa, Argentina, the Falklands, South Georgia and Chile (Lichter 1986). Brownell (op. cit.) also lists records from the South Shetlands and the Antarctic Peninsula. McCann (1962) suggested that *B. arnuxii* winters in the Antarctic, but moves into warmer latitudes to calve and mate during summer. Ross *et al.* (in prep.) suggest that the distribution of *B. arnuxii* is centred around the southern Pacific between 30°S and Antarctic waters and that the southern African records arise from a "sporadic occurrence" in these waters.

Berardius arnuxii has only been recorded in southern African waters from three strandings, including the record published by McLachlan *et al.* (1966). All are of single animals found on beaches during the warmer months (one each in October, December and January) and, although the records are themselves insufficient to draw any conclusions as to seasonality, they would confirm McCann's (1962) suggested movement patterns. The strandings occurred at 32°40′S, 18°16′E, 33°53′S, 18°24′E and 34°10′S, 24°50′E.

The lack of sightings of the species implies that *Berardius* is not common in southern African waters, although summer pelagic search effort off both the East and West coasts is extremely limited.

THE GENUS *MESOPLODON*

The known distributions of the *Mesoplodon* species have undergone considerable revision in the past 20 years. Moore (1966) stated that Blainville's beaked whale *M. densirostris* was the only *Mesoplodon* species which could be found in both northern and southern hemispheres. Mead (1981), in describing the global pattern of distribution of the genus *Mesoplodon*, stated that *M. densirostris* is a species of temperate and tropical oceans, that three species appear to be limited to tropical and warm temperate waters (*M. pacificus* and *M. ginkgodens* in the Indopacific and *M. europaeus* in the Atlantic) and that two species (*M. bidens* and *M. stejnegeri*) are confined to cold temperate waters of the Atlantic and Pacific respectively. Five species (*M. hectori, M. grayi, M. mirus* and *M. bowdoini*, the latter through, Mead suggests, its possible conspecific *M. carlhubbsii*) have general distributions in southern temperate oceans and in at least one of the northern oceans. Mead (op. cit.) further suggests that *M. layardii* should be placed in this latter group because it is likely to be recorded from the northern hemisphere.

Five species of *Mesoplodon* (*M. layardii, M. densirostris, M. mirus, M. hectori* and *M. grayi*) have been recorded from the coasts of southern Africa. All sightings of these (and possibly other *Mesoplodon* species) are analysed as "*Mesoplodon* species" because of the difficulty of differentiating positively between them at sea, although three incidental sightings of *M. layardii* were analysed as such because their distinctive adult colour pattern was noted. The 11 scientific sightings of a total of 32 individuals of *Mesoplodon* species were all made during January and February; their distribution is shown in Figure 6a. Group size of the schools ranged from one to six with a mean of 2,91 (±*SD* 1,70). All sightings of *Mesoplodon* species were limited to waters deeper than 2 000 m in Area 3 and deeper than 1 000 m in Area 4, confirming that the members of this genus are essentially deep-water animals (Fig. 6a).

Layard's beaked whale, M. layardii — This species has been recorded from Australia, New Zealand, South Africa, Uruguay, Argentina and Chile, and its distribution has been described by Goodall (1978), Ross (1984) and Lichter (1986). Ross *et al.* (in prep.) maintain that *M. layardii* has a circumpolar distribution in cold temperate waters of the southern hemisphere between 30 and 53°S, the only records north of these latitudes being within the cold Benguela system. Three incidental sightings of *M. layardii* were made off the coast of Natal during whaling operations in March

1973, two of which were at the same position (Fig. 6a). Two of these groups were of four animals and one was of six; all were in waters more than 2 000 m deep.

The distribution of 33 specimens of *M. layardii* is plotted on Figure 6a. Although the distribution of incidental sightings and specimens suggests a cosmopolitan distribution in southern African waters, specimen records are only from west of 28°E. Known months in which these specimens were collected include January (4), February (3), March (5), April (17), May (1) and June (2). Ross *et al.* (in prep.) note a marked increase in specimens during summer and autumn and suggest that this results from an inshore movement then. They further suggest a possible northward shift in distribution during winter. The pattern of stranding records under review in this study suggests that the species is limited to the area between Namibia and the Eastern Cape, which is in accord with Ross's (1984) statement that the South Coast distribution of *M. layardii* is limited to cool water inshore of the Agulhas Current. However, the incidental sightings off the Natal coast extend the range and are surprising given the apparent cold-water preference of the species elsewhere.

Blainville's beaked whale, M. densirostris — Moore (1958) notes that, of the 11 records at that time, 10 were from the tropics or from coasts adjacent to warm oceanic currents. Ross (1984) states that *M. densirostris* is a widely distributed species and notes records from the northern and southern Atlantic Ocean, from the northern Pacific and Indian oceans and from around Australasia. He suggests that the animals found off southern Africa either inhabit or are transported by the warmer water of the Agulhas Current. Ross *et al.* (in prep.) find *M. densirostris* to be distributed in tropical waters north of 35°S, and the large sample from southern Africa may arise from the warm Agulhas Current extending tropical conditions into higher latitudes.

The distribution of 48 specimen records of *M. densirostris* (Fig. 6a) suggests that this species is limited to the warm temperate waters of the South Coast and the mixed waters of the South-West Coast. The species is recorded elsewhere from the tropical waters of the Indian Ocean and the lack of records from off Natal is therefore surprising. It is thought that the animals stranded in the Southern Cape have their origin in the Agulhas Current.

True's beaked whale, M. mirus — Talbot (1960) published a stranding record of *M. mirus* from Wilderness (34°S, 22°34′E) in May 1959. McCann and Talbot (1963–1964) stated that, prior to the finding of that specimen, the known distribution of this species was restricted to the North Atlantic Ocean. Moore (1966) considered the Wilderness record to be "curious" and defined the distribution as the northern Atlantic. However, a stranding of a pregnant cow and a calf at the mouth of the Maitland River (33°58′S, 25°17′E) in 1969 (Ross 1969) gave evidence of the existence of a breeding population in the southern hemisphere. There have since been a further 20 records of *M. mirus* from South Africa (Fig. 6b). Animals were distributed between St Helena Bay (33°S) on the West Coast and the coast of northern Natal (Fig. 6b). Ross *et al.* (1985) note that the stranding record of PEMN 1010 at 28°29′S, 32°25′E extends the eastern limit of the species but, as with the Natal *K. simus* record, it may be attributable to abnormally high water temperatures around southern Africa in 1982. Elsewhere in the southern hemisphere, *M. mirus* has only been recorded from Australia (Baker 1983).

Gray's beaked whale, M. grayi — Southern hemisphere records of *M. grayi* exist for Australia, New Zealand, the Chatham Islands, South Africa, Argentina, Uruguay and Chile. Ross *et al.* (in prep.) state that *M. grayi* has a circumpolar distribution in cold temperate waters of the South Atlantic, Indian and Pacific oceans between 30 and 53°S, except for records north of these latitudes in the cold Benguela system. One stranding has been reported in the Netherlands (Boschma 1951), and Ross (1984) states that it was either a vagrant from the southern hemisphere or a representative of a separate population in the northern Atlantic Ocean.

The distribution of 12 *M. grayi* specimens is plotted on Figure 6b, and it would appear that, off southern Africa, the species is restricted to the West Coast and the coast of the Southern Cape. All strandings were of single animals except one group of three found dead on the coast near Still Bay (34°24′S, 21°12′E). The strandings occurred between January and October, and Ross *et al.* (in prep.) found no evidence of seasonal movement between latitudes.

Hector's beaked whale, M. hectori — Specimens of *M. hectori* are known from Tasmania, New Zealand, South Africa, the Falklands, Argentina, Chile and California (Lichter 1986), and Mead (1981) reports two probable sightings off the coast of California. Ross *et al.* (in prep.) state that the species has a circumpolar distribution in cold temperate waters. One stranding of two juvenile *M. hectori* occurred at 34°S, 23°45′E during March 1967, but the animals were very decomposed when found (Ross 1970). Ross *et al.* (in prep.) note a second South African stranding of *M. hectori* at 34°03′S, 22°50′E; it is not included in the current database because it occurred after June 1986. Ross *et al.* (op. cit.) note a strongly seasonal (Decem-

ber–March) incidence of strandings in the southern hemisphere, suggestive of inshore movement during summer.

Delphinidae

KILLER WHALE *ORCINUS ORCA*

Killer whales occur in all major oceans of the world (Budylenko 1981). Dahlheim (1981) notes that they appear to be most prevalent in cooler waters of both hemispheres, with centres of abundance within 800 km of major continents. However, there are several references to their migratory habits. Mikhalev *et al.* (1981) suggest that southern killer whales live in low latitudes during winter and migrate to high latitudes during summer, the southward migrations beginning in September/October and ending by January and the northern migrations beginning in February/March. Bigg *et al.* (1987) found two forms ("resident" and "transient") of killer whales in Puget Sound on the west coast of the United States. Ross (1984) defines the species as cosmopolitan and notes that it occurs throughout the year off the south-east coast of southern Africa.

There were 10 confirmed scientific sightings of a total of 48 *O. orca* from the study area (Fig. 7a). Group size of these confirmed sightings ranged from 3 to 11 with a mean of 5,33 (±*SD* 3,24). Sightings were made during January (2), February (3), April (1), May (1) and August (2). A further 46 incidental sightings of killer whales were made (Fig. 7a). These sightings occurred throughout the year and group size ranged from 1 to 12 with a mean of 4,54 (±*SD* 3,03). Also shown on Figure 7a are the localities of 41 specimens of killer whales reviewed in this study.

The scientific and incidental sightings and specimen records show that the killer whale is found at all water depths off southern Africa (Fig. 7a). The clump of incidental sightings west of the Cape Peninsula results from reports from ski-boat anglers. In that case, it is possible that the whales had been attracted to the boats (they have been reported to take fish off lines) or that both anglers and whales are attracted to frontal areas where gamefish occur.

The occurrence of the remains (nails and vibrissae) of at least three southern elephant seals *Mirounga leonina* in the stomach of a killer whale taken at Durban (some 1 000 miles from the nearest rookery) and the seasonality of killer whales on the whaling grounds (Findlay 1989) suggest that some at least of the animals in southern African waters are highly migratory. However, the cosmopolitan year-round occurrence of killer whales in these waters implies that at least some killer whales may be resident.

FALSE KILLER WHALE *PSEUDORCA CRASSIDENS*

Ross (1984) states that the false killer whale is an oceanic species found in tropical and temperate waters of all oceans. Six dedicated scientific sightings of a total of 100 *Pseudorca crassidens* in southern African waters were all made during summer (one in January and five in February). Group size ranged from 1 to 50 with a mean of 16,0 (±*SD* 22,9). One incidental sighting of approximately 68 animals was reported off the Cape Peninsula (33°53′S, 18°03′E) from a private fishing vessel during February 1985. Strandings of false killer whales have been recorded from just south of Lüderitz to the East Coast (Fig. 7b). Five of the stranding incidents of *P. crassidens* involved mass strandings of 5, 65, 120, 200 and 58 animals respectively. For another stranding of four animals, no information was available as to the category of the stranding. All mass strandings occurred over a limited area of coastline in the South-Western Cape, two of them on the same stretch of beach in St Helena Bay (32°50′S, 18°05′E) — Best (1982).

