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Current status of Odontocetes in the Antarctic

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Abstract: The current status of Antarctic Odontocetes – sperm whales *Physeter catodon*, killer whales *Orcinus orca*, long-finned pilot whales *Globicephala melaena*, hourglass dolphins *Lagenorhynchus cruciger* and poorly known species of beaked whales (family Ziphiidae) – were studied in Antarctic waters using data gathered in sighting surveys conducted from 1976/77 to 1987/88. Temporal variation in density demonstrated the different migration patterns by species, especially between sperm whale and killer whale. Spatial distributions during mid-summer demonstrated different peaks of occurrence for each species by latitude that suggest possible segregation between the species. Killer whales occur mainly in the very southernmost areas, sperm whales in the southern half of the study area, beaked whales (mostly southern bottlenose whales *Hyperoodon planifrons*) ranged over a wide area, and long-finned pilot whales and hourglass dolphins were mainly in the northern regions of Antarctic waters. Several longitudinal peaks of occurrence and apparent distribution gaps were identified for sperm, beaked and killer whales. Abundance estimates for south of the Antarctic Convergence in January are based on line transect theory and were 28 100 animals (coefficient of variation CV 0.18) sperm whales, 599 300 (0.15) beaked whales (mostly southern bottlenose whales), 80 400 (0.15) killer whales, 200 000 (0.35) long-finned pilot whales, and 144 300 (0.17) hourglass dolphins. Based on this, biomass of these species were estimated as 0.77 (sperm whales), 2.70 (beaked whales), 0.32 (killer whales), 0.16 (long-finned pilot whales) and 0.01 (hourglass dolphins) million tonnes. Consumption of food (mostly squid) by the Odontocetes is estimated as 14.4 million tonnes with 67% of the total consumed by beaked whales. Indirect consumption of Antarctic krill through the predation of squid by beaked whales is estimated to be *c.* 24 million tonnes. This value is similar to the estimate of krill consumption by penguins in the Antarctic (33 million tonnes). Odontocetes, especially southern bottlenose whales, are suggested to have a much greater role in the Antarctic ecosystem than has previously been considered.

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Key words: Odontocetes, distribution, Antarctic, ecosystem impact, consumption

Introduction

Nine species of Odontocetes (toothed whales and dolphins) are known to occur in Antarctic waters (Brown & Lockyer, 1984, Kasamatsu *et al.* 1988). Since the start of modern commercial whaling in the Antarctic in 1904, substantial information has been gathered on the commercially valuable large baleen whales (Mackintosh 1965), but the abundance and distribution of Antarctic Odontocetes other than the sperm whale *Physeter catodon* have remained largely unassessed (Klinowska 1991). Studies of the Southern Ocean ecosystem have advanced through programmes of the Scientific Committee of Antarctic Research (SCAR) and the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The BIOMASS programme has increased the overall knowledge of the ecology of the Antarctic phytoplankton, zooplankton, fish, seals and seabirds, but with the exception of the southern minke whales *Balaenoptera acutorostrata,* our understanding of the ecology of whales has improved little. Antarctic marine ecosystem models have therefore been developed with little or no regard for the possible influence of Odontocetes consumers other than the sperm whale (e.g. Laws 1977a, Everson 1984, Clark 1985).

Since 1976, data on the distribution and density of Odontocetes in the Antarctic have been accumulated from the two ship-based sighting survey programmes. The present study provides basic information on the distribution and abundance of the following Odontocetes as regular inhabitants of Antarctic waters: sperm whales, beaked whales (family Ziphiidae), killer whales *Orcinus orca,* long-finned pilot whales *Globicephala melaena* and hourglass dolphins *Lagenorhynchus cruciger.* Some of the Odontocetes, especially sperm and beaked whales, make very long dives which may cause them to be undetected in the survey area. Abundance estimates based on the line-transect model could be substantially underestimated for the long-diving species if the probability of an animal being seen on the trackline, $\hat{g}(0)$, is not considered. Estimates of $\hat{g}(0)$ were made in this study using a simulation model of the sighting process of the cruises.

Materials and methods

In this study Antarctic waters are defined as waters south of the Antarctic Convergence generalized as the area south of 50°S latitude between 60°W–160°E longitude (South Atlantic–Indian Ocean Sector) and south of 60°S latitude between 160°E–60°W longitude (South Pacific Sector), (see Deacon 1937).

Sighting surveys and data

The data were collected from two separate research programmes: the Japanese sightings survey programme started in 1976/77 season and the International Whaling Commission/ International Decade of Cetacean Research (IWC/IDCR) Southern Hemisphere Minke Whale Assessment Cruises (IDCR cruises) started in 1978/79 season. To avoid the possible effects of weather and sea conditions on density, searching effort in both surveys was restricted to times when sea conditions were Beaufort 5 or less. The total search distances and the noon positions for all the survey vessels in waters south of 50°S are presented in Table I and Fig. 1.

IDCR Cruises

These sighting surveys used two or three Japanese research vessels. An additional Soviet ship was used for ice reconnaissance and special experiments. All ships were converted whale catchers (750–900 gross tonnes). The IDCR cruises were conducted in one of six management areas each season. Each area was divided into four to six strata (Fig. 2). The surveys extended mainly from 60°S to the pack ice edge in most of the areas. The vessels normally kept a constant speed of 12 kns with a constant watch for whales from 04h00–20h00 each day, weather permitting. Two observers on watch in the foremast barrel had the primary responsibility to find whales assisted by two or three crew members on the upper bridge. All the observers used 7 x 50 binoculars for scanning the sea ahead of, and up to about 90° on either side. The vessels travelled along pre-planned tracklines diverting and accelerating to 15 kns to approach sighted animals to identify species and count all animals.

