

## FEEDING HABITS AND POSSIBLE MOVEMENTS OF SOUTHERN BOTTLENOSE WHALES (*HYPEROODON PLANIFRONS*)

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**Abstract:** Stomach contents of two southern bottlenose whales (*Hyperoodon planifrons*) were examined in detail; a 6.43 m male caught off the east coast, and a 6.55 m lactating female stranded alive on the west coast of South Africa. Both stomachs contained only squid remains. All lower squid beaks were counted (1995 in the male, 1912 in the female), each beak was identified, and the original dorsal mantle length and weight were calculated. A total of 36 species in 14 families of squids was identified, all of which were oceanic species. Four Antarctic squids (*Kondakovia longimana*, *Galiteuthis glacialis*, *Alluroteuthis antarcticus* and *Mesonychoteuthis hamiltoni*) and four subantarctic species (*Gonatus antarcticus*, *Moroteuthis knipovitchi*, *Moroteuthis ingens* and *Histioteuthis eltaninae*) were present. In weight percentage, the stranded female had more Antarctic and subantarctic squids in its stomach (72.4%) than the captured male (43.7%), but by number both animals contained similar percentages (28.1% for the female and 29.2% for the male). The rest of the squid species found in the stomachs may occur in South African waters. Sightings of southern bottlenose whales off Durban between February and October showed strong seasonality with peaks in February and October. The beaks of Antarctic and subantarctic squids in the stomachs, plus the presence of cold water skin diatoms *Bennettella* [= *Cocconeis*] *ceticola* on the male, suggest that the animals had arrived comparatively recently in South African waters from higher latitudes. Therefore, the February peak in sightings might represent a northward movement of southern bottlenose whales from the Antarctic.

### 1. Introduction

Southern bottlenose whales (*Hyperoodon planifrons*) are distributed in the Southern Hemisphere between Antarctica and about 20°S (LEATHERWOOD and REEVES, 1983). They are believed to be the second most frequently encountered cetacean in high latitudes of the Southern Ocean, and thus may play an important role in the Antarctic marine ecosystem (F. KASAMATSU, private com.).

Relatively little is known about the biology of southern bottlenose whales, compared to northern bottlenose whales (*Hyperoodon ampullatus*). In the North Atlantic bottlenose whales are distributed in deep water in cold temperate to arctic seas (LEATHERWOOD and REEVES, 1983). Their main diet is squid, primarily *Gonatus fabricii* (BENJAMINSEN and CHRISTENSEN, 1979; CLARKE and KRISTENSEN, 1980), but some fish, such as herring (*Clupea harengus*) and redfish (*Sebastes* sp.), were also found in

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their stomachs (BENJAMINSEN and CHRISTENSEN, 1979). Many researchers suggested that northern bottlenose whales fed near the bottom because their stomachs sometimes contained bottom-dwelling animals, stones and clay (BENJAMINSEN and CHRISTENSEN, 1979).

Northern bottlenose whales are deep divers and sometimes submerge for more than one hour (OHLIN, 1893 reviewed by MEAD, 1989; BENJAMINSEN and CHRISTENSEN, 1979), presumably when foraging. F. KASAMATSU (private com.) described the diving patterns of southern bottlenose whales in the Antarctic. Their submergence times ranged from 11–46 min with an average of 25.3 min.

However, the feeding habits of southern bottlenose whales are poorly known. HALE (1931) found a large number of cephalopod beaks in a stranded animal in Australia, but he only guessed that they might be "*Polypus variolatus*" because of their large size. FRASER (1947) reported cephalopod lenses from the stomach of a male caught near South Georgia. Squid remains (soft parts, lenses and beaks) were found in the stomachs of three animals caught between 45 and 58°S (ZEMSKII and BUDYLENKO, 1970), and a stranded male in New Zealand contained 200 squid beaks (BAKER, 1983). CLARKE (1986a) identified squid beaks from the stomach of an animal stranded in Tierra del Fuego, but only to family level. The main prey items were Cranchiidae (66.8% by number), Neoteuthidae (16.2%) and Enopteuthidae (8.8%).

Northern bottlenose whales have a north-south migratory pattern, and are distributed in higher latitudes in summer (LEATHERWOOD and REEVES, 1983). A whale stranded on the Faroe Islands had a beak of the warm water squid *Vampyroteuthis infernalis* in the stomach, which indicated migration from at least 1000 km further south (CLARKE and KRISTENSEN, 1980). ROSS (1984) described the seasonal occurrence (summer months) of southern bottlenose whales in South African waters, and noted that there are insufficient records from elsewhere to determine their migration patterns.

In this study, stomach contents of two southern bottlenose whales are examined in detail, and records of the aerial sightings of cetaceans off Durban are analyzed to examine the seasonal occurrence of this species in South African waters. From a combination of these results, a possible migration pattern for southern bottlenose whales is described.

## 2. Materials and Methods

The first stomach was from a 6.43 m male (ZM37146) caught off East London on the east coast of South Africa (33°36'S, 28°06'E) on 19 January 1975. The second was from a 6.55 m lactating female (ZM40855) stranded alive at St Helena Bay on the west coast of South Africa (32°47'S, 18°08'E) on 10 January 1990 (Fig. 1).