All scientific sightings of *P. crassidens* were made in water depths of more than 1 000 m, although the one incidental sighting was made in water 100–200 m deep in Area 2 (Fig. 7b). This incidental sighting in such shallow waters is somewhat surprising, given the species preference for deep water elsewhere.

It would appear from scientific sightings that this species occurs seasonally throughout southern African waters. However, little search effort was carried out off the East Coast during winter or in pelagic waters off the West Coast, and this may explain the paucity of winter records. All mass strandings took place between August and December.

PYGMY KILLER WHALE *FERESA ATTENUATA*

This species appears to be confined to tropical, subtropical and warmer temperate waters of the world. In reporting a specimen from the eastern tropical Pacific, Perrin and Hubbs (1969) note that the distribution remained almost undetermined until Yamada (1954) described an animal from Japan and Fraser (1960) one from Senegal. Nishiwaki *et al.* (1965) reported that 14 specimens were caught in Japan and Pryor *et al.* (1965) described one caught from Hawaii. Best (1970) recorded strandings in South Africa and Namibia. Van Waerebeek and Reyes (1988) reported two records of *Feresa attenuata* from the coast of Peru in the Humboldt Current and summarized the known distribution in the

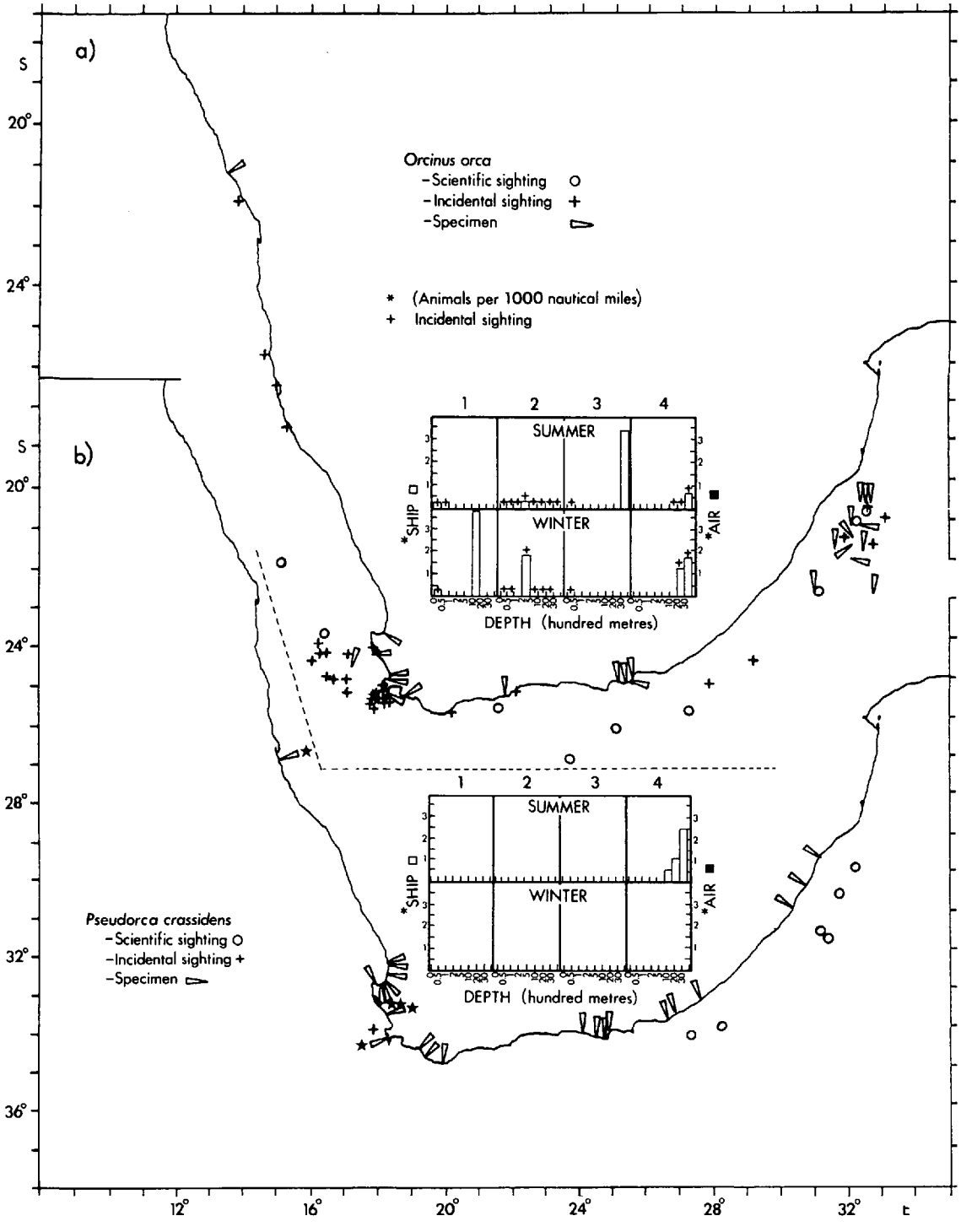

Fig. 7: Localities of scientific and incidental sightings and specimens of (a) *Orcinus orca* and (b) *Pseudorca crassidens*. The insets show densities of each species sighted during scientific cruises and flights and the occurrence of incidental sightings, by depth interval in each area. Stars indicate provenances of mass strandings

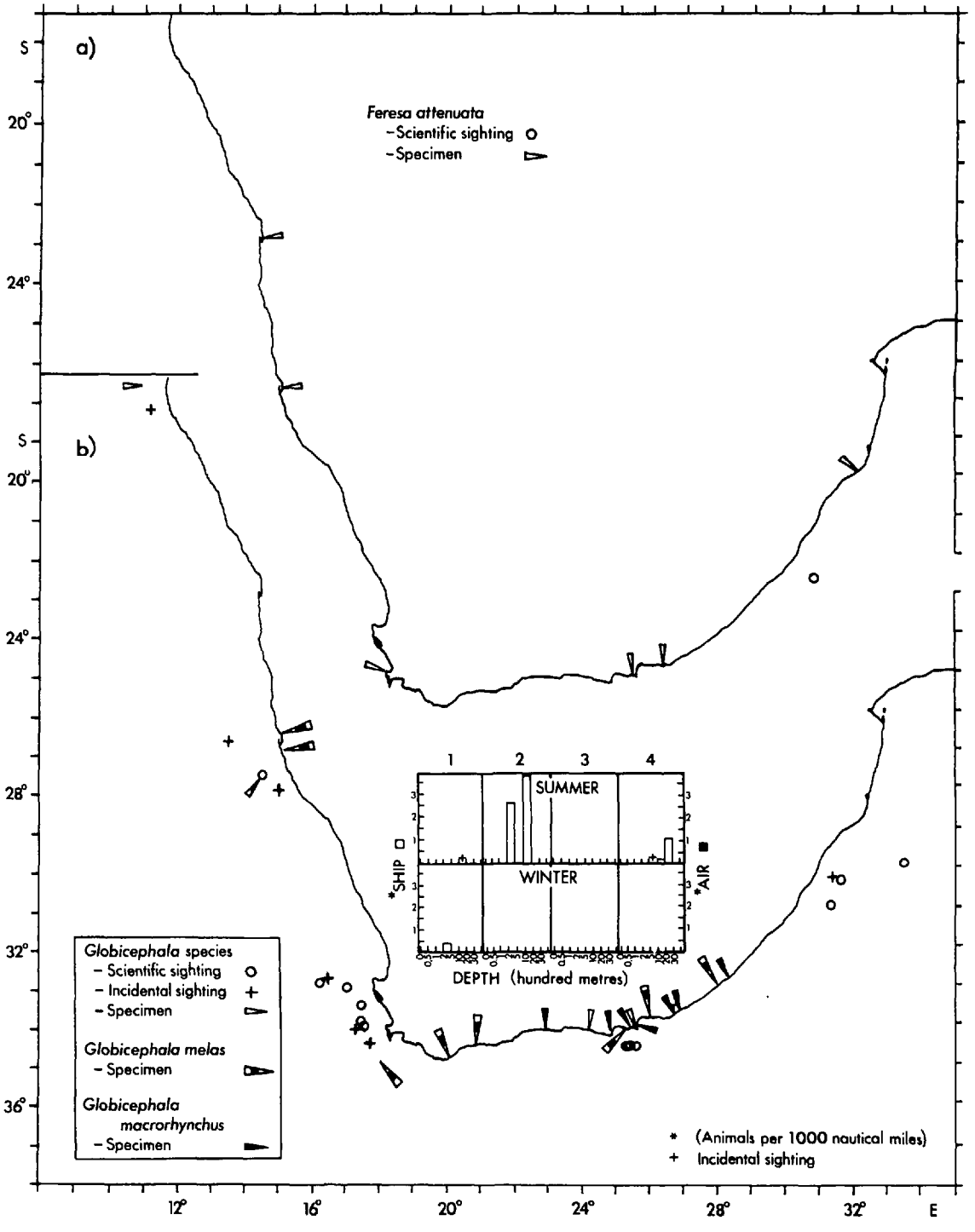

Fig. 8: Localities of (a) scientific sightings and specimens of *Feresa attenuata* and (b) scientific and incidental sightings and specimens of *Globicephala* species and provenances of specimens of *G. melas* and *G. macrorhynchus*. The insets show densities of each species sighted during scientific cruises and flights and the occurrence of incidental sightings, by depth interval in each area

eastern Pacific.

One dedicated scientific sighting of 11 *Feresa attenuata* was made off the coast of Natal (31°S, 29°E) in August 1969 (Best 1970). This sighting was made in water 1 000–2 000 m deep (Fig. 8a). There have also been 6 strandings of 11 *F. attenuata* along the coast of southern Africa (Fig. 8a), with a marked absence of strandings between the Cape Peninsula and Algoa Bay, given the number of observers on this coast. This is possibly caused by the greater width of the continental shelf there. The records from Namibia as far north as 23°S are surprising given the reputed preference of the species for warm temperate waters. However, these animals probably originate from warmer offshore waters.

MELONHEADED WHALE *PEPONOCEPHALA ELECTRA*

P. electra is a tropical pelagic species, and Perrin (1976) summarized its worldwide distribution. There is only one record from South Africa, a single animal that stranded alive at Hout Bay (34°04′S, 18°21′E) in July 1976. Best and Shaughnessy (1981) note that, because this species is usually found in tropical and subtropical waters, this animal must have been at the extreme southern limit of its range. The only other Atlantic Ocean records were made north of the equator (Van Bree and Cadenat 1968), apart from a report of a mass stranding of 240 individuals in Brazil (Siciliano *et al.* 1987).

THE GENUS *GLOBICEPHALA*

Two species of pilot whales, the long-finned (*G. melas*) and the short-finned (*G. macrorhynchus*) have been recognized worldwide, the former having an antitropical distribution in cold temperate waters of the North Atlantic and the southern hemisphere, and the latter being cosmopolitan in tropical and warm temperate waters (Leatherwood and Reeves 1983). Both species are found off the coast of southern Africa. Van Bree *et al.* (1978) found that *G. macrorhynchus* appears to predominate on the East Coast and *G. melas* on the West Coast, with an area of overlap from strandings between East London and Mossel Bay. The record of *G. macrorhynchus* from Mossel Bay, however, was based on a skull in a local museum without any provenance.