Species identification was frequently difficult for beaked whales due to their prolonged dives, wariness of vessels, limited distinguishing physical characteristics, and, for some species, lack of available physical descriptions of the animals in the wild. The data collected from the IDCR cruises reflected this difficulty, especially during the early years of the programme, as many sightings were identified only to the family Ziphiidae. Data from the cruises have therefore been pooled for the entire family Ziphiidae rather than treating

Table I. Total search distances (n miles) by latitude and longitude square derived from the Japanese sighting surveys and the IWC/IDCR Southern Hemisphere Minke Whale Assessment Cruises, combined, during 1976/77–1987/88.

Longitude interval	Latitude 50–60°S	Latitude S of 60°S
0–10°E	758	1757
10–20°E	216	2211
20–30°E	1740	1802
30–40°E	943	2267
40–50°E	2076	2538
50–60°E	752	3321
60–70°E	1537	3634
70–80°E	2216	8219
80–90°E	5815	5405
90–100°E	4704	4772
100–110°E	3190	8373
110–120°E	2743	5512
120–130°E	1691	5569
130–140°E	1299	5161
140–150°E	3886	4156
150–160°E	1865	5431
160–170°E	1515	4890
170–180°E	1602	5905
180–170°W	3033	7057
170–160°W	3665	6673
160–150°W	3578	5675
150–140°W	2974	4177
140–130°W	2604	4395
130–120°W	2402	5572
120–110°W	1476	2916
110–100°W	384	1256
100–90°W	931	1588
90–80°W	888	1111
80–70°W	1852	1385
70–60°W	2107	1703
60–50°W	1027	1432
50–40°W	580	1910
40–30°W	366	2966
30–20°W	809	2587
20–10°W	498	3413
10–0°W	434	4007

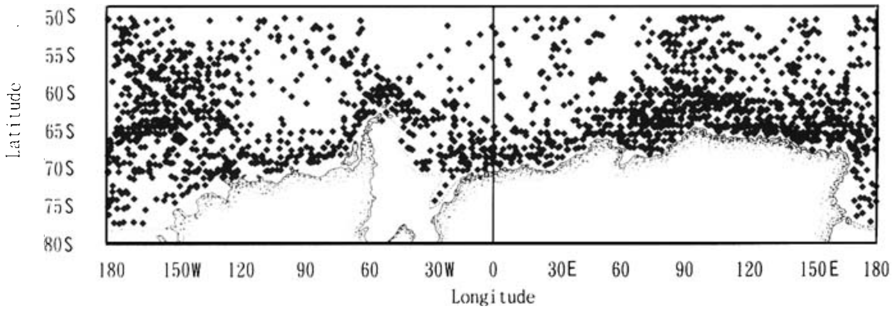

Fig. 1. Noon positions of sighting vessels during 1976–88 in waters south of 50°S.

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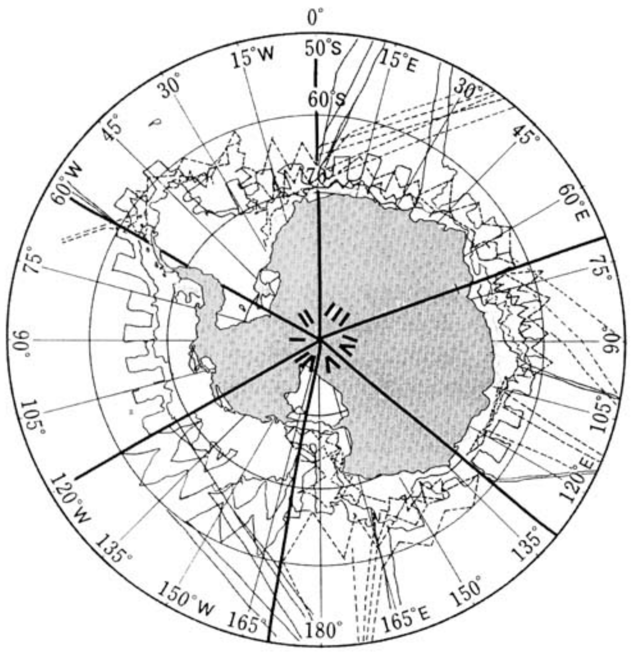

Fig. 2. Cruise tracks of the IWC/IDCR Southern Hemisphere Minke Whale Assessment Cruises, 1978/79–1983/84 (bold line) and 1985/86–1987/88 (broken line).

each species separately. Based on the composition of confirmed species identification, the majority (93%) of the beaked whales observed in Antarctic waters were southern bottlenose whales *Hyperoodon planifrons* (Kasamatsu *et al.* 1988). Sightings from the IDCR cruises were divided into two categories: sightings made when full searching effort was being applied (primary sighting), and all other sightings (secondary sightings). Only primary sightings from the Japanese vessels were used to estimate abundance. Search effort was recorded whenever there was any change that affected the effort, and environmental conditions were recorded hourly. Complete details of the cruises are found in Best & Butterworth (1980), Kasamatsu *et al.* (1988) and Kasamatsu (1993). Data from the first decade of the IDCR cruises (1978/79–1987/88) were used for the present analyses.

Japanese cruises

Starting in 1976, the Japanese Government has sponsored sightings and marking surveys in the Southern Hemisphere from October–March (November–February in Antarctic waters), with most effort in waters south of 40°S. Two or three sighting vessels were used independently of the whaling operations that were occurring concurrently in the Antarctic waters (Ohsumi & Yamamura 1982). In 1978, and continuing until 1983, two of the three ships dedicated to the Japanese programme were made available to the IDCR programme from mid-December–mid-February. Starting in 1983, all ships were dedicated to the IDCR programme during that time frame. This resulted in the Japanese survey being conducted at different times and in different areas from those of the IDCR cruises. While most of the IDCR surveys were concentrated in the area south of 60°S and during the period of late December–February, the Japanese sightings surveys had a much greater geographical and temporal range.