Stomachs were ligatured at the oesophageal and duodenal ends at collection, and kept in a freezer until analysis later in a laboratory. After thawing and trimming off the spleen and membranes, each stomach was weighed intact. After opening, all contents of each compartment were sorted, weighed and recorded. Cephalopod mandibles ("beaks") were kept separately in ethanol until counting and identification by one of the authors (N.K.). Enumeration and identification were based on the lower beaks. Beaks were identified to the lowest possible taxon by comparison with material held in

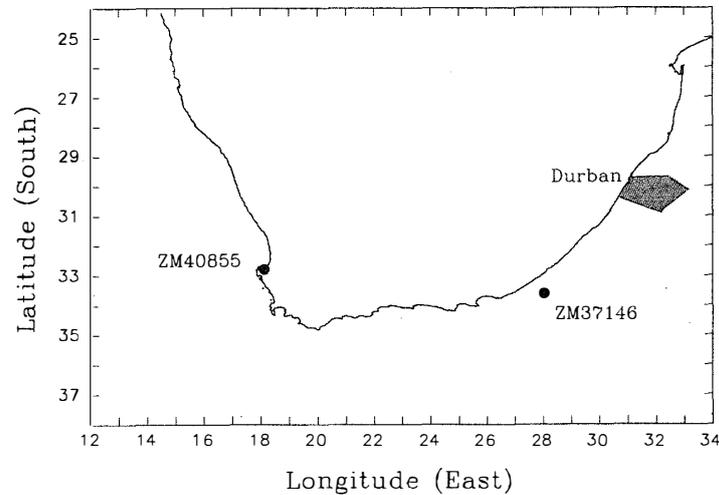


Fig. 1. Map of southern Africa, showing the locations where two specimens of southern bottlenose whales were collected and the shaded area off Durban corresponding to the east coast whaling ground.

the reference collections of the Port Elizabeth Museum and by use of CLARKE (1986b). Lower rostral lengths (LRL) (CLARKE, 1962) of the beaks were measured to the nearest 0.1 mm using Vernier calipers. Regressions (CLARKE, 1986b; RODHOUSE *et al.*, 1990; Port Elizabeth Museum unpublished data) were used to estimate dorsal mantle lengths (DML) and weights of cephalopods from LRL. Because no reliable weight data is available for *Mesonychoteuthis hamiltoni*, we used the generalised regression “(curve  $x$ )” from CLARKE (1962) to estimate weights for this species from LRL values. However, these estimated weights are not accurate, since the coefficients of this regression have very wide confidence limits.

When not all squid beaks could be measured, the total weight of a prey item in the stomach was calculated from the average weight of those whose beaks were measured, multiplied by the number of lower beaks present. In most cases the average weights were calculated for the same prey species in the same stomach, but for some prey species there were no regressions relating beak lengths to weight data available. For Cranchiidae species (other than *Mesonychoteuthis hamiltoni*) and *Discoteuthis* sp, the average weights were calculated for other species in the same family present in the stomachs (107.4 g and 66.5 g respectively). Because the few beaks available for *Ancistrocheirus lesueuri* were damaged and could not be measured, the average weight of the same prey in similar sized species of Odontoceti (766.0 g) was used instead.

Records of cetacean sightings were made from the spotter aircraft (a Cessna 310) working for the Union Whaling Company in the east coast whaling ground off Durban (Fig. 1). Between 1972 and 1975, 628 daily flights were made, representing about 430000 nautical miles searched off the Natal coast between the months of February and October inclusive. The altitude and speed of the aircraft were usually 500 feet and 135 knots respectively, although these were weather dependent. The crew usually consisted of a pilot and one spotter. Positions of sightings were fixed by radio beacon as bearings and distances from Durban harbour. The flight paths and species, number

and position of each sighting were entered into a data retrieval file for each flight undertaken. Flight paths were entered from the daily chart as a startpoint, waypoints and an endpoint for each flight, while the positions of the sightings were entered from a separate diary log as bearings and distances from Durban harbour.

Positions of sightings were converted from bearings and distances to latitudes and longitudes. Because of the imprecise navigational positions, effort and sightings were analysed per 10 min square of latitude and longitude. Densities were calculated on an "encounter-rate" basis (as the number of whales seen per nautical mile searched).

The distribution of cephalopods follows ROPER *et al.* (1984), FISCHER and HUREAU (1985), RODHOUSE and CLARKE (1986), and KUBODERA (1989). Cephalopod prey species are categorized into four areas; Antarctic (species occur south of the Antarctic Convergence), subantarctic (south of the Subtropical Convergence), temperate-tropical (north of the Subtropical Convergence), and cosmopolitan (species widespread).

### 3. Results

#### 3.1. Stomach content analysis

The weight of the total stomach contents was 1.2 kg for the male and 3.0 kg for the female. Both stomachs contained squid beaks, squid pens and eyes. The female also contained 48.2 g of nematodes, and some sand which was possibly ingested at stranding.

A total of 1995 squid lower beaks was counted from the male's stomach, and 1912 squid lower beaks from the female. Among them, 21 beaks from the male and 290 beaks from the female were unidentified. All identified squids (36 species in 14 families) were oceanic species (Table 1). The stomach of the female contained more prey species (29) than the male (23).

Four Antarctic squids (*Kondakovia longimana*, *Galiteuthis glacialis*, *Alluroteuthis antarcticus* and *Mesonychoteuthis hamiltoni*) and four subantarctic species (*Gonatus antarcticus*, *Moroteuthis knipovitchi*, *Moroteuthis ingens* and *Histioteuthis eltaninae*) were found, although *K. longimana* and *M. ingens* were only present in the female's stomach (Fig. 2). In percentage by weight, the stranded female had more Antarctic and subantarctic squids in its stomach (72.4%) than the captured male (43.7%), but by number both animals contained similar percentages (28.1% for the female and 29.2% for the male).