Owing to the difficulty of distinguishing between the two species at sea, scientific sightings have been recorded simply as *Globicephala* species. All 13 dedicated scientific sightings were associated with the shelf-edge or in waters >1 000 m deep (Fig. 8b). Two were of unconfirmed group size, but excluding these, group size ranged from 2 to 25 with a mean of 7,33 (±*SD* 4,61). Seven incidental sightings were made in southern African waters. Group sizes of these ranged between 1 and approximately 120. A number of the schools of *Globicephala* were associated with schools of *Tursiops*. Four dedicated sightings of pilot whales were made in the same localized area as three sightings of bottlenose dolphins on one day, and two incidental sightings of *Globicephala* were made with *Tursiops*.

Figure 8b also shows the distribution of nine specimens of *G. melas* and 29 specimens of *G. macrorhynchus* respectively.

Sightings of *Globicephala* have been made throughout southern African pelagic waters. However, although they cannot be differentiated into species, the pattern of strandings of both species and the distribution of the genus in relation to water masses appear to confirm the distribution patterns advanced by Van Bree *et al.* (1978) that *G. melas* is a cold-water species found on the South and West coasts, whereas *G. macrorhynchus* is a warm-water species found on the East Coast. The area of overlap of the two species (between 25 and 28°E) apparent from the stranding records would reflect the movement of *G. macrorhynchus* westwards with the Agulhas Current and the eastward movement of *G. melas* in cooler water inshore of that current system. Nores and Pérez (1988) found that the two species existed allopatrically off the coast of Spain, with *G. melas* inhabiting cooler waters than *G. macrorhynchus*.

RISSO'S DOLPHIN *GRAMPUS GRISEUS*

Leatherwood *et al.* (1980) state that Risso's dolphin is distributed worldwide in tropical and temperate waters, but Davies (1963) defines the distribution as largely tropical, extending its range polewards to overlap with temperate species. Kruse *et al.* (1991) found the species to be distributed throughout the central and northern Indian Ocean and particularly along and seawards of the continental shelf. Ross (1984) found that, off the south-east coast of southern Africa, *G. griseus* occurred well offshore, but that there was some possible association with the 1 000 m isobath.

A total of 43 sightings of Risso's dolphin was made during scientific cruises (Fig. 9a). Group sizes of these sightings ranged from 1 to 80 with a mean of 11,09 (±*SD* 13,37). The majority (37) were made in summer. In all, 25 incidental sightings of Risso's dolphin have been made (Fig. 9a) and the mean group size of these was 10,36 (±*SD* 8,70). The localities of 100 specimens of Risso's dolphin are also shown in Figure 9a.

The sightings of *G. griseus* were made between 31°S on the West Coast and 29°S on the East Coast. The paucity of sightings off the West Coast is prob-

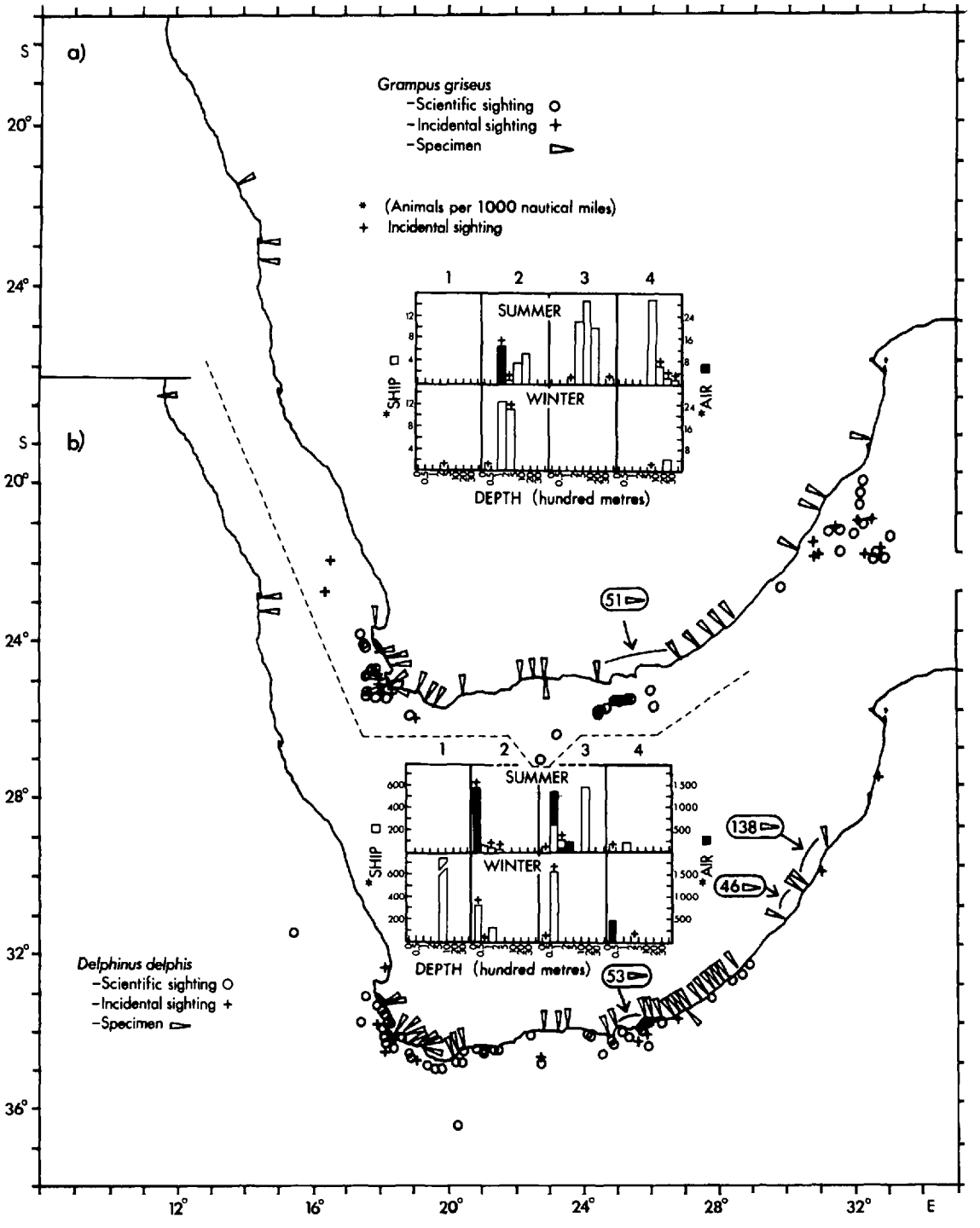

Fig. 9: Localities of scientific and incidental sightings and specimens of (a) *Grampus griseus* and (b) *Delphinus delphis*. The insets show densities of each species sighted during scientific cruises and flights and the occurrence of incidental sightings, by depth interval in each area

ably an artifact of the low offshore search effort, because three strandings took place between 23°18′ and 21°35′S. The scientific and incidental sightings of Risso's dolphins reveal the species to be associated with the shelf-edge and pelagic waters (Fig. 9a inset). The one incidental sighting of Risso's dolphin made nearshore was in the vicinity of Simonstown harbour. This animal was presumed about to strand, and therefore its position must be considered anomalous. Risso's dolphins are found throughout southern African pelagic waters but, as suggested by Leatherwood *et al.* (1984), the species appears to have some association with the shelf-edge.

COMMON DOLPHIN *DELPHINUS DELPHIS*

Evans (1982) notes that *D. delphis* is a highly mobile species distributed over a wide range of water temperatures (10–28°C) and that it appears to adapt to a wide range of habitats, from enclosed waters (Black Sea) to a pelagic existence. Gaskin (1968) states that, in the southern hemisphere, *D. delphis* appears to be confined to north of the Subtropical Convergence; he suggests a minimum surface temperature of about 14°C. Dohl *et al.* (1986) found that *D. delphis* off the coast of California followed features of bottom topography in response to seasonally fluctuating water temperature, and Hui (1979) found *D. delphis* distribution to be related to regions of high topographical relief and that ocean floor plains are avoided. Hui (op. cit.) notes, however, that this utilization of areas of high topographical relief is probably related to prey distribution, because such areas are regions of upwelling. He concludes that, as upwelling (and therefore productivity) is not related to ocean depth, *D. delphis* should be distributed without regard to depth. Norris and Prescott (1961) found a seasonal movement of *D. delphis* off California, animals moving inshore in autumn and winter and offshore in spring and summer; they suggest this to be food-related. Evans (op. cit.) found a southward movement of the species in Californian waters between December and June. Ross (1984) suggests that the presence of *D. delphis* in Natal waters during winter is associated with the "sardine run".

In all, 52 scientific sightings of common dolphins have been made off southern Africa (Fig. 9b). Group size of these sightings ranged from 1 to approximately 1 000 animals with a mean of 267 (±*SD* 287,2). Most of the sightings were made during summer, but this appears to be a reflection of timing of effort in areas where common dolphins occur. A total of 21 incidental sightings of common dolphins has been reported (Fig. 9b), of which the largest school recorded was estimated to be between 1 000 and 5 000 animals (Ross 1984). The mean group size for these confirmed incidental sightings was 174,3 (±*SD* 206,9). The distribution of 431 specimens of common dolphin is also shown in Figure 9b.

The pattern of sightings of common dolphins implies that the species is distributed from about 31°S on the West Coast to north of 28°S on the East Coast (Fig. 9b). However, strandings as far north as Walvis Bay and an incidental capture at 18°S confirm the occurrence of common dolphins off Namibia. The lack of sightings on dedicated searches both there and inshore along the west coast of South Africa north of c. 32°S implies that the distribution is largely offshore, where there was little search effort. Therefore, it appears that common dolphins prefer the warmer deep waters off the West Coast and avoid cooler inshore waters. Conversely, on the East Coast, there are very few sightings offshore, despite a great deal of winter shipboard effort. Evans (1982) found two separate stocks of common dolphin in the north-east Pacific Ocean. These were a long-snouted neritic form and a short-snouted pelagic form. More recently, consistent differences in the pigmentation pattern have also been found for these two forms (Heyning and Perrin 1989). Although there have been no studies on the onshore/offshore movements of the species off southern Africa, two colour morphs have been identified from strandings.

The one dedicated sighting of *D. delphis* in Area 1 was made in water 500–1 000 m deep, further confirming the species' preference for deep water off the West Coast (Fig. 9b). The majority of sightings in the remaining three Areas were in waters shallower than 500 m, although one further pelagic sighting was made in water south of the Agulhas Bank. All incidental sightings were made inshore of the 500 m isobath.

Common dolphins are found off the South Coast throughout the year. Despite Ross' (1984) contention that they follow the winter "sardine run" into Natal waters, common dolphins have been sighted (as both dedicated and incidental sightings) off the East Coast during both summer and winter. Only one sighting was made offshore (in waters >500 m deep) north of 32°S on the West Coast, and this sighting was made in winter. Specimens of common dolphin were recorded off the West Coast during both summer and winter, but it is not known if these originate from inshore or offshore populations.