The procedures used in the Japanese surveys were similar to those used in the IDCR cruises. However, the sightings data from these surveys before 1987 included only the total number of schools seen, total number of whales seen by species each day, total distance searched each day, and weather and sea conditions at noon each day, but did not include details on each sighting. There was no separation of primary and secondary sightings in the daily records, although such separation has been made since 1987.

Estimation of abundance

The estimation of abundance from the sighting data was based on a line transect method (Burnham *et al.* 1980, Hiby & Hammond 1989). The following equation was used:

$$\hat{P} = \frac{n\bar{s}A\hat{f}(0)}{2L\hat{g}(0)} \qquad (1)$$

where $\hat{P}$ is the abundance estimate; n is the number of schools seen; $\bar{s}$ is mean school size; A is the size of the area covered; L is the distance search; $\hat{f}(0)$ is the estimated probability density of perpendicular distances, evaluated at zero, calculated from fitting the Hazard rate model (Hayes & Buckland 1983, Buckland 1985) with truncation (T) at 3.0 n miles (for sperm whales) and 1.5 n miles (for other species) for perpendicular distance; $\hat{g}(0)$ is the probability of an animal being seen on the trackline.

Effective search half-width is $1/\hat{f}(0)$. The coefficient of variation for the abundance estimate $\hat{P}$ was calculated using the following formula:

$$CV^2(\hat{P}) = CV^2\left(\frac{n}{L}\right) + CV^2(\hat{f}(0)) + CV^2(\bar{s}) + CV^2\{\hat{g}(0)\} \qquad (2)$$

For all the toothed whales except the hourglass dolphin, $\hat{g}(0)$, was estimated from the model of the sighting process developed and modified by Doi *et al.* (1982, 1983), and Kishino & Kasamatsu (1987).

Encounter rate

To analyse the temporal and spatial occurrence of Odontocetes, encounter rate (number of animals seen per one nautical mile search distance) was used as an index of abundance. This avoids bias associated with any possible geographic-dependent school size heterogeneity. The coefficient of variation of the encounter rate was calculated based on variation in distance searched and number of animals seen per day:

$$\text{Encounter rate} = w/L \qquad (3)$$

with coefficient of variation

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$$CV^2\left(\frac{w}{L}\right) = \left(\frac{k}{w}\right)^2 \frac{1}{k(k-1)} \sum_{i=1}^{k}\left(w_i - \frac{w}{L}L_i\right)^2 \qquad (4)$$

where w is total whales seen in area; k is number of research day; w_i number of animals seen in i th day; L_i distance searched in i th day (Kasamatsu *et al.* 1990, 1991, Kishino *et al.* 1991, Kasamatsu *et al.* 1995).

Estimation of mean school size

Previous studies have shown that the probability of detecting a whale is a function of school size and that the observed mean school size could be overestimated because larger schools are more easily detected than smaller schools (Best & Butterworth 1980, Kasamatsu *et al.* 1990, 1991, Kishino *et al.* 1991). Mean school size was therefore estimated using the following formula:

$$\bar{s} = \left\{\frac{\text{estimated total number of animals}}{\text{estimated total number of schools}}\right\}$$
$$= \frac{\frac{A}{2L}\left\{1\cdot n_1\cdot \hat{f}_1(0) + 2\cdot n_2\cdot \hat{f}_2(0) + \ldots + i\cdot n_i\cdot \hat{f}_i(0)\right\}}{\frac{A}{2L}\left\{n_1\cdot \hat{f}_1(0) + n_2\cdot \hat{f}_2(0) + \ldots + n_i\cdot \hat{f}_i(0)\right\}} \qquad (5)$$
$$= \frac{\left\{\Sigma i\cdot n_i\cdot \hat{f}_i(0)\right\}}{\left\{\Sigma n_i\cdot \hat{f}_i(0)\right\}}$$

The variance of $\bar{s}$ was assumed to be the variance of school size observed within a truncated perpendicular distance of T. An adequate sample size for beaked whales permits the calculation of the mean school size by each stratum of each management area, but this is not possible for other species. The mean school size of killer whales was calculated by two strata (northern and southern strata) but for combined areas since there was no significant difference (at the 5% level) for the observed mean school size between areas. The mean school size of hourglass dolphin was calculated for combined strata and area. Sample size was too small for long-finned pilot whales, so the observed mean school size was used. The mean school size of sperm whales was 1.0 because only mature solitary male sperm whales migrate into the Antarctic waters (Best 1974).

Results and discussion

Temporal variability in the Antarctic

Both the IDCR data and the Japanese survey data were used to estimate the seasonal density by month and half-month during the period of November–February.

Sperm whales

Fig. 3a suggests that sperm whales migrate into and out of Antarctic waters over an extended period. Best (1974) demonstrated a seasonality of occurrence of male sperm whales (>13.7m body length) off Durban with a peak in June–July. This pattern is complementary to the pattern observed in Antarctic waters and suggests that adult male sperm whales regularly migrate between high and low latitude.