The rest of the squid species found in the stomachs occur in South African waters. Of these species, *Histioteuthis meleagroteuthis* was the most important numerically for the male (20.1%) and comprised 10.2% by weight, but it did not occur in the female. *Histioteuthis* sp. was the most important species by number and *Taonius pavo* was the most important by weight for the female (23.7% and 6.5% respectively) (Fig. 2).

*Teuthowenia megalops* was contained in the stomach of the female in relatively high percentages (9.9% by number and 3.0% by weight), but was not present in the male. *Onychoteuthis* spp. were also only found in the stomach of the female (1.1% by number and 2.5% by weight). There were some other prey species not present in both animals; but their percentages by either number or weight were less than one, so that they seemed to be relatively minor items in the diet.

Table 1. The list of prey species eaten by two bottlenose whales (*Hyperoodon planifrons*), the numerical percentages (N%) of each species in the total number of identified lower beaks, and their average sizes (with standard deviations) estimated from lower beak sizes.

| Prey   |                  | N%                |                     | Average size |       |               |         |
|--|------------------|-------------------|---------------------|--------------|-------|---------------|---------|
| Species                                      | Family           | ZM37146<br>(Male) | ZM40855<br>(Female) | DML<br>(cm)  | s.d.  | Weight<br>(g) | s.d.    |
| <i>Bathyteuthis abyssicola</i>               | Bathyteuthidae   |                   | 0.25                | 7.33         | 4.61  | 119.83        | 140.83  |
| <i>Chiroteuthis</i> sp.                      | Chiroteuthidae   | 17.63             | 2.47                | 10.61        | 1.34  | 31.89         | 14.29   |
| <i>Galiteuthis glacialis</i>                 | Cranchiidae      | 11.04             | 10.85               | 19.25        | 1.75  | 68.07         | 15.02   |
| <i>Liocranchia reinhardti</i>                | Cranchiidae      |                   | 0.55                | 24.90        | 3.33  | 81.14         | 22.51   |
| <i>Liocranchia</i> sp.                       | Cranchiidae      | 0.10              |                     | 36.01        | 21.15 | 225.75        | 242.47  |
| <i>Megalocranchia</i> sp.                    | Cranchiidae      | 0.61              | 4.01                | 19.65        | 5.98  | 42.17         | 31.55   |
| <i>Mesonychoteuthis hamiltoni</i>            | Cranchiidae      | 0.81              | 3.02                | 69.58        | 25.78 | 4080.72       | 3641.88 |
| <i>Taonius megalops</i>                      | Cranchiidae      | 0.10              |                     | 40.55        | 4.92  | 148.70        | 37.70   |
| <i>Taonius pavo</i>                          | Cranchiidae      | 14.29             | 20.47               | 34.91        | 8.27  | 113.73        | 5.84    |
| <i>Teuthowenia megalops</i>                  | Cranchiidae      |                   | 9.86                | 22.17        | 4.66  | 102.76        | 56.47   |
| <i>Teuthowenia pellucida</i>                 | Cranchiidae      | 0.41              |                     | 18.55        | 1.25  | 61.61         | 10.39   |
| Cranchiidae sp.                              | Cranchiidae      | 3.60              |                     | –            | –     | –             | –       |
| <i>Discoteuthis discus</i>                   | Cycloteuthidae   |                   | 3.70                | 10.33        | 0.85  | 66.48         | 16.53   |
| <i>Discoteuthis</i> sp.                      | Cycloteuthidae   | 0.10              |                     | –            | –     | –             | –       |
| <i>Cycloteuthis</i> sp.                      | Cycloteuthidae   |                   | 0.12                | 46.19        | 1.32  | 1284.40       | 71.28   |
| <i>Ancistrocheirus lesueuri</i>              | Enoploteuthidae  |                   | 0.06                | –            | –     | –             | –       |
| Enoploteuthidae sp.                          | Enoploteuthidae  |                   | 0.06                | 5.01         | –     | 4.50          | –       |
| <i>Gonatus antarcticus</i>                   | Gonatidae        | 9.57              | 7.09                | 25.32        | 5.93  | 256.04        | 127.27  |
| Gonatidae sp.                                | Gonatidae        | 0.15              |                     | 23.63        | 3.86  | 99.42         | 47.23   |
| <i>Histioteuthis bonellii corpusculata</i>   | Histioteuthidae  | 0.30              |                     | 4.90         | 0.73  | 54.77         | 13.46   |
| <i>Histioteuthis eltaninae</i>               | Histioteuthidae  | 5.37              | 1.60                | 5.90         | 0.90  | 77.69         | 22.12   |
| <i>Histioteuthis macrohista</i>              | Histioteuthidae  | 0.41              |                     | 4.42         | 0.77  | 45.80         | 13.98   |
| <i>Histioteuthis meleagroteuthis</i>         | Histioteuthidae  | 20.11             |                     | 5.49         | 0.73  | 67.53         | 16.29   |
| <i>Histioteuthis</i> sp.                     | Histioteuthidae  | 6.18              | 23.68               | 5.40         | 1.71  | 70.77         | 48.45   |
| <i>Pholidoteuthis boschmai</i>               | Lepidoteuthidae  | 0.05              | 0.37                | 29.60        | 2.51  | 646.11        | 159.52  |
| <i>Lycoteuthis diadema</i>                   | Lycoteuthidae    |                   | 0.06                | 8.53         | –     | 29.64         | –       |
| <i>Mastigoteuthis</i> sp.                    | Mastigoteuthidae |                   | 1.23                | 10.79        | 1.48  | 57.29         | 20.70   |
| <i>Alluroteuthis antarcticus</i>             | Neoteuthidae     | 1.57              | 0.49                | 40.13        | 14.06 | 417.54        | 140.58  |
| <i>Octopoteuthis rugosa</i>                  | Octopoteuthidae  |                   | 1.05                | 15.02        | 2.20  | 179.58        | 59.26   |
| <i>Octopoteuthis</i> sp.                     | Octopoteuthidae  | 0.41              |                     | 16.64        | 2.34  | 226.39        | 6.92    |
| <i>Taningia danae</i>                        | Octopoteuthidae  | 1.37              | 0.55                | 18.92        | 13.04 | 825.03        | 816.67  |
| <i>Todarodes sagittatus</i>                  | Ommastrephidae   |                   | 0.06                | 39.82        | –     | 1437.80       | –       |
| <i>Todaropsis eblanae</i>                    | Ommastrephidae   | 0.05              |                     | 7.14         | –     | 20.90         | –       |
| <i>Kondakovia longimana</i>                  | Onychoteuthidae  |                   | 3.64                | 46.94        | 6.95  | 2568.70       | 1034.71 |
| <i>Moroteuthis ingens</i>                    | Onychoteuthidae  |                   | 0.31                | 70.36        | 5.02  | 3756.56       | 621.27  |
| <i>Moroteuthis knipovitchi</i>               | Onychoteuthidae  | 0.86              | 1.05                | 22.10        | 3.49  | 386.45        | 115.90  |
| <i>Moroteuthis robsoni</i>                   | Onychoteuthidae  | 1.42              | 1.97                | 20.71        | 8.36  | 48.05         | 35.67   |
| <i>Moroteuthis</i> sp.                       | Onychoteuthidae  | 3.50              | 0.31                | 22.42        | 4.42  | 410.96        | 154.57  |
| <i>Onychoteuthis banksi</i>                  | Onychoteuthidae  |                   | 0.49                | 21.36        | 9.73  | 502.90        | 500.10  |
| <i>Onychoteuthis</i> sp.                     | Onychoteuthidae  |                   | 0.62                | 29.26        | 5.24  | 936.80        | 534.96  |
| Total number of identified squid lower beaks |                  | 1974              | 1622                |              |       |               |         |
| Unidentified squid lower beaks               |                  | 21                | 290                 | –            | –     | –             | –       |