DUSKY DOLPHIN *LAGENORHYNCHUS OBSCURUS*

Würsig and Würsig (1980) note that *L. obscurus* populations are distributed in coastal waters of the southern hemisphere and most notably off the coasts of New Zealand, South Africa and South America. Brownell (1965) states that *L. obscurus* has a circumpolar distribution north to approximately 30°S, but

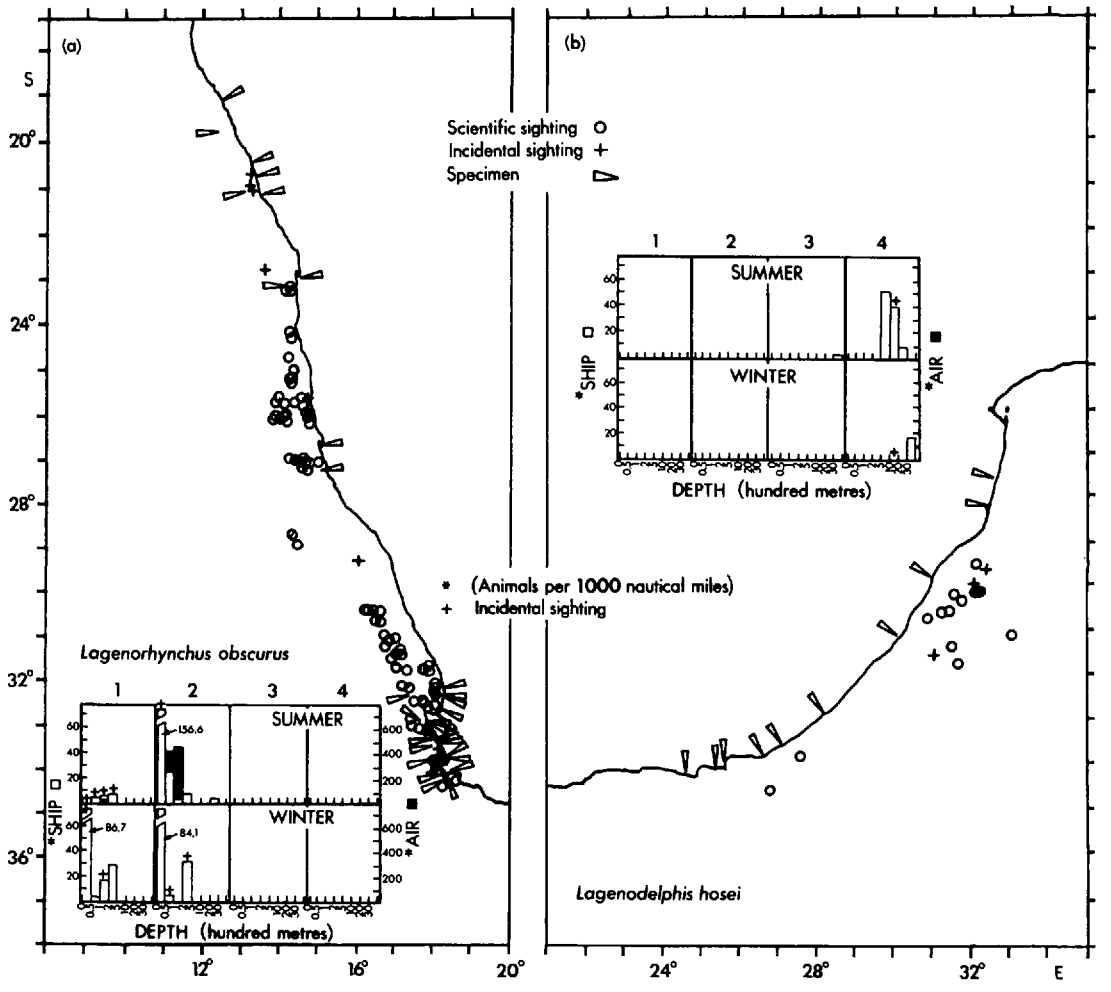

Fig. 10: Localities of scientific and incidental sightings and specimens of (a) *Lagenorhynchus obscurus* and (b) *Lagenodelphis hosei*. The insets show densities of each species sighted during scientific cruises and flights and the occurrence of incidental sightings, by depth interval in each area

Gaskin (1968) regards this distribution with caution and maintains that there is no evidence that the species occurs east of the Chatham Islands. Gaskin (op. cit.) further suggests that the population of *L. obscurus* off New Zealand is associated with the subtropical convergence and rapidly disappears north and south of it.

In all, 100 sightings of dusky dolphin were made on scientific cruises (Fig. 10a). The sightings were made throughout the year, and the size of confirmed schools ranged from 2 to 800 with a mean of 35,32 (±*SD* 104,46). Würsig and Würsig (1980) found a seasonal difference in group size off Argentina, but no such differences were apparent in the current data by summer (December–February), autumn (March–May), winter (June–August) and spring (September–November) — $F = 2{,}448$, $p > 0{,}05$. In all, there were 71 incidental sightings of dusky dolphins, including 41 made during live-capture attempts for oceanaria. Mean group size of the confirmed incidental sightings was 29,2 (±*SD* 48,3). A further 62 specimens of dusky dolphin have been recorded from the West Coast (Fig. 10a).

All sightings of *L. obscurus* were made west of 19°E (Fig. 10a). Brownell (1974) maps *L. obscurus* as occurring along the south coast as far east as Algoa Bay. This, however, is based on a misinterpretation of a statement made by Tayler and Saayman (1972) and on a personal communication by Prescott (in Brownell

op. cit.). Prescott has no knowledge of this personal communication (Prescott *in litt.*). A hiatus in the West Coast distribution is apparent between about 27 and 30°S, only two sightings being recorded between these latitudes (slightly farther offshore than the majority of other sightings), despite substantial search effort there. A further gap is apparent between 21 and 23°S. Although the distribution of *L. obscurus* overlaps the upwelling cells noted by Shannon (1985) off the Cape Peninsula, Cape Columbine and Lüderitz, the larger southern hiatus overlaps the Namaqua upwelling cell. The most northern record known from the West Coast is from Lobito Bay, Angola (12°S) made by Kramer (1961), but this may not be the northernmost limit of the distribution. Read *et al.* (1988) record catches of dusky dolphins as far north as Huacho (approximately 11°S) off the coast of Peru.

Most scientific sightings of *L. obscurus* were in water shallower than 500 m (Fig. 10a). This may, however, reflect some bias towards the nearshore in that there was little offshore search effort on the West Coast. The species was recorded offshore of the 2 000 m isobath in Area 2 in 1963, but the highest densities were recorded within the 0–50 m depth interval (Fig. 10a inset). Würsig and Bastida (1986) found that, of nine dusky dolphins marked off Argentina, eight kept to within 20 km of the shore and one moved up to 50 km offshore.

In conclusion, *L. obscurus* is a year-round resident of the west coast of southern Africa, being found predominantly over the shelf in shallow waters, but also off the shelf-edge. Unfortunately, insufficient search effort was expended in deep water off the West Coast to establish pelagic densities more accurately.

FRASER'S DOLPHIN *LAGENODELPHIS HOSEI*

Prior to 1971, Fraser's dolphin was only known from a skeleton collected in 1895 from Sarawak, Borneo. Perrin *et al.* (1973) reported at-sea sightings of the species off the coast of southern Africa, as well as recording specimens from the tropical Eastern Pacific, off Durban, South Africa, and from New South Wales, Australia. Robison and Craddock (1983) suggest that the species has a pan-tropical distribution. Ross (1984) notes that the species has been recorded from widespread localities in tropical waters of the Pacific and Atlantic oceans, and states that, despite sightings and strandings occurring at the same time of the year on the south-east coast of South Africa, the data are insufficient to show seasonality.

A total of 14 dedicated scientific sightings of *L. hosei* have been made off the coast of South Africa (Fig. 10b). It must be noted that a number of these sightings were made prior to the report of Perrin *et al.* (1973), but subsequent identifications of the particular animals were made from field notes and sketches, given the greater knowledge of the animal's appearance. The majority (13) of the sightings were in summer (the one winter sighting was made during August). Group size ranges from 7 to 1 000 animals with a mean of 183,1 (±*SD* 277,1). Incidental sightings of *L. hosei* have been reported during April (150 animals), August (about 100) and September (25). All incidental and dedicated sightings of *L. hosei* were made in water >1 000 m deep (Fig. 10b).

The distribution of 10 strandings of 14 animals covers a stretch of coastline slightly longer than that covered by sightings (Fig. 10b).

L. hosei is found off the shelf-edge off the East Coast (Fig. 10b), and it may well have a localized occurrence strongly associated with the subtropical component of the Agulhas Current. No sightings of this species were made farther offshore (outside the study area) on the 1973/74 whale-marking cruise that covered a large part of the south-eastern Indian Ocean (Gambell *et al.* 1975).

HEAVISIDE'S DOLPHIN *CEPHALORHYNCHUS HEAVISIDII*

Marcuzzi and Pilleri (1971) erroneously map *C. heavisidii* as occurring in waters off Natal and the Southern Cape and in a trans-oceanic band into the south-western Atlantic (where it is mapped as occurring sympatrically with *C. commersonii* off the Argentinian coast). Best (pers. comm. in Mitchell 1975) defines the distribution as from Cape Cross to Cape Point on the west coast of the African subcontinent, and Watkins *et al.* (1977) state that it is found in coastal waters off the west coast of southern Africa from about 18°S to Cape Point. Rice and Saayman (1984) reviewed incidental sightings between Table Bay (33°54′S, 18°25′E) and northern Namibia (17°23′S, 11°55′E), all of which were within five miles of the shore.

In all, 149 scientific sightings of 482 Heaviside's dolphins were recorded from the West Coast (Fig. 11a). Group size ranged from 1 to 30 with a mean of 3,15 (±*SD* 3,07). Incidental sightings of Heaviside's dolphin total 40 (Fig. 11a). Group sizes of these sightings also range between 1 and 30 with a mean of 3,97 (±*SD* 4,92). The distribution of 59 specimens of Heaviside's dolphin is also plotted on Figure 11a.

All records of Heaviside's dolphin are from west of Cape Point (Fig. 11a), although there is one unconfirmed incidental sighting approximately one mile east of Cape Point. The farthest north this species has been recorded is 17°09′S, but the accuracy of the position is uncertain. No data are available from Angola. The