Beaked whales

Only the IDCR cruises provided systematic information on the density of beaked whales, so data are limited to the time period of late December to February (Fig. 3b). Southern bottlenose whales are known to be at least present in Antarctic

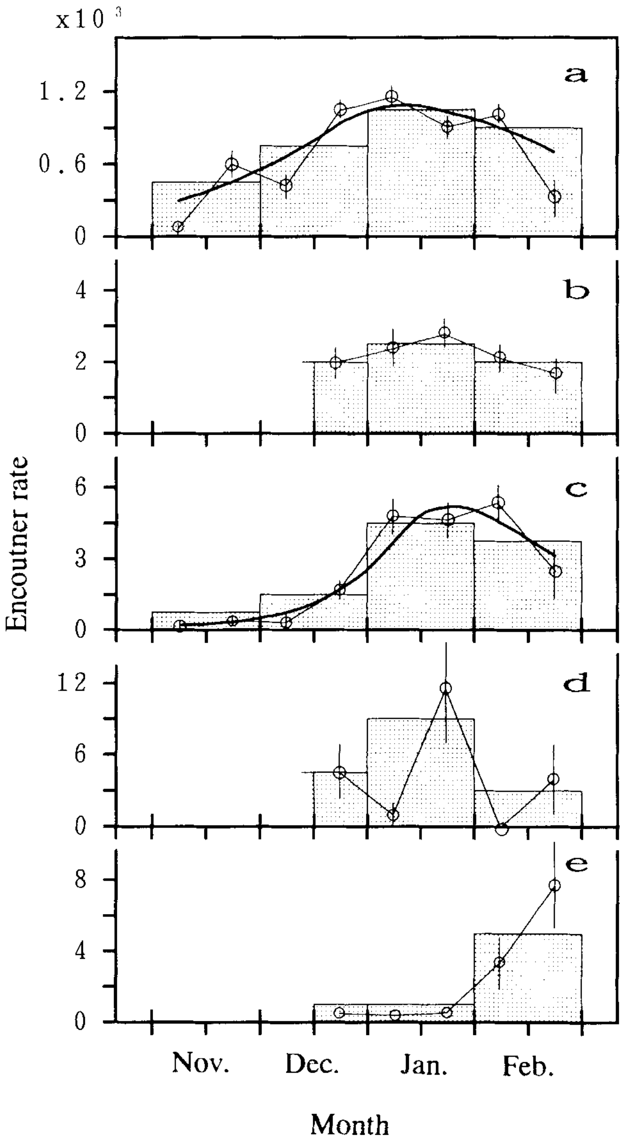

Fig. 3. Seasonal occurrences of Odontocetes in the Antarctic waters. Shaded areas show mean encounter rate by month and open circles with vertical lines show mean encounter rate by half-month and their standard errors. **a.** sperm whale. **b.** beaked whale. **c.** killer whale. **d.** long-finned pilot whale. **e.** hourglass dolphin.

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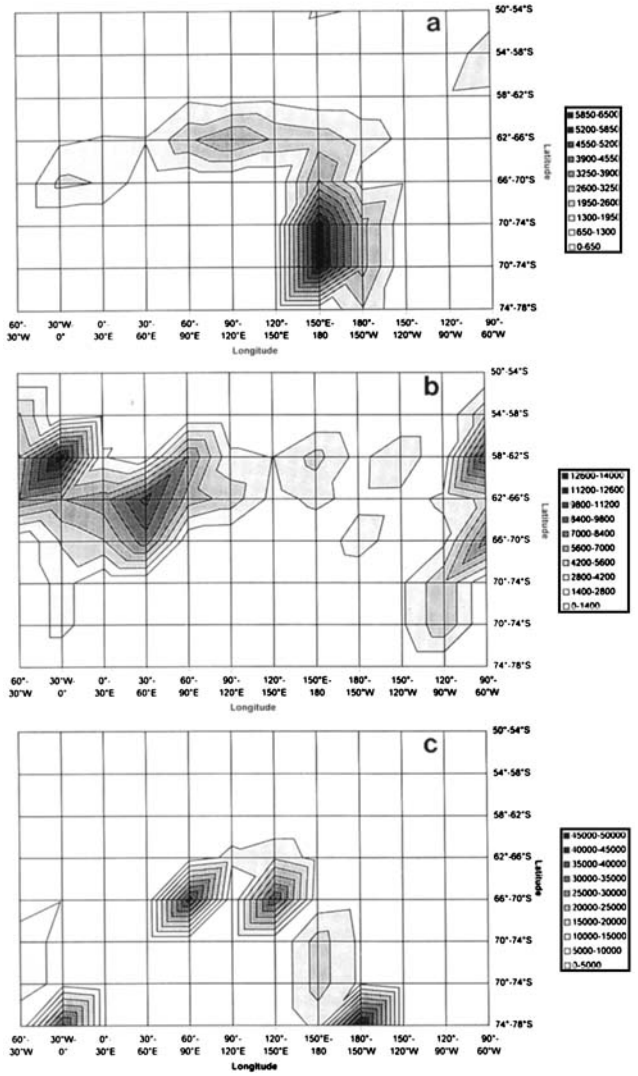

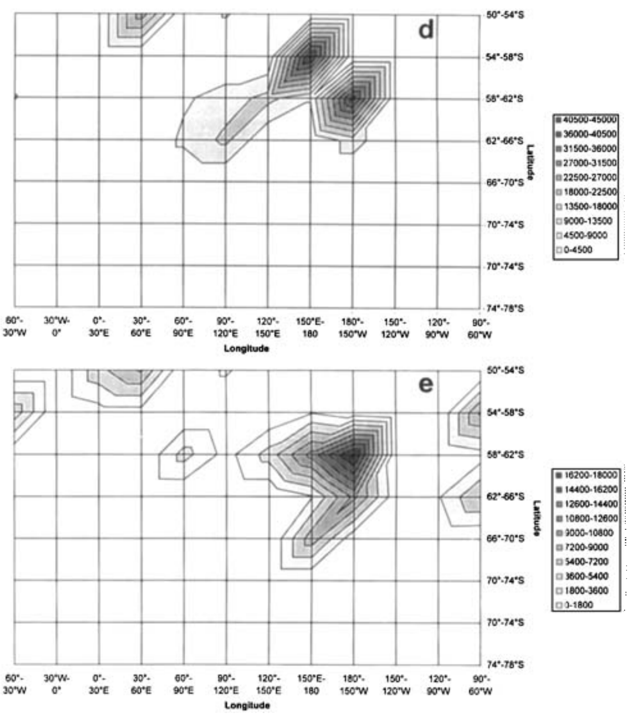

Fig. 4. Spatial occurrence of Odontocetes in the Antarctic waters during mid-December to mid-February. **a.** sperm whale. **b.** beaked whale. **c.** killer whale. **d.** long-finned pilot whale. **e.** hourglass dolphin.