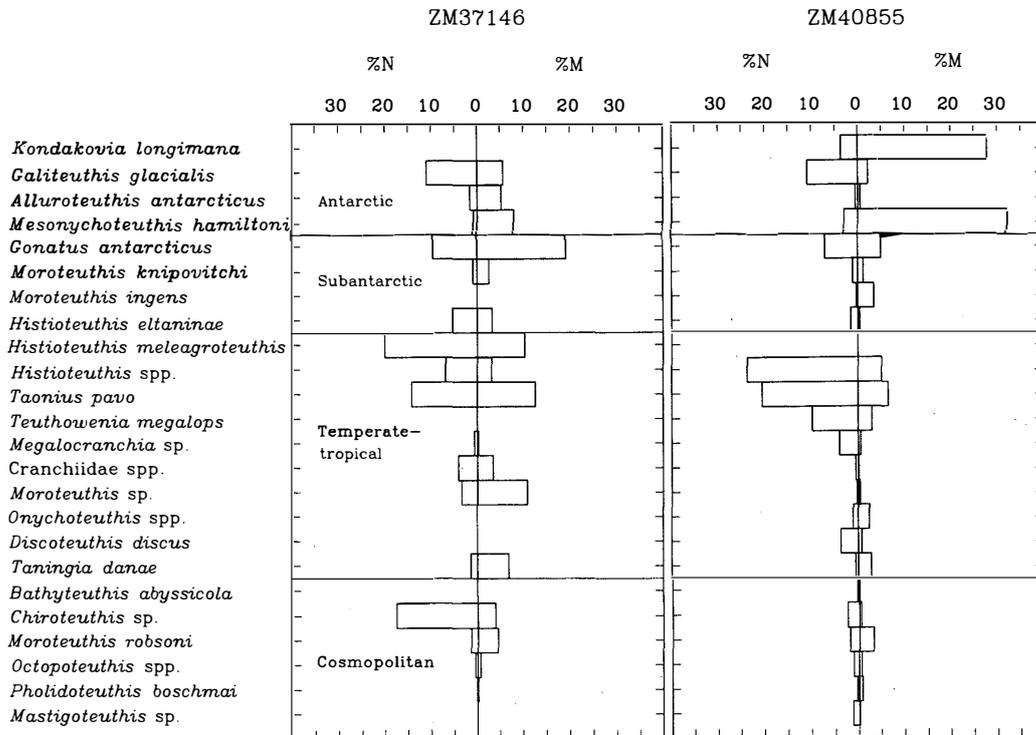


Fig. 2. The percentage compositions (by both number and weight) of prey items taken by two southern bottlenose whales; ZM37146 (male) and ZM40855 (female). *Histiototeuthis* spp. includes *H. bonellii* corpusculata and *H. macrohista*; *Cranchiidae* spp. includes *Licranchia* spp., *Taonius megalops* and *Teuthowenia pellucida*; *Onychoteuthis* spp. includes *O. banksi*; *Octopoteuthis* spp. includes *O. rugosa*. Other prey species that comprised less than 1% of those eaten are not shown. Unidentified squid beaks were omitted from the calculation.