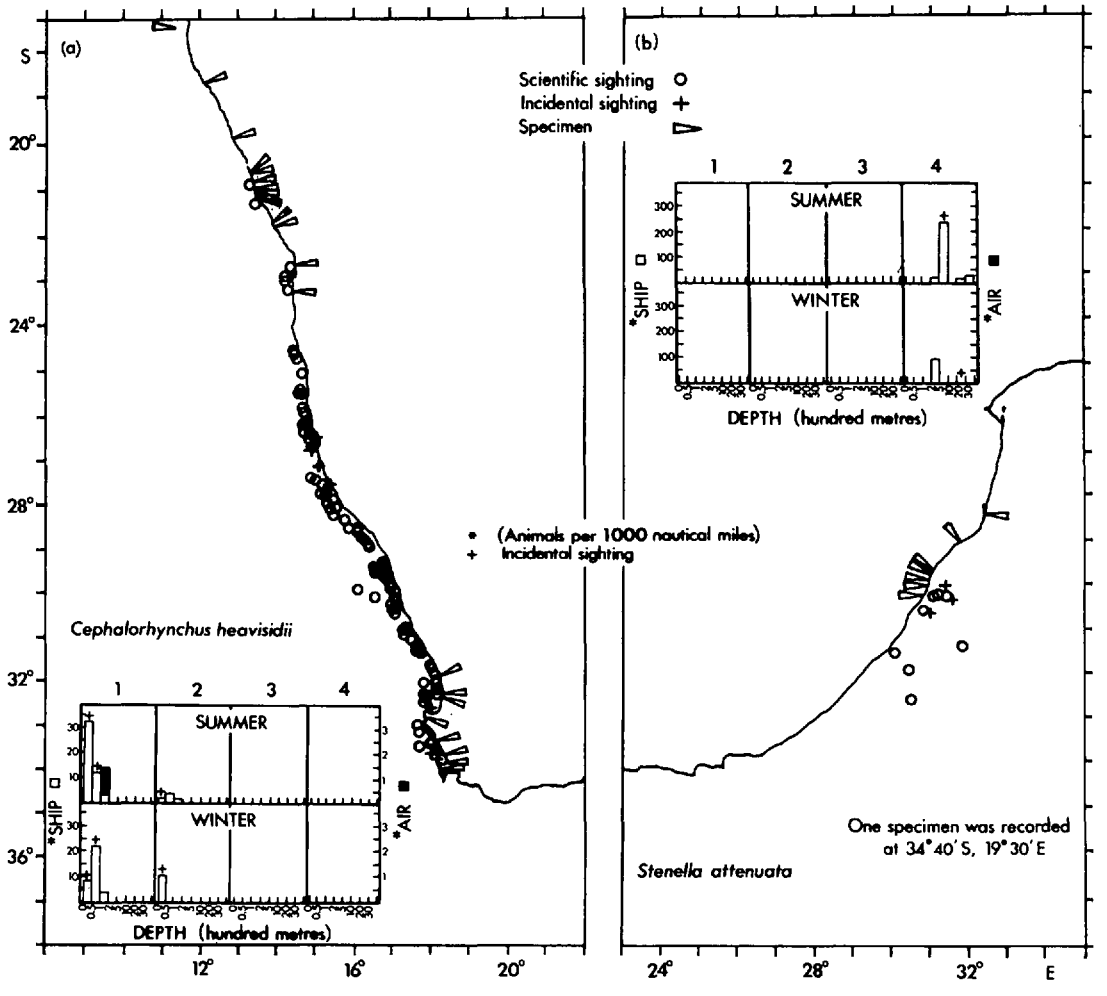

Fig. 11: Localities of scientific and incidental sightings and specimens of (a) *Cephalorhynchus heavisidii* and (b) *Stenella attenuata*. The insets show densities of each species sighted during scientific cruises and flights and the occurrence of incidental sightings, by depth interval in each area

species has been seen up to 45 miles from the coast, but all dedicated and incidental sightings of *C. heavisidii* were made in waters shallower than 200 m, the highest densities being inshore of the 100 m isobath (Fig. 11a). Therefore, *C. heavisidii* is a resident of nearshore waters of the west coast of southern Africa.

THE GENUS *STENELLA*

The taxonomy of the genus *Stenella* is complex. Three groups or superspecies can be distinguished (Rice and Scheffer 1968, Rice 1977). These are: the spinner dolphins, which are found in all three oceans and include *S. longirostris* from the Pacific, Indian and Atlantic oceans and *S. clymene* occurring allopatrically with *S. longirostris* in the Atlantic (Perrin *et al.* 1981); the spotted dolphins, including the pan-tropical *S. attenuata* and *S. frontalis*, which is restricted to the Atlantic (Perrin *et al.* 1987); the striped dolphin *S. coeruleoalba*. All spotted dolphins from the study area have so far been referred to the pan-tropical species *S. attenuata*, and there are no records of the short-snouted spinner dolphin *S. clymene*.

Perrin *et al.* (1978) suggest that the great diversity of *Stenella* in the Atlantic may have resulted from movements of the genus from the Indian Ocean around the African subcontinent via the Agulhas Current into the Atlantic Ocean during interglacial

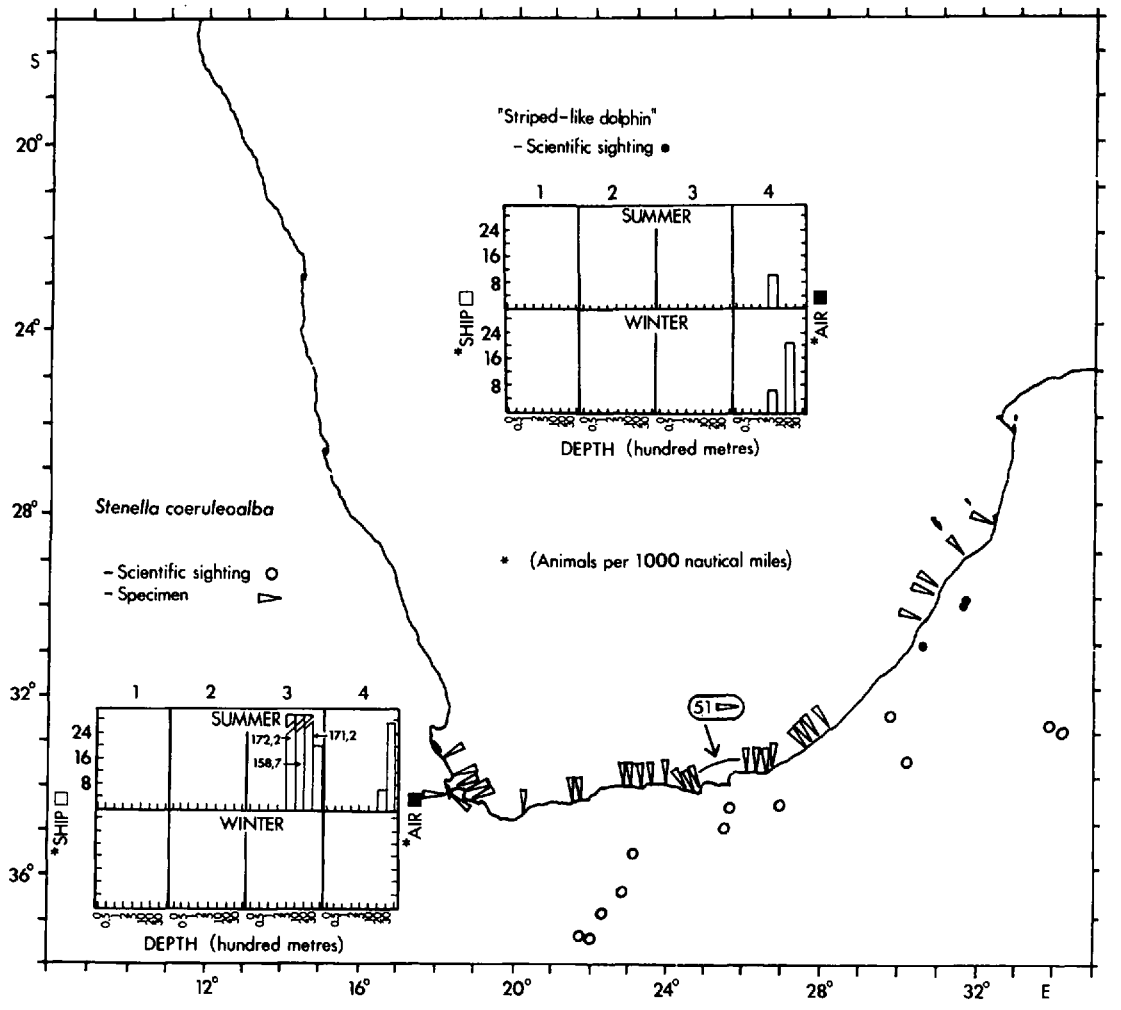

Fig. 12: Localities of scientific sightings and specimens of *Stenella coeruleoalba* and "striped-like dolphin". The insets show densities of each species sighted during scientific cruises and flights, by depth interval in each area

periods. Miyazaki *et al.* (1974) found *S. attenuata* to be distributed in slightly warmer waters than *S. coeruleoalba* off Japan, and Perrin *et al.* (1983) state that *S. longirostris* may be more restricted to tropical conditions than *S. attenuata* in the eastern Tropical Pacific.

Spotted dolphin, S. attenuata — Eight dedicated scientific sightings of a total of 663 *S. attenuata* are on record off southern Africa. All these sightings were east of 29°00'E (Fig. 11b) and mean group size of confirmed sightings was 93,86 (±*SD* 92,4). Three incidental sightings of a total of 125 animals were made in the same region (Fig. 11b). The distribution of 12 specimens of *S. attenuata* is also plotted on Figure 11b; all are east of 30°E. One live stranding at 34°40'S, 19°30'E, well west of any other sighting or stranding, is not illustrated in Figure 11b because it is possible that the specimen was a stray.

All scientific sightings of *S. attenuata* were made in water >200 m deep, whereas the incidental sightings were all made in waters of 500–2 000 m (Fig. 11b). Ross *et al.* (1987) suggest that *S. attenuata* may feed closer inshore than the 200 m isobath.

Striped dolphin, S. coeruleoalba — In all, 12 dedicated scientific sightings of a total of 1 020 *S. coeruleoalba* were recorded (Fig. 12). All sightings were made during

summer, in December (1), January (9) and February (2). Mean group size of these sightings was 74,5 (±*SD* 57,2). Three scientific sightings of "striped-like dolphin" were made. Two of these were in August (of 100 and of 4 animals) and one in February (22 animals). No incidental sightings of striped or "striped-like dolphins" were made. A total of 87 specimens of striped dolphins was reviewed, and the localities of these are plotted on Figure 12. All sightings of striped and "striped-like dolphins" were made in water depths greater than 500 m (Fig. 12).

The distribution of *S. coeruleoalba* appears to be strongly associated with the Agulhas Current (Fig. 12). As with the distribution of *H. planifrons* (Fig. 5b), the western boundary appears to be determined by the edge of the shelf of the Agulhas Bank. Strandings of striped dolphins around the Cape Peninsula and as far west as Yzerfontein (33°22′S, 18°09′E) on the West Coast suggest that animals may move around the Cape Peninsula into the Benguela system with eddies of Agulhas Current water, or alternatively that *S. coeruleoalba* also occurs offshore on the West Coast (where there has been relatively little search effort). One sighting of a single animal with a group of 15 dusky dolphins was made in July 1986 at c. 30°20′S, 16°15′E, in 200–220 m of water, but it was not included in this database.

Spinner dolphin, S. longirostris — Two incidental sightings of *S. longirostris* have been documented by Ross *et al.* (1985). Both of these were made close inshore off the north coast of Natal and no school sizes are given. Ross (1984) notes that there are three other possible records of *S. longirostris* off southern Africa, but none of the localities of these animals can be accurately verified and as such were omitted from this database. The two incidental sightings were made inshore of the 50 m isobath.

Despite much search effort within the area, no spinner dolphins have been recorded on the East Coast whaling grounds farther south than those documented by Ross *et al.* (1985). Therefore, northern Natal may represent the southernmost limit of the distribution of spinner dolphins in the western Indian Ocean. The nearshore distribution of these records may reflect the closeness of the tropical Agulhas Current to the coast there, or perhaps the species' behaviour of resting in shallow waters, as recorded off Hawaii (Norris and Dohl 1980).