waters from October (Ensor 1989) and March (Kasamatsu *et al.* 1993). From data on ectoparasites and stomach contents Sekiguchi *et al.* (1993) suggested that southern bottlenose whales undertake seasonal migrations between sub-tropical and colder waters with sightings off Durban (30°S) showing peaks in February and October which they interpreted as representing northward and southward migration. In the present study, the observed density of beaked whales in Antarctic waters decreased after mid-January (Fig. 3b). When combined with the observations off Durban, this indicates that southern bottlenose whales leave temperate waters in October for the cold-water area of the Southern Ocean, and leave for temperate seas starting in early February.

Killer whales

This pattern (Fig. 3c) is substantially different from that of sperm whales, the only other species with data gathered over the same period. It indicates that most of the killer whales migrate into Antarctic waters at approximately the same time (in early January) and leave in late February. The pattern is synchronous with the migration pattern of the southern minke whale, which is one of the major prey species of killer whales in Antarctic waters (Mikhalev *et al.* 1981). Although evidence for the northward migration of killer whales in the autumn in inconclusive (IWC 1982), the clear reduction in encounter rate is suggestive of a distinctive onset of a northern autumn migration.

Long-finned pilot whales and hourglass dolphin

No clear seasonality for long-finned pilot whales was identified, but the small sample size limits this analysis. Seasonality cannot be discounted however, as the highest encounter rates were recorded in the second half of January (Fig. 3d).

The increase for the hourglass dolphin that starts in early February and continues until the end of the study period (Fig. 3e) corresponds to the increase in sea surface temperature in Antarctic waters, with peaks in March. This pattern may be due to thermoregulatory considerations related to the small body size of this species or to prey availability and is the first evidence of possible seasonal variation in density for hourglass dolphin.

Spatial distribution in the Antarctic

Spatial distribution by species was examined for the period mid-December and mid-February. Encounter rates, pooled in bins of 4° latitude and 30° longitude for waters south of 50°S, are presented in Fig. 4a–e. In addition, encounter rates

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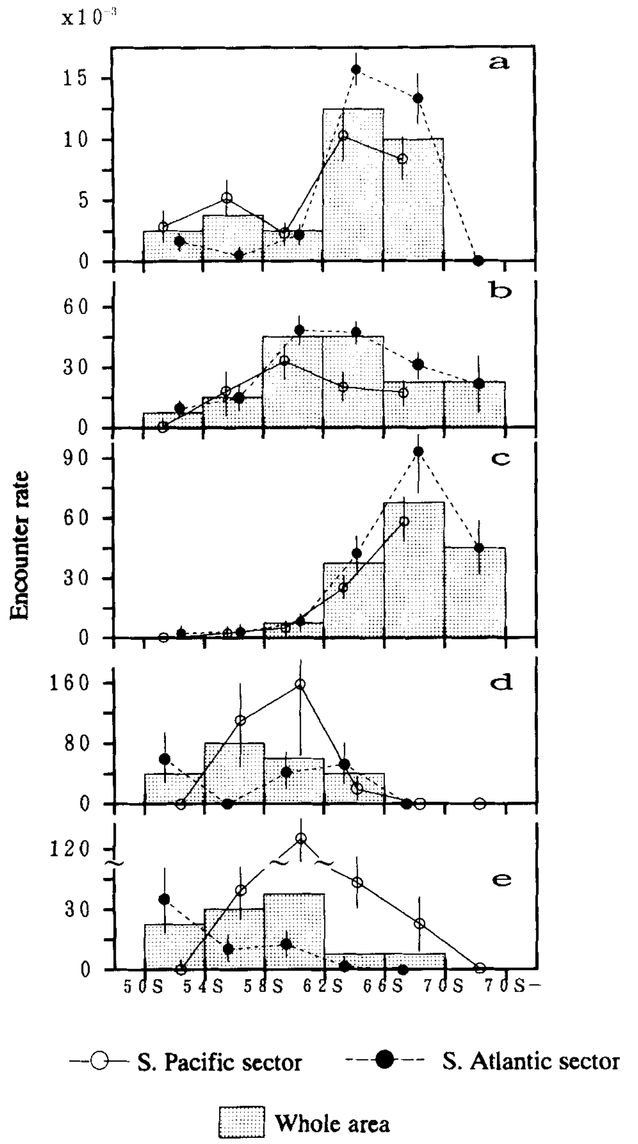

Fig. 5. Latitudinal occurrence of Odontocetes in the Antarctic waters during mid-December to mid-February. Vertical lines show the standard errors. **a.** sperm whale. **b.** beaked whale. **c.** killer whale. **d.** long-finned pilot whale. **e.** hourglass dolphin.