Table 1 shows the mean estimated DML and weight of each prey species found in the stomachs. The range of the mean DML was between 4.4 and 70.4 cm, and of the mean weight was between 4.5 and 4080.7 g. Although the estimated weights of *Mesonychoteuthis hamiltoni* are not as reliable as for the other species, this squid was the largest individual prey item eaten by both the male (5350.1 g, 85.4 cm DML) and the female (13842.3 g, 120.4 cm DML). The average weight of this squid species was large (4080.7 g), so that its percentages in the diet were low by number but high by weight (Fig. 2). Other Antarctic and subantarctic squids, except *Galiteuthis glacialis* and *Histiototeuthis eltaninae*, also had relatively large average weights (2568.7 g for *Kondakovia longimana*, 417.5 g for *Alluroteuthis antarcticus*, 256.0 g for *Gonatus antarcticus*, 386.5 g for *Moroteuthis knipovitchi*, and 3756.6 g for *Moroteuthis ingens*).

However, most of the prey items eaten by both whales were rather small (Fig. 3). Prey items weighing less than 100 g comprised 66.6% of the total number of measured prey for the male (n=1683), and 65.8% for the female (n=1203). Squids weighing more than 1000 g comprised only 0.7% of the diet by number for the male and 7.5% for the female.

Figure 4 shows the frequency distributions of weight for the major prey items.

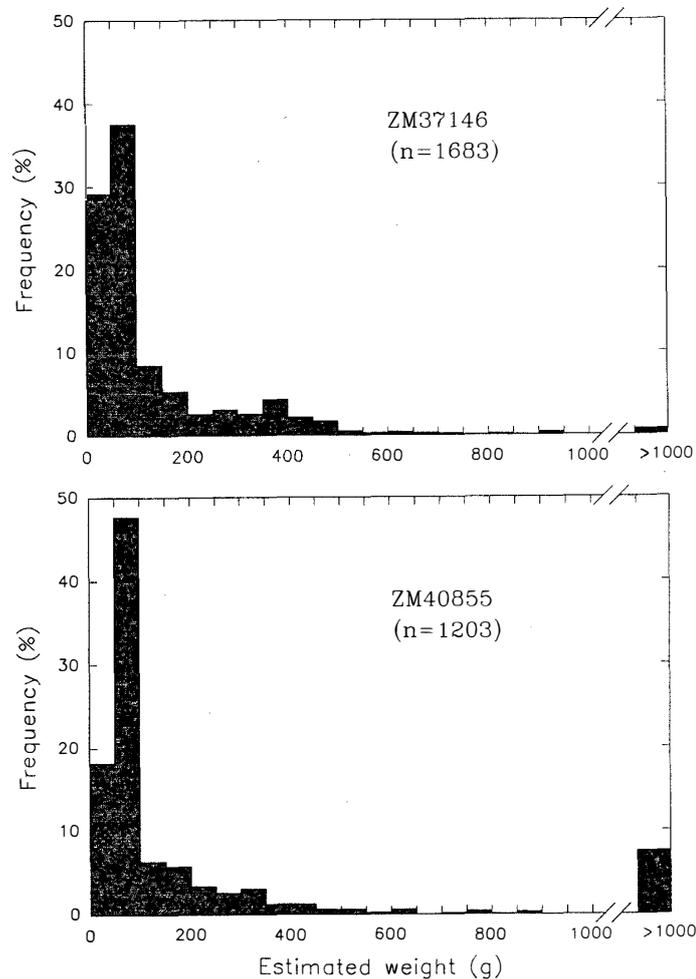


Fig. 3. The distributions of estimated weights of identified squids eaten by two southern bottlenose whales; ZM37146 and ZM40855. The total number of identified and measured lower squid beaks ( $n$ ) is shown in the figure.

Both the captured male and the stranded lactating female consumed similar-sized individuals of each prey species eaten except *Mesonychoteuthis hamiltoni*. Both whales tended to take smaller size classes of a prey species. The frequency distributions of weight for *Kondakovia longimana*, *M. hamiltoni* and *Gonatus antarcticus* were different from those of the other prey, and had wider ranges (359.3 to 5289.2 g for *K. longimana*, 91.7 to 13842.3 g for *M. hamiltoni* and 6.1 to 672.1 g for *G. antarcticus*).

Among these major prey items (Fig. 4), some of the individuals eaten were probably larger juvenile and smaller mature squids. The nidamental gland of *Kondakovia longimana* shows rapid growth at 50 cm DML (about 3000 g) (CLARKE, 1980), and 24.4% of the total number of *K. longimana* eaten by the female southern bottlenose whale were over 3000 g in weight, and so probably mature. *Taonius pavo* with lower rostral lengths of more than 0.5 cm were "mature" (CLARKE and KRISTENSEN, 1980), corresponding to about 74.5 g in weight. *T. pavo* weighing more than 74.5 g composed 83.3% of the total number of this species eaten by the male and 39.0% by the female.