SOUTHERN RIGHT WHALE DOLPHIN *LISSODELPHIS PERONII*

The recorded distribution of this species is limited to the cooler waters of the southern hemisphere (Gaskin 1968, Brown 1973). It has been recorded from 58 to 64°S off the coast of South America (Fraser 1955) and Brownell (1974) noted that all observations except two are from the South-West Atlantic, South-Pacific and Australian waters. Gaskin (1968) stated that the presence of this species in water of surface temperatures 9–15°C suggests that it is distributed south of the Subtropical Convergence, but north of the Antarctic Convergence. Fraser (op. cit.) maintains that *L. peronii* probably has a circumpolar distribution in the southern hemisphere and that it has a "predilection" for the West Wind Drift, because records to the north are close to the Subtropical Convergence and there is only one sighting record for the Antarctic Ocean. Kasamatsu *et al.* (1988) documented three sightings of *L. peronii* south of 58°S and these sightings were associated with temperatures of 1,4–13,8°C. Van Waerebeek *et al.* (1991) found *L. peronii* to be distributed as far north as 12°30′S off the coast of Peru. Barnard (1954) suggested it might well occur off the coast of South Africa, and Brown (1973), on the basis of sea surface temperature and records in the Peru Current as far north as 19°S, suggested that it may be found in the Benguela system. Brownell (1974) states that *L. peronii* is an epipelagic species, whereas Aguayo (1975) defines it as a pelagic and coastal species.

There are no recorded scientific sightings of this species from southern Africa. However, there are 12 incidental sightings (Fig. 13a), including those published by Cruickshank and Brown (1981). A further record was published by Brown (1982) but no precise locality was given. Group size ranged between 3 and 250 with a mean of 52,25 (±*SD* 82,59). Eight of the sightings were made in summer, January (3), February (3), November (1) and December (1), and two in each of autumn and winter, in April (2) and August (2) — Fig. 13a. Cruickshank and Brown (1981) note that the seven sightings before 1981 were made in water where the surface temperature was between 15,5 and 20,1°C and the depths were 300–500 m. However, the position given for the group of 200–300 animals sighted on 24 January 1979 (26°40′S, 14°49′E) lies in water shallower than 200 m. Water depths of the remaining 11 sightings ranged from the 100–200 to the 1 000–2 000 m depth intervals.

Further records of the species off southern Africa were published by Rose and Payne (1991) but, as these were made after June 1986, they have not been considered here. The majority of those records were from a similar region to those reviewed here, but one was from south of the Orange River mouth. Therefore, it would appear that *L. peronii* occurs in a small area off Namibia, perhaps associated with the Lüderitz upwelling cell (Rose and Payne op. cit.). The rarity of sightings in South African waters implies that the population may be resident in Namibian waters.

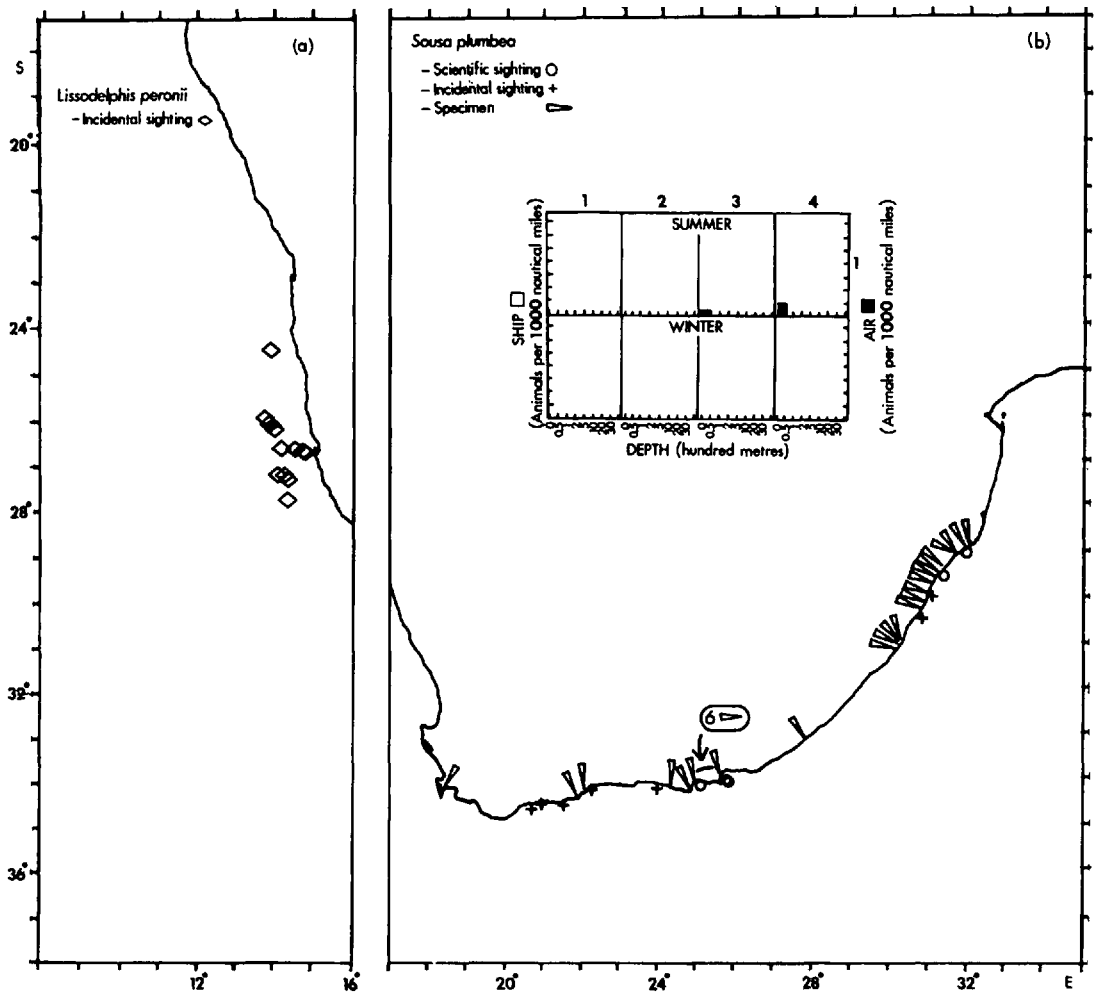

Fig. 13: Localities of (a) incidental sightings of *Lissodelphis peronii* and (b) scientific and incidental sightings and specimens of *Sousa plumbea*. The inset shows densities of *Sousa plumbea* (numbers·100 miles^{-1}) sighted during scientific cruises and flights, by depth interval in each area

INDIAN OCEAN HUMPBACK DOLPHIN *SOUSA PLUMBEA*

Ross (1984) lists *S. plumbea* as occurring in the western and northern Indian Ocean, between the Gulf of Siam and South Africa. Off southern Africa, *S. plumbea* may be found in the coastal waters of Natal and the Eastern and Southern Cape. Ross (op. cit.) states that the western limit is uncertain and that, apart from a skull found at Muizenberg (34°07′S, 18°28′E) in 1896 (Tietz 1963), which is presumed to have been a vagrant, there are no records west of the mouth of the Gouritz River (21°53′E). Saayman and Tayler (1979) found that humpback dolphins ranged within a kilometre of the coast and foraged in the vicinity of reefs.

Six dedicated scientific sightings of a total of 41 *S. plumbea* have been made during the aerial surveys for dolphins carried out by the Port Elizabeth Museum (Fig. 13b). Group size ranged between 5 and 10 with a mean of 6,83 (±*SD* 1,94). A further 12 incidental sightings of *S. plumbea* have been reported. Group size of these sightings ranged from 1 to 10 with a mean of 4,83 (±*SD* 3,04). Of three sighting records west of the mouth of the Gouritz River, the farthest west is off De Hoop (20°30′E). There are also another 57 specimen records of *S. plumbea* from the South and East coasts, the localities of which are plotted on Figure 13b. All sightings of *S. plumbea* were made in waters shallower than 50 m (Fig. 13b). The lack of dedicated shipboard sightings presumably reflects the fact that the vessels used for dedicated searches were too large to survey such shallow depths, as well as the

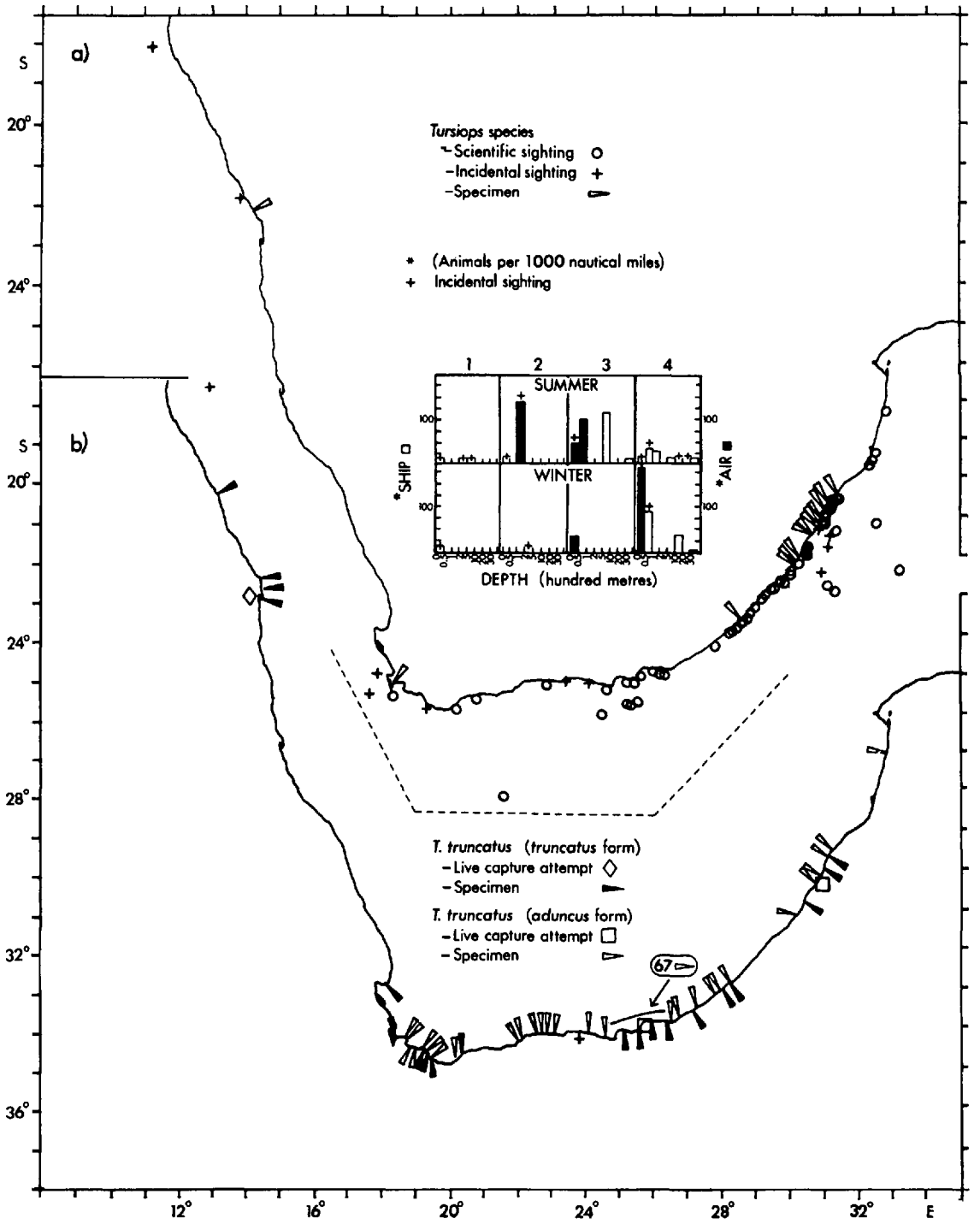

Fig. 14: Localities of (a) scientific and incidental sightings and specimens of *Tursiops* species and (b) catch attempts and specimens of the *tursiops* and *aduncus* forms of *Tursiops truncatus*. The inset shows densities of bottlenose dolphins sighted during scientific cruises and flights and the occurrence of incidental sightings, by depth interval in each area

vessel avoidance behaviour of the species. The distribution of *S. plumbea* is limited to nearshore waters in tropical, subtropical and warm temperate regions. Saayman *et al.* (1972) found that the occurrence of humpback dolphins in Plettenberg Bay was not affected by variation in sea surface temperature, because the species was present in the bay all year round.