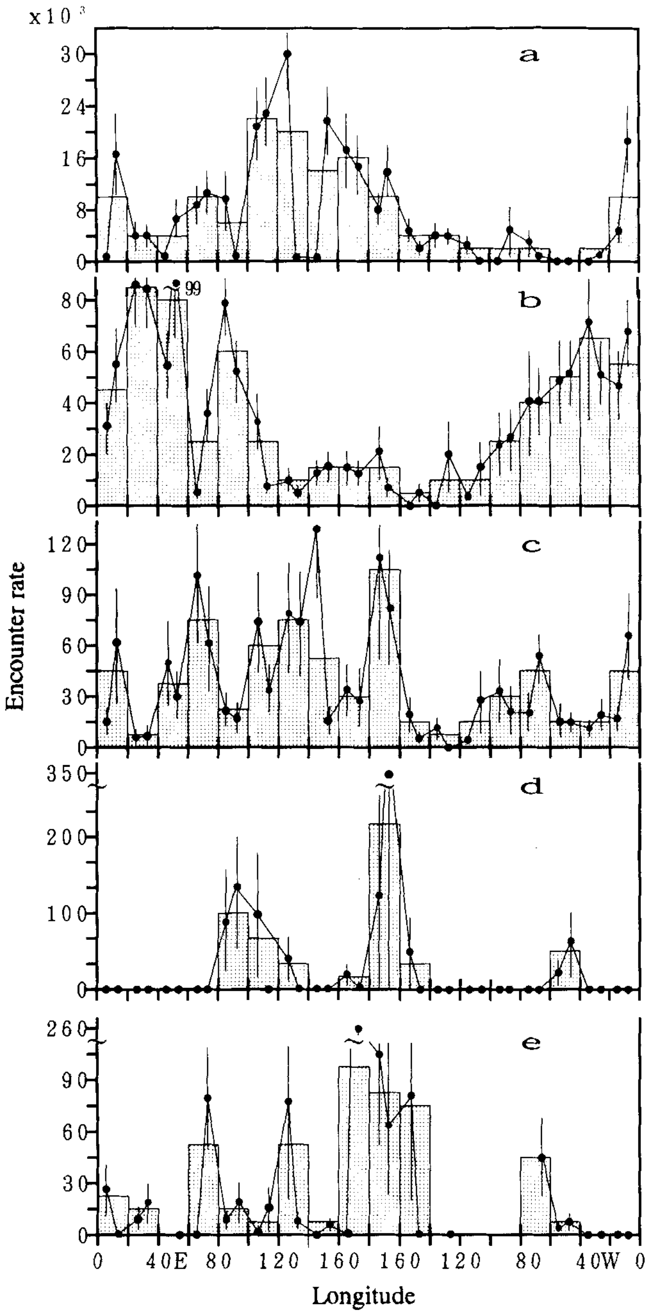

Fig. 6. Longitudinal occurrences of Odontocetes in the Antarctic waters during mid-December to mid-February. Shaded areas shows mean encounter rates in 20° bands and closed circles with vertical lines show the encounter rates in 10° bands and their standard errors. **a.** sperm whale. **b.** beaked whale. **c.** killer whale. **d.** long-finned pilot whale. **e.** hourglass dolphin.

were stratified in bands of 4° latitude (longitude combined, Fig. 5a–e) and 10–20° longitude (latitude combined, Fig. 6a–e) to investigate latitude-dependent or longitude-dependent distribution patterns. When examining the longitudinal variation of density using 10–20° longitudinal bands the search effort in waters outside the major latitudinal range of each species were not considered, to avoid possible underestimation of the encounter rate. Encounter rates by the 10–20° longitude bands were thus calculated in main latitudinal distribution range.

Sperm whale

Highest densities were observed in the area bounded by 62–66°S, 90–120°E, and south of 66°S, 150–180°E (Fig. 4a). It is obvious that sperm whales tend to prefer the southern portion of Antarctic waters (Fig. 5a) with southernmost

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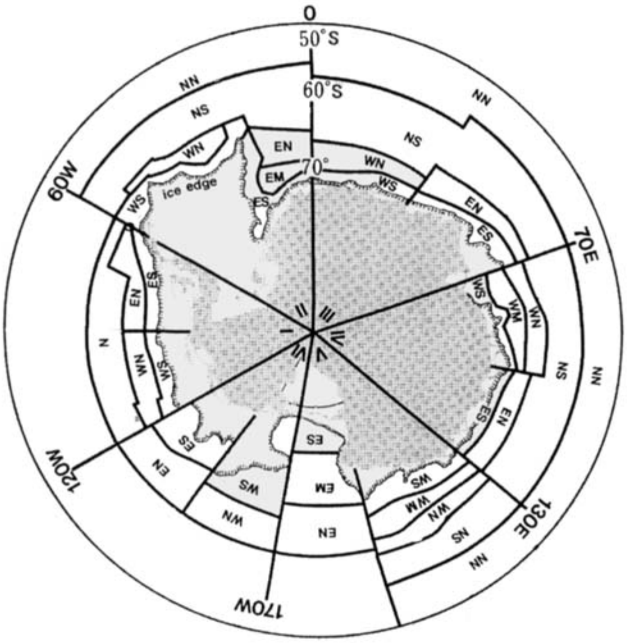

Fig. 7. Strata used in the estimation of Odontocetes abundance. Details of strata and their definition can be seen in Kasamatsu *et al.* (1988) and Joyce *et al.* (1988).

sightings of sperm whales at 74°S in the Ross Sea. Encounter rates in the Indian Ocean sector were higher than those in South Atlantic and South Pacific sectors (Fig. 6a). Bannister (1969) suggested a western limit of distribution of a Tasman Sea–South Pacific stock at 146°E, based on catch positions. Best (1969) suggested boundaries at 30°W and 35°E for a putative West African stock. Cushing *et al.* (1963) suggested on the basis of blood-type frequency that sperm whales between 40 and 55°E might differ from whales occurring between *c.* 60 and 90°E. On the basis of this information, the IWC adopted nine stock boundaries at 20°E, 60°E, 90°E, 130°E, 160°E, 170°W, 100°W, 60°W and 30°W (IWC 1971). Data from this study demonstrated very low or zero densities at about 20°E, 60°E, 90°E, 130°E, 100°W, 60°W and 30°W but no apparent gap at 160°E and 170°W.