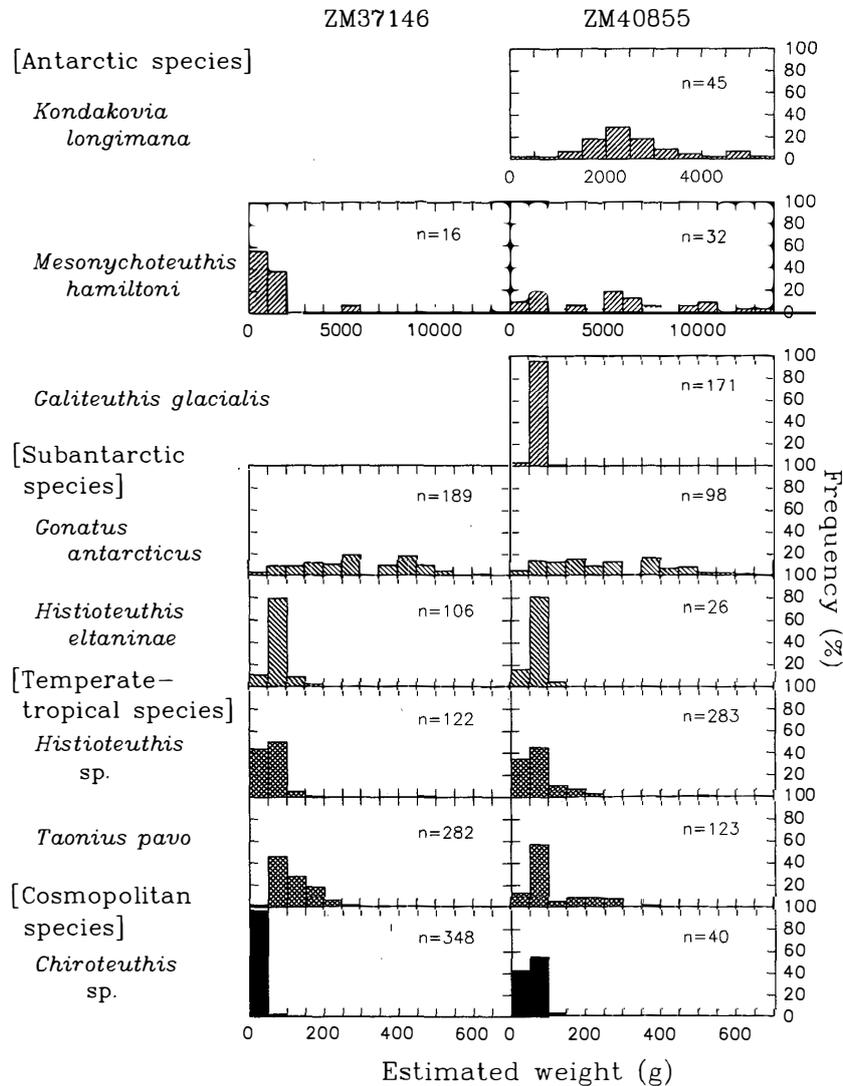


Fig. 4. The distributions of estimated weights of eight major prey species eaten by two southern bottlenose whales; ZM37146 and ZM40855. The total number of identified and measured lower squid beaks (n) for each species is shown in each figure.

A *Mesonychoteuthis hamiltoni* of 117 cm DML taken at 2000–2200 m depth was a mature female (RODHOUSE and CLARKE, 1985). FISCHER and HUREAU (1985) stated that the mantle size of mature individuals was over 100 cm, corresponding to a weight of 25 to 30 kg. The maximum size of *M. hamiltoni* eaten by southern bottlenose whales was estimated as 120.4 cm DML and 13842.3 g weight, so it could be mature. *M. hamiltoni* with a DML of more than 100 cm comprised 21.9% of the total number of this species eaten by the female.

*Gonatus antarcticus* and *Histioteuthis eltaninae* preyed upon by southern bottlenose whales included some individuals with DML's up to 39.9 cm and 7.1 cm, respectively, estimated from beaks. Although size at maturity in these species is unknown, these maximum DML's slightly exceed the size of the largest whole specimens in scientific collections (35 cm and 6.6 cm) (FISCHER and HUREAU, 1985).

*Galiteuthis glacialis* of 255 mm DML caught at 1000–1205 m depth were immature (RODHOUSE and CLARKE, 1986). The maximum estimated DML for this species eaten by two southern bottlenose whales was 236.5 mm; so it is assumed that most of the squid of this species eaten were immature.

### 3.2. Aerial sightings

One hundred and thirty eight sightings of a total of 584 “like-bottlenose whales” were recorded by aerial spotters off Durban between 1972 and 1975. Group size of these sightings ranged between one and 12 animals with a mean of 4.34 animals (s.d.  $\pm 2.28$ ). The abundance of sightings off Durban imply a marked seasonality between October and February (Fig. 5), although the lack of data for the summer months makes it unclear whether there is one or more peaks. All of these sightings in the east coast whaling ground were in water depths of over 500 m and mostly over 1000 m. The highest densities were recorded in water of 3000 m or deeper (Fig. 6). Although it was not possible to identify animals positively from the air, they had the same characteristic appearance, and the specimen ZM37146 was specially taken to confirm species identity.

## 4. Discussion

Southern bottlenose whales appear to be oceanic squid feeders, with a definite off-shore distribution in deep water in the east coast whaling ground (Fig. 6). Although there is no direct evidence to show at what depths they feed, the maturity of prey squids found in the stomachs may suggest the feeding depth of this whale species. RODHOUSE and CLARKE (1985) caught adult *Mesonychoteuthis hamiltoni* in deeper water than young ones.