BOTTLENOSE DOLPHINS, GENUS *TURSIOPS*

There is some doubt over the taxonomy of the genus *Tursiops*. Ross (1977) identified two species of *Tursiops* off the coast of southern Africa, *T. truncatus* and *T. aduncus*, and maintained that they existed allopatrically. However, he found no evidence of competitive exclusion. Ross (1984) stated that the smaller *T. aduncus* is widely distributed in Indian Ocean coastal waters, but he was uncertain of the western limit of its distribution. It has been found inshore along the south-eastern coast of South Africa, whereas the larger *T. truncatus* has been found offshore on the South and South-East coasts and inshore on the West Coast. Ross *et al.* (1987) found that all the *T. aduncus* sighted during an aerial census along the east coast of South Africa were inshore of the 50 m isobath, whereas during boat censuses in Algoa Bay, *T. aduncus* was rarely seen outside of the 40 m isobath. There is recent evidence to suggest that the two forms are not separate species, but should be referred to as forms of *Tursiops truncatus* (Ross and Cockcroft 1990); this approach has been followed in this study.

There were a total of 86 dedicated sightings of *T. truncatus* that could not be identified as to form (Fig. 14). Of these, 73 were confirmed sightings of a total of 2 434 animals, the mean group size being 33,34 (±*SD* 52,68). Excluding capture attempts for oceanaria (in which the form was identified), 23 incidental sightings of a total of 682 *T. truncatus* were made. Mean group size was 29,62 (±*SD* 36,43). Eight specimen records of bottlenose dolphins could not be identified to *truncatus* or *aduncus* forms. All these records were distributed throughout southern African waters (Fig. 14).

Tursiops truncatus, "truncatus" form — A total of 11 live capture attempts of the *truncatus* form was made in Walvis Bay in 1975, 1976 and 1983, and a further 39 records of specimens of this form can be identified. The distribution of these is shown in Figure 14. Records of this form are from 30°S on the East Coast to almost 33°S on the West Coast and then again in the vicinity of Cape Cross and Walvis Bay, Namibia (Fig. 14). Apart from an extreme inshore population occurring in the region of Walvis Bay and to the north at least as far as Cape Cross, it is assumed that the remainder of these records represent an offshore population, as described by Ross (1984) for the East Coast.

No scientific sightings of *Tursiops* were made during the largely inshore search effort along the West Coast, possibly because the survey vessels were too large to traverse the extreme inshore region. However, there are no incidental records inshore south of Walvis Bay either. Although there was a lack of offshore search effort, incidental sightings of *Tursiops* have been made offshore (on or outside the shelf-edge) on the West Coast, from about 17°S to west of Cape Point (Fig. 14a), frequently associated with schools of long-finned pilot or false killer whales. These animals may be contiguous (through one scientific sighting near the tip of the Agulhas Bank) with the population of this form occurring off the South-East Cape and Natal.

Differentiation between stranded individuals of the offshore and inshore populations of the *truncatus* form may be possible if differences in parasite infestation found in the inshore and offshore populations in the eastern U.S.A. (Mead and Potter 1990) and off Peru (Van Waerebeek *et al.* 1990) also apply to southern Africa.

Tursiops truncatus, "aduncus" form — In all, 20 capture attempts of the *aduncus* form were made, 17 from Algoa Bay and three from Durban (Fig. 14). A total of 26 published sightings of *T. aduncus* from the Tsitsikamma National Park (Saayman *et al.* 1972, original data supplied by D. Bower) is included as incidental sightings. School size of these sightings ranged from 1 to 1 500 with a mean for confirmed sightings of 76,2 (±*SD* 84,98). The "school" of 1 500 animals actually consisted of three groups, but no individual group sizes were noted and this group has not been included in the calculation of mean group size. The distribution of 267 specimen records of the *aduncus* form is shown in Figure 14. Ross (1984) stated that the western limit of this form's distribution is uncertain, because there are only three records west of Cape Agulhas. The sample size, however, is not much larger, and the westernmost record under review in this study is a stranding in False Bay (34°06′S, 18°48′E), with inshore sightings of *Tursiops* extending as far west as Gans Bay (34°35′S, 19°20′E).

Figure 14 reflects the distribution of scientific and incidental sightings of *Tursiops* species by depth and area. Marked neritic and pelagic densities are evident in Area 4, and comparison of the shipboard and aerial results in Area 3 show similar trends in neritic and pelagic peaks of occurrence. These would presumably correspond to the allopatric existence of the *truncatus* and *aduncus* forms of *Tursiops truncatus*.

To summarize, the distribution of the neritic *aduncus* form extends from the East Coast westwards as far as

False Bay, whereas the distribution of the neritic *truncatus* form appears to extend from Walvis Bay northwards. An offshore *truncatus* form occurs off the East Coast and may have a continuous offshore distribution around the whole coast, although the origin of stranded *truncatus* forms on the West Coast is unknown.

ROUGH-TOOTHED DOLPHIN *STENO BREDANENSIS*

Two confirmed specimen records of *S. bredanensis* are on record for southern Africa. The provenance of the first of these specimens was 1 km north of Sheffield Beach (29°28′S, 31°16′E; Ross *et al.* 1985), but the provenance of the second specimen, found in a collection at Möwe Bay, Namibia (19°20′S, 12°35′E) in 1986, is unknown but assumed (from the remote and relatively inaccessible nature of this site) to have been local. Ross *et al.* (op. cit.) note that, historically, a further three specimens were attributed to the Cape of Good Hope, but that two of these may have been collected elsewhere by a vessel *en route* to England via the Cape Colony and mistakenly "attributed" to South Africa, whereas the third has been re-identified as the "*aduncus*" form of *Tursiops truncatus* (Van Bree 1966). There have been no sightings of this species in South African or Namibian waters, and the single records from East and West coasts may represent individuals at the extreme southern limits of their range, the rough-toothed dolphin being generally considered a tropical and warm temperate species living in waters warmer than 25°C (Leatherwood and Reeves 1983).

DISCUSSION

Ekman (1967), noting the wide spectrum of zoogeographic components in southern African waters, stated that the faunistic patterns are complex as a result of the diverse oceanographic conditions. The mixing of the tropical and subtropical waters brought in from the east by the Agulhas Current with the cold temperate waters of the West Coast results in a strong longshore cline of surface water temperatures (descending from east to west). Christensen (1980) found marked changes in sea surface temperature off Cape Point, Cape Agulhas and Transkei and noted the important faunal discontinuities in these regions. Certain species of odontocete cetaceans are strongly confined to particular water masses and faunistic boundaries coincide with temperature fronts. Within the longshore temperature cline, the offshore distribution patterns of regional species are strongly associated with water depth, which may be a reflection of the distribution of prey items within the longshore distribution. The resident cetacean fauna of the region can be divided into species occurring in 11 different habitats, which may be defined by both water temperatures and depth (Fig. 15).

Cosmopolitan component (the entire study area in Fig. 15)

Orcinus orca (Fig. 7a) is the only species with a true cosmopolitan distribution in these waters. Although *Pseudorca crassidens* (Fig. 7b) and *Grampus griseus* (Fig. 9a) appear to have cosmopolitan patterns of distribution, they are largely confined to pelagic waters (although *G. griseus* also appears to be strongly associated with the shelf-edge). The distribution of sightings and strandings of *Mesoplodon layardii* (Fig. 6a) off both the West and East coasts suggest that it too has a pelagic cosmopolitan distribution, although the distribution of stranding records only confirms Ross' (1984) finding that the South-East Coast is the eastern limit of its distribution. It would seem from the specimen records that *Ziphius cavirostris* (Fig. 5b), *Feresa attenuata* (Fig. 8a) and *Kogia breviceps* (Fig. 4b) should be grouped as pelagic cosmopolitan, but the paucity of sightings makes confirmation of these distribution patterns difficult.

Two further species, *Delphinus delphis* (Fig. 9b) and *Tursiops truncatus* (Fig. 14), appear to be found throughout southern African waters, but because different forms (in the case of *Tursiops*) or possible forms (in the case of *Delphinus*) are found at different depths off the West, South and East coasts they cannot be considered truly cosmopolitan. *Delphinus delphis* occurs over the Agulhas Bank on the South Coast (inshore of the 500 m isobath) and in similar water depths on the East Coast, and the records of common dolphin off the continental shelf on both South and West coasts would suggest that an offshore population of this species does indeed occur in those waters. Further evidence of an offshore population of the species on the West Coast is implied from the records of strandings. Bottlenose dolphins are found both inshore (the *aduncus* form) and offshore (the *truncatus* form) off the East and South coasts. As far as their West Coast distribution is concerned, there is a strong indication that the *truncatus* form is distributed both offshore and in extremely localized nearshore waters in the region of Walvis Bay and to the north.

Ross and Cockcroft (1990) suggest that the larger *truncatus* form is found in cooler waters than the smaller *aduncus* form. These temperature associations are not apparent in the present data, because:

(i) the West Coast *truncatus* form was not recorded on dedicated surveys;
(ii) the East Coast *truncatus* form was found in