Table II. Estimated search half-widths by species and by school size.

Species	School size	half-width (n miles)	CV
Sperm	1	1.87	0.04
Beaked	1	0.26	0.33
	2-3	0.54	0.08
	>=4	0.54	0.32
	All	0.43	0.09
Killer	1-9	0.52	0.41
	10-19	0.73	0.30
	>=20	1.41	0.20
	All	0.64	0.18
Pilot	All	0.61	0.26
Hourglass	1-5	0.34	0.17
	>=6	0.57	0.17
	All	0.41	0.13

Beaked whales

Relatively high encounter rates were seen from the South Atlantic to the eastern part of the Indian Ocean (90°W–120°E), and low encounter rates were observed in the western and central South Pacific (Fig. 4b). Fig. 5b shows high rates between 58°S and 62°S in both sectors. Beaked whales appear to have a wide distribution between the Antarctic Convergence and the pack ice edge. The southernmost sighting of a southern bottlenose whale was at 73°S in the Ross Sea. This is the first time a latitudinal variation in density for these whales has been demonstrated. The longitudinal distribution of encounter rates (Fig. 6b) is substantially different from that for sperm whales. There is little published information on the longitudinal distribution of either the Ziphiidae in general or of southern bottlenose

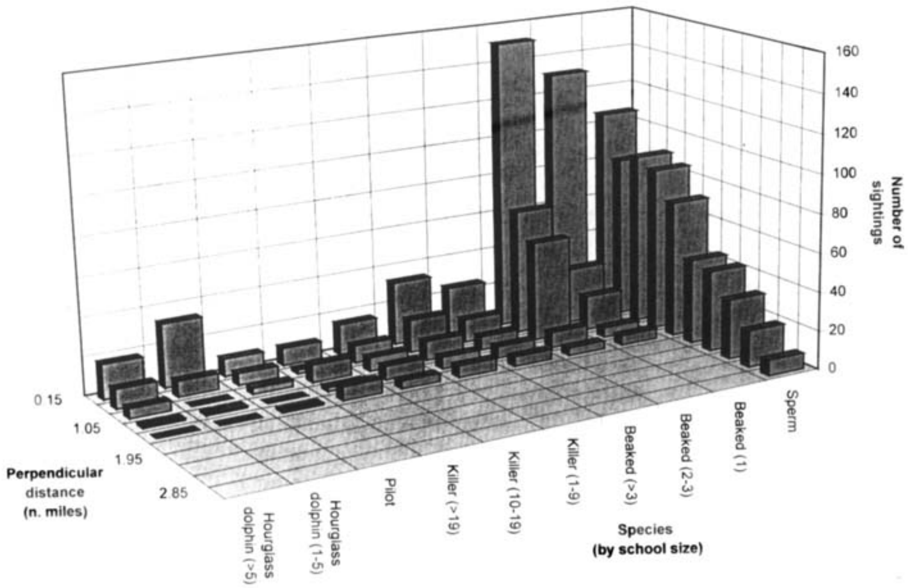

Fig. 8. Frequency distribution of pooled perpendicular sighting distance by school size and by species.

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Table III. Size of area, search distance, number of schools seen (n), mean school size ($\bar{s}$) and encounter rate (ER) by stratum.

Area	Stratum*		Size area (n m²)	Search dist. (n m)	Sperm whale n	Sperm whale $\bar{s}$	Sperm whale ER	Sperm whale CV	Beaked whales n	Beaked whales $\bar{s}$	Beaked whales CV	Beaked whales ER	Beaked whales CV
I	W	WS	25600	1354					11	1.92	0.14	0.008	0.45
		WM	163900	1426	3	1.0	0.002	0.95	4	2.02	0.28	0.003	0.42
	E	ES	32500	916					22	2.04	0.11	0.024	0.31
		EM	148900	1047					17	2.15	0.16	0.002	0.37
	N	N	406700	1122	15	1.0	0.013	0.55	5	2.02	0.43	0.005	0.57
II	W	WS	22600	3314					155	1.77	0.07	0.047	0.19
		WM	95300	550					20	2.02	0.19	0.036	0.64
	E	ES	83300	2062	12	1.0	0.006	0.46	30	1.79	0.21	0.015	0.35
		EMS	69900	1472	17	1.0	0.012	0.58	35	1.80	0.11	0.024	0.29
		EMN	124000	847	10	1.0	0.012	0.37	34	1.71	0.11	0.040	0.25
	N	NS	651100	2122					17	2.17	0.10	0.008	0.32
		NN	656200	825	2	1.0	0.002	0.89					
III	W	WS	74800	1256	32	1.0	0.026	0.67	28	3.61	0.47	0.022	0.45
		WN	148800	889	5	1.0	0.006	0.48	41	1.86	0.16	0.046	0.26
	E	ES	87800	1211	18	1.0	0.015	0.59	43	1.80	0.21	0.036	0.42
		EM	168900	1067	8	1.0	0.005	0.76	16	1.77	0.17	0.015	0.43
	N	NS	772400	5541	11	1.0	0.002	0.46	24	1.99	0.09	0.004	0.24
		NN	907700	2464	1	1.0	0.001	0.93	11	1.94	0.15	0.005	0.40
IV	W	WS	53200	1682	48	1.0	0.029	0.56	57	1.68	0.08	0.034	0.23
		WMS	73900	2063	27	1.0	0.003	0.31	69	2.08	0.12	0.034	0.18
		WMN	185200	1771	13	1.0	0.007	0.37	38	2.38	0.24	0.022	0.17
	E	ES	27600	1456	9	1.0	0.006	0.42	8	1.63	0.29	0.006	0.55
		EM	156800	2149	4	1.0	0.002	0.87	13	1.85	0.19	0.006	0.41
	N	NS	603100	5049	6	1.0	0.001	0.49	24	1.90	0.09	0.005	0.17
		NN	657200	5878	9	1.0	0.002	0.43	13	1.54	0.17	0.002	0.28
V	W	WS	104800	1601	32	1.0	0.020	0.38	2	2.42	0.33	0.001	0.71
		WMS	166300	840					9	1.63	0.20	0.011	0.36
		WMN	139000	1057	1	1.0	0.001	0.91	11	1.64	0.13	0.010	0.28
	E	ES	107300	1753					1	1.86	0.03	0.001	0.97
		EMS	165900	1771	33	1.0	0.019	0.49	14	5.85	0.36	0.004	0.39
		EMN	279600	1718	15	1.0	0.009	0.66	18	2.29	0.15	0.009	0.27
	N	NS	262600	2392	2	1.0	0.001	0.73	1	2.16	0.12	0.001	0.98
		NN	328600	2338					2	2.09	0.22	0.001	0.73
VI	W	WS	156500	2637	20	1.0	0.008	0.41	6	1.84	0.27	0.002	0.79
		WM	207700	958					4	1.65	0.20	0.004	1.95
	E	ES	158900	2735	6	1.0	0.002	0.56	14	2.14	0.13	0.005	0.44
		EM	23700	881	1	1.0	0.001	0.91	1	1.90	0.05	0.001	1.03