The two stomachs contained some squids of the same families that were found in the stomach from Tierra del Fuego (CLARKE, 1986a). For the Tierra del Fuego whale,

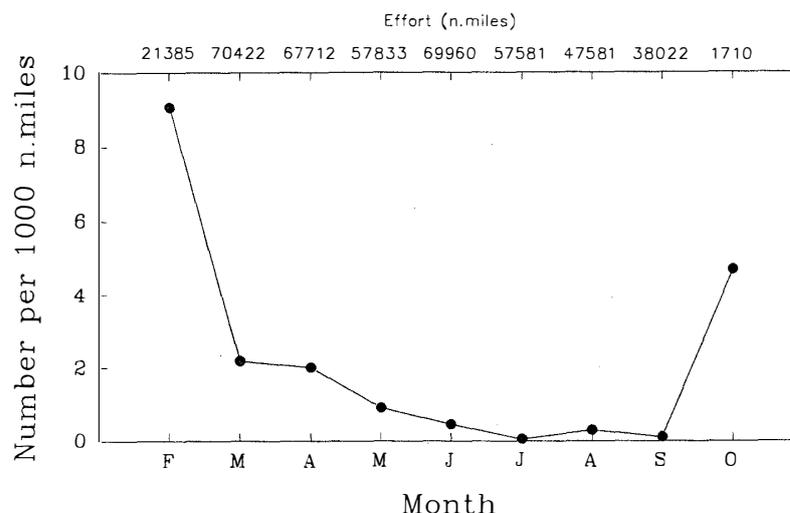


Fig. 5. The seasonal abundance of “like-bottlenose whales” sighted by spotter aircraft on the east coast whaling grounds between 1972 and 1975. Searching distance (n. miles) for each month is also shown.

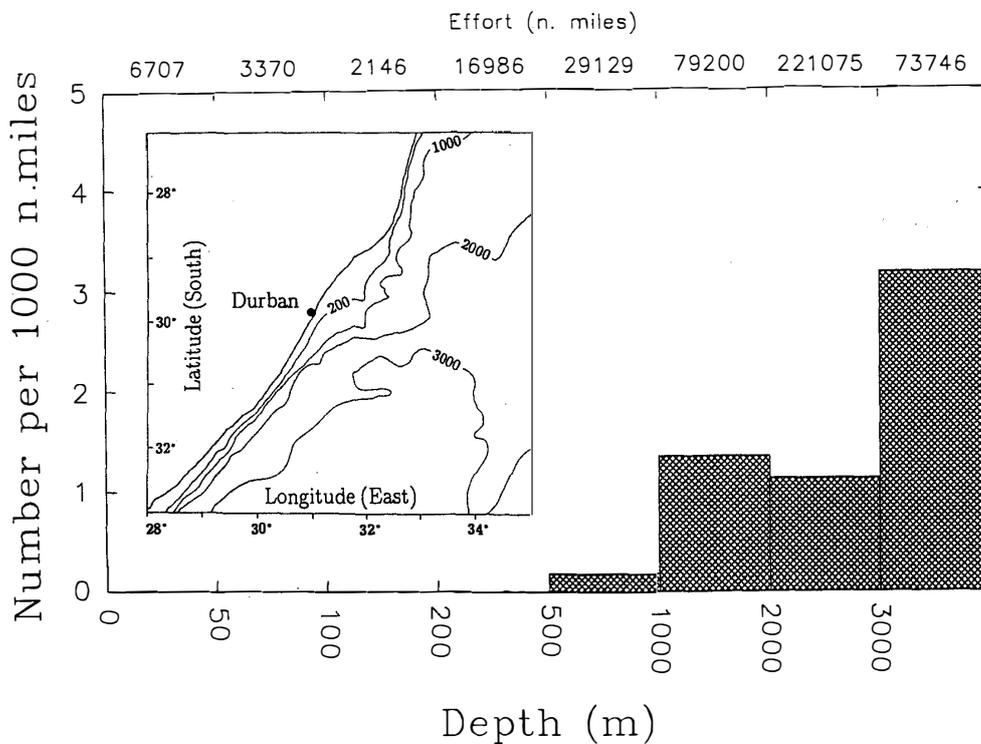


Fig. 6. The depth distribution of "like-bottlenose whales" sighted by the spotter aircraft on the east coast whaling grounds between 1972 and 1975. Searching distance (n. miles) for each depth category is also shown. The map shows the bathymetry of the east coast whaling ground (isobaths are in meters).

the main prey family was Cranchiidae (66.8% by number), as it was in this male and female, but with a numeric percentage about half (31.0 and 48.8% respectively). By contrast, Histioteuthidae were the second most frequently consumed squids in the two South African whales (32.4% in the male and 25.3% in the female by number), but were not found in the Tierra del Fuego whale. Although CLARKE found one fish out of 327 lenses in the Tierra del Fuego whale, no fish remains were found in either ZM37146 or ZM40855.

Some prey species (*Taonius pavo*, *Taonius megalops* and *Todarodes sagittatus*) of southern bottlenose whales were the same as found in northern bottlenose whales (CLARKE and KRISTENSEN, 1980). *Taonius pavo*, the second most important prey for the northern bottlenose whales, was one of the major prey items found in the two southern bottlenose whales examined. However, the size of prey was somewhat larger for southern bottlenose whales, the mean weight for *Taonius pavo* being 81 g for the northern bottlenose whale, but 113.7 g for southern bottlenose whales (Table 1).

The stomach contents of both southern bottlenose whales consisted not only of squid species that occur in South African waters but also included the beaks from eight species of Antarctic and subantarctic squids, of which one was the most dominant species by weight in both whales. Sperm whales (*Physeter macrocephalus*) caught off Durban, which probably migrated from the Antarctic, contained only 4.5% Antarc-

tic and subantarctic squids by number (CLARKE, 1980). Because whales vomit the accumulated beaks in their stomach (CLARKE, 1980), the presence of a high percentage (29.2% and 28.1% by number) of higher-latitude squid beaks in bottlenose whale stomachs might suggest that these whales collected in January arrived very recently in South African waters from higher latitudes.

NEMOTO *et al.* (1980) found cold water skin diatoms *Bennettella* [= *Cocconeis*] *ceticola* on the male ZM37146. This diatom species is common on cetaceans in Antarctic and subantarctic waters, and they therefore suggested that southern bottlenose whales might migrate from higher latitudes to warmer waters, a conclusion in agreement with that inferred from stomach contents in this paper.