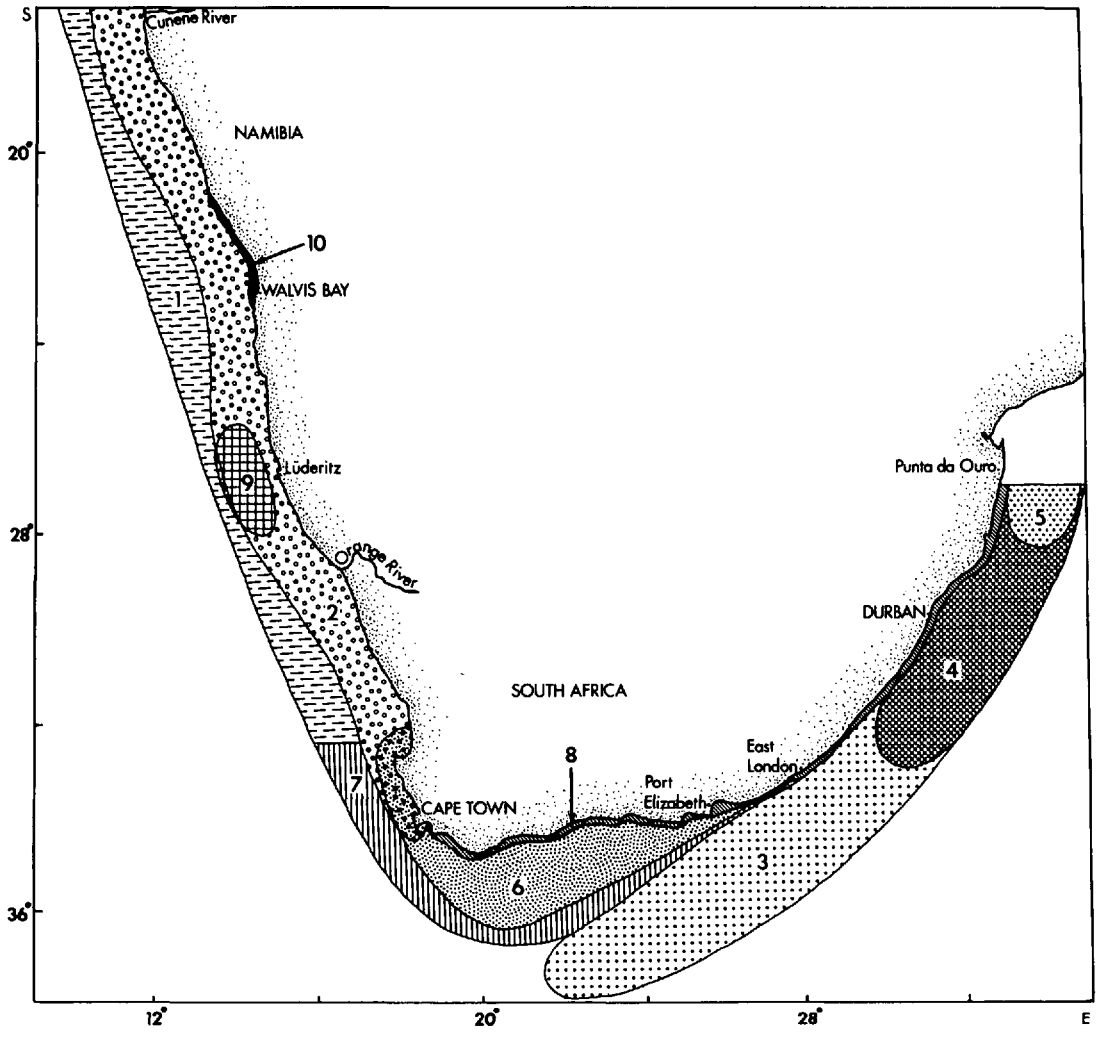

Fig. 15: Diagrammatic representation of the distribution patterns of small odontocetes in southern African waters (Numbers 1–10 are as defined in text)

deeper water than the *aduncus* form.

The analyses performed in this study were carried out with sea surface temperatures, but it is suggested by Ross and Cockcroft (1990) that, much of the time, the offshore *truncatus* form is utilizing deeper, cooler water, of a similar temperature range to that on the West Coast.

Species associated with the Agulhas Current (3, 4, 5, 8 on Fig. 15)

The northernmost species associated with the Agulhas Current is *Stenella longirostris*, which has been sighted inshore off the coast of northern Natal, although the data are too few to define a distribution pattern (apart from a possible southern boundary) or to comment on seasonality within the study area. The species has been recorded from the tropical Indian Ocean (Howell and Pearson 1977), and its occurrence off northern Natal is possibly linked to the tropical component of the Agulhas Current. The one specimen of the tropical *Steno bredanensis* from the northern Natal coast would suggest that the region may also represent the extreme southern limit of that species' distribution in the western Indian Ocean.

Smith (1965) stated that the southern limit of the subtropical fish and invertebrate fauna on the East Coast was in the region of the mouth of the Great Kei River (32°45'S, 28°30'E), whereas Ekman (1967) found that Algoa Bay represented a region of disconti-

nuity of the inshore fauna, presumably caused by the Agulhas Current's movement offshore there. Two of the pelagic cetacean species associated with the Agulhas Current *Lagenodelphis hosei* (Fig. 10b) and *Stenella attenuata* (Fig. 11b), are confined to the east of this region, whereas two others (*Hyperoodon planifrons* plus "bottlenose-like whales" — Fig. 5b, and *Stenella coeruleoalba* — Fig. 12) also tolerate the more temperate Agulhas Current conditions to the south of the subcontinent. The western limit (from sightings) of these last two species is defined by the eastern shelf-edge of the Agulhas Bank (which in itself plays an important role in defining the path of the Agulhas Current). Two other pelagic species, *Mesoplodon densirostris* (Fig. 6a) and *Globicephala macrorhynchus* (Fig. 8b) are recorded from the East and South coasts as strandings. Sightings of both these species have only been recorded to genus level, and distribution patterns are difficult to define. It is possible that, as a result of the prevailing currents of the South Coast, strandings of these species have occurred to the west of their normal range.

Gaskin (1982) states that continental Africa has functioned as a barrier to some warm-water cetacean species, and the extent of this barrier has depended on their varying abilities to penetrate the cool waters off the Southern Cape. Certain pan-tropical genera have penetrated this barrier and have both Atlantic and Indo-Pacific distributions; they include *Sousa, Feresa, Steno, Peponocephala, Lagenodelphis* and *Stenella*. Perrin *et al.* (1978) have suggested that the high diversity of *Stenella* species in the Atlantic Ocean has resulted from the Cape acting as a "variable one way filter" in the movement of *Stenella* into the Atlantic Ocean. Strandings of both *Stenella attenuata* (Fig. 11b) and *S. coeruleoalba* (Fig. 12) recorded herein and of *H. planifrons* subsequent to June 1986 suggest that these species may have been able to move around the Cape Peninsula in cells of Agulhas Current water moving into the Benguela system.

Three species are found inshore of the Agulhas Current on the East Coast. Both *Tursiops truncatus* (*aduncus* form) and *Sousa plumbea* (Fig. 13b) are found from the coast of northern Natal to the South Coast west of Cape Agulhas. *D. delphis* may move into Natal inshore waters from the south following the annual winter sardine run (Ross 1984).

The warm temperate component of the South Coast (6 and 7 on Fig. 15)

Both Ekman (1967) and Stephenson (1948) define the South Coast as a warm temperate region, and Ekman notes that inshore waters are cooler than the more offshore Agulhas Current. He therefore defines the region as an independent zoogeographical province. Ross (1984) maintains that cool waters intrude westwards inshore of the Agulhas Current on the South Coast. The Algoa Bay region does not determine the western boundaries of the East Coast neritic species *Sousa plumbea* and the *aduncus* form of *T. truncatus* (Fig. 14). Ross (1984) also suggests that this is due to the presence of sheltered shallow bays along the South Coast, which provide warm water in extreme proximity to the coast where these two species are found. However, the region does appear to determine the eastern limit of three groups.

(i) The South Coast neritic form of *Delphinus delphis*, which apart from some winter movement into Natal, is largely confined to the west of the Algoa Bay faunal discontinuity.

(ii) A group of pelagic species (recorded from strandings only), including *Mesoplodon mirus* (Fig. 6b), *Berardius arnuxii* and *Kogia simus* (Fig. 5a), distributed from about Cape Columbine to the Eastern Cape. Ross (1984) maintains that both *K. simus* and *M. mirus* are closely associated with regions of highly mixed waters and notes that Moore (1966) suggests an association between *M. mirus* and the deeper waters of the continental shelf of the eastern seaboard of the U.S.A. However, Ross (op. cit.) argues that *M. mirus* is an oceanic species and therefore probably not associated with the Agulhas Bank and that it appears to be confined to the area of overlap between *M. densirostris* and *M. layardii* (Fig. 6a). Ross (1979) suggested some association between the Agulhas Bank and the distribution of *K. simus*, and later suggested (Ross 1984) that the continental shelf is utilized as a nursery area by *K. simus*. The longshore distribution of strandings of *K. breviceps* overlaps that of *K. simus*, and unless the two species are confined to water of different depths, they must be considered sympatric within the range of *K. simus*.

(iii) A second group of pelagic species which appears to tolerate the cooler waters between Namibia and the Eastern Cape, where they intrude eastwards inshore of the Agulhas Current, includes *Globicephala melas* (Fig. 8b) and *Mesoplodon grayi* (Fig. 6b). Ross (1984) states that the South Coast distribution of *Mesoplodon layardii* is associated with cool water inshore of the Agulhas Current. The results of the present study, however, have demonstrated incidental sightings from the East Coast, so that this species is not included in this grouping.

The inshore West Coast (2, 9 and 10 on Fig. 15)

Ekman (1967) suggests that the Cape of Good Hope

(1 km west of Cape Point) forms a boundary between two temperate regions, and the distribution patterns of the neritic cetaceans do indeed show a faunal discontinuity in the region of the Cape Peninsula. Two neritic species, *Lagenorhynchus obscurus* (Fig. 10a) and *Cephalorhynchus heavisidii* (Fig. 11a), are associated with the cold temperate waters of the West Coast and have not been recorded east of False Bay and Cape Point respectively. Conversely, *Sousa plumbea* and the *aduncus* form of *Tursiops truncatus* have not been recorded farther west than strandings in False Bay, at Muizenberg (34°07′S, 18°28′E) and The Strand (34°16′S, 18°48′E) respectively. (The definition of the western limit of the distribution range of *Sousa plumbea* from this stranding, however, must be regarded with caution because there are no recent records west of Cape Agulhas.)

The inshore distribution of *Delphinus delphis* does not extend much farther north than about 32°S on the West Coast (although there are offshore records of this species farther north). Surprisingly, the inshore distribution of *D. delphis* does overlap the upwelling cells off the Cape Peninsula and Cape Columbine, where sea surface temperatures would be lower than the 14°C lower tolerance level suggested by Gaskin (1968). The longshore distribution pattern of *Cephalorhynchus heavisidii* (in the cool temperate inshore waters of the West Coast) corresponds to Ekman's (1967) "Namaqua zone" between Cape Point and 18°S, whereas *Lagenorhynchus obscurus* tolerates slightly warmer and deeper water, and has been recorded as far north as 12°S. The extreme nearshore distribution of the *truncatus* form of bottlenose dolphins (Fig. 14) off the West Coast appears to be confined to the vicinity of Walvis Bay and farther north, one nearshore incidental sighting at Cape Cross having been reported. There have been no dedicated sightings of this nearshore population, but probably this is due to the lack of search effort there, the water depth being too shallow for the survey vessels. The extremely localized occurrence of *Lissodelphis peronii* off Lüderitz (Fig. 13a and Component 9 on Fig. 15) is associated with the shelf-edge and possibly with the Lüderitz upwelling cell. The rarity of sightings from South African waters suggests that the population is resident off Namibia. The fact that the majority of sightings of this species were made in summer must be regarded with caution because all sightings were incidental and may reflect seasonality of the search effort in the region.

The offshore West Coast (1 on Fig. 15)

The offshore distributions of cetaceans on the West Coast are difficult to define because of the lack of search effort off the shelf (in a number of cases they are inferred from strandings, the lack of sightings over the shelf and the pelagic habits of these species off other coasts). Such species include the pelagic cosmopolitan species *Globicephala melas*, *Mesoplodon grayi* (both recorded between Namibia and the Eastern Cape) and the pelagic form of the common dolphin.

The distribution of *Tursiops truncatus* (*truncatus* form) in pelagic waters of the West Coast is uncertain. The occurrence of this form in extreme nearshore waters of the northern West Coast has been noted, and all strandings in the region have been attributed to the *truncatus* form. However, it is not known if the stranding records originate from the nearshore population or from an offshore population indicated by incidental sightings.

The record of *Steno bredanensis* on the West Coast probably arises from a population north of Namibia in tropical waters of the eastern Atlantic. Unfortunately, little data are available as to the distribution of small cetaceans off Angola and farther north.

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