During the summer (December to February) southern bottlenose whales are very abundant in higher latitudes of the Antarctic (F. KASAMATSU, private com.). In a cruise in lower latitudes of the Indian Ocean during summer, bottlenose whale-like animals were not seen between 20 and 30°S, and were seen four times as frequently between 35 and 40°S as between 30 and 35°S (GAMBELL *et al.*, 1975). Aerial sightings off Durban (~30°S) showed much higher sighting rates of bottlenose whales in February and October than from March to September (Fig. 5). If the main population of southern bottlenose whales is south of 30°S in summer, and individuals are moving north to South African waters in January, the February peak at Durban could be interpreted as a general movement northward out of the Antarctic in late summer. The subsequent virtual disappearance of bottlenose whales at Durban in winter could therefore mean that the migration continues further to the north, but there is no data available on the winter distribution of bottlenose whales in the Indian Ocean, although ALLING (1986) reported two sightings of possible *Hyperoodon planifrons* off the north-east coast of Sri Lanka in April 1983 and 1984, at between 9 and 10°N. T. MIYASHITA (private com.) and B. PITMAN (private com.) report the presence of an unidentified beaked whale in the central, western and eastern tropical Pacific which they conclude is *Hyperoodon* (and possibly *H. planifrons*). Of the 15 sightings they list, 13 were made between May and October, and extend from the equator to 34°N. If their identification as *H. planifrons* is correct (and this is not a resident population), it is conceivable from the seasonality of the sightings that these are Southern Hemisphere animals on their wintering grounds. The October peak in aerial sightings at Durban could therefore represent the animals on their southern migration back to high latitudes.

Scientific sightings along the east coast of South Africa in summer (December to February) showed that the distribution of southern bottlenose whales and "like-bottlenose whales" was in water over 1000 m deep and was strongly associated with the Agulhas Current (FINDLAY *et al.*, 1992). During summer months, northern bottlenose whales are found off the continental shelf in waters of more than 1000 m depth. BENJAMINSEN and CHRISTENSEN (1979) suggested this distribution might be related to the occurrence and distribution of the whale's prey. Because a large proportion (about 70% by number, 27–56% by weight) of the prey in the stomachs of these southern bottlenose whales occurs in South African waters, the offshore distribution of this whale species also may be related to their migration route and prey distribution.

Among the eight Antarctic and subantarctic squids which were found in the two bottlenose whales, *Kondakovia longimana*, *Mesonychoteuthis hamiltoni*, *Gonatus*

*antarcticus* and *Moroteuthis knipovitchi* also occur in sperm whale stomachs as major prey items in Antarctica (23.3, 21.5, 4.4 and 30.1% by number; 17.8, 76.9, 0.2 and 4.0% by weight respectively—CLARKE, 1980). However, southern bottlenose whales ate smaller individuals of these species than sperm whales (average weights 2568.7, 4080.7, 256.0 and 386.4 g for southern bottlenose whales; 5225, 24399, 334 and 917 g for sperm whales respectively). Sperm whales which feed on these squid species are mostly large males (BEST, 1979; CLARKE, 1980), so it is possible that sperm whales select larger squids, or, if larger squids live in deeper water (NEMOTO *et al.*, 1985), that sperm whales are feeding at a greater depth than southern bottlenose whales. Among these eight Antarctic and subantarctic squid species, the most important prey by number was *G. glacialis* for both the male (11.0%) and the female (10.9%); and by weight was *G. antarcticus* (19.1%) for the male and *M. hamiltoni* for the female (32.1%) (Fig. 2).

*Kondakovia longimana* was present only in the female's stomach where it formed 27.8% by weight of all prey eaten (Fig. 2). The average weight of these squids was very large (2568.7 g; Table 1). This female also fed on larger sized *Mesonychoteuthis hamiltoni* than the male (Figs. 2 and 4), although the estimated weights of this squid are not accurate. We speculate that these large squids might have been selected by the lactating female to meet nutritional needs (BERNARD and HOHN, 1989).

As large, squid-feeding predators, southern bottlenose whales may play an important role in the Antarctic marine ecosystem (KASAMATSU and JOYCE, *private com.*) similar to that of sperm whales. Sperm whales in the Antarctic are mostly large males with an average body length of about 15 m (BEST, 1979). A sperm whale of this size would weigh about 30 t (LOCKYER, 1976; LAWS, 1977), while the male southern bottlenose whale ZM37146 weighed 3.69 t in pieces. For a variety of animals, ingestion rates vary as the body weight raised to the power of  $\sim 0.75$  (INNES *et al.*, 1987). On this assumption, a southern bottlenose whale would consume about 1/5 of the food that a sperm whale takes per day. During the southern summer in the Antarctic region, it is estimated that there are 30000–60000 sperm whales (KLINOWSKA, 1991) compared to an estimated 224000–377000 beaked whales (F. KASAMATSU, *private com.*), most (93%) of which are probably southern bottlenose whales (KASAMATSU, 1991). If these estimates are correct, then the daily food consumption by the southern bottlenose whale population is larger than that of the sperm whale population in the Antarctic. CLARKE (1987) estimated the daily consumption of cephalopods by sperm whales in the Antarctic as  $96.7 \times 10^3$  t, but this is based on a population of 85000 whales and a daily feeding rate derived from captive small cetaceans. Although it is not known how long sperm and southern bottlenose whales stay in the Antarctic region during summer, southern bottlenose whales may be as important predators of Antarctic cephalopods as sperm whales.

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