*See Fig. 7.

whales in particular, apart from Kasamatsu *et al.* (1988). Encounter rates were higher in the South Atlantic–Indian Ocean sector than in the South Pacific sector.

Killer whales

Fig. 4c and Fig. 5c show that encounter rates increased south of 62°S, with a peak south of 66°S. The southernmost sighting was at 78°S in the Ross Sea. The peak of occurrence in both sectors corresponded to the general position of the northern edge of the pack ice. As noted by Kasamatsu *et al.* (1988) and Kasamatsu (1993) the pack ice edge is an area inhabited by large numbers of southern minke whales, seals, and penguins, all of which are major prey of killer whales. Sightings of killer whales indicate an essentially circumpolar distribution, with only one apparent gap at 120–130°W (Fig. 6). The density of killer whales in the South Pacific and Indian Ocean sector is higher than that in the South Pacific sector as for beaked whales. Although two different breeding areas of this species in tropical waters of the eastern and

Table III. Cont.

Area	Stratum*		Killer whale *n*	$\bar{s}$	CV	ER	CV	Pilot whale *n*	$\bar{s}$	CV	ER	CV	Hourglass dolphin *n*	$\bar{s}$	CV	ER	CV
I	W	WS	2	8.79	0.17	0.002	0.66										
		WM	5	9.02	0.12	0.004	0.48						1	6.70	0.11	0.001	0.97
	E	ES	6	8.79	0.17	0.007	0.34										
		EM	3	9.02	0.12	0.003	0.72						8	6.70	0.11	0.008	0.53
	N	N						2	72.9	0.45	0.002	0.67	4	6.70	0.11	0.004	0.91
II	W	WS	9	8.79	0.17	0.003	0.39										
		WM	1	9.02	0.12	0.002	0.76										
	E	ES	6	8.79	0.17	0.003	0.39										
		EMS	4	8.79	0.17	0.003	0.72										
		EMN	3	9.02	0.12	0.004	0.91										
	N	NS	4	9.02	0.12	0.002	0.42	1	72.9	0.45	0.001	1.02	6	6.70	0.11	0.003	0.42
		NN	1	9.02	0.12	0.001	1.00										
III	W	WS	2	8.79	0.17	0.002	0.63										
		WN															
	E	ES	1	8.79	0.17	0.001	0.84										
		EM	2	9.02	0.12	0.002	0.84										
	N	NS	6	9.02	0.12	0.001	0.38						3	6.70	0.11	0.001	0.83
		NN	1	9.02	0.12	0.001	0.94						5	6.70	0.11	0.002	0.71
IV	W	WS	3	8.79	0.17	0.002	0.65	1	72.9	0.45	0.001	0.96					
		WMS	5	8.79	0.17	0.002	0.45										
		WMN	3	9.02	0.12	0.002	0.65	1	72.9	0.45	0.001	0.99	17	6.70	0.11	0.010	0.35
	E	ES	16	8.79	0.17	0.011	0.35	1	72.9	0.45	0.001	0.96					
		EM	4	9.02	0.12	0.002	0.69	2	72.9	0.45	0.001	0.65	4	6.70	0.11	0.002	0.65
	N	NS	1	9.02	0.12	0.001	0.98	4	72.9	0.45	0.001	0.54	10	6.70	0.11	0.002	0.33
		NN	2	9.02	0.12	0.001	0.69	8	72.9	0.45	0.001	0.61	11	6.70	0.11	0.002	0.48
V	W	WS	11	8.79	0.17	0.007	0.49										
		WMS	1	8.79	0.17	0.001	0.96										
		WMN	1	9.02	0.12	0.001	0.85						2	6.70	0.11	0.002	0.63
	E	ES	5	8.79	0.17	0.003	0.54										
		EMS	4	8.79	0.17	0.002	0.44										
		EMN											28	6.70	0.11	0.016	0.33
	N	NS	1	9.02	0.12	0.001	0.98	2	72.9	0.45	0.001	0.68	5	6.70	0.11	0.002	0.70
		NN	2	9.02	0.12	0.001	0.71						4	6.70	0.11	0.002	0.61
VI	W	WS	5	8.79	0.17	0.002	0.78										
		WM	2	9.02	0.12	0.002	0.69	1	72.9	0.45	0.001	0.96	2	6.70	0.11	0.002	0.60
	E	ES	5	8.79	0.17	0.002	0.79										
		EM	1	9.02	0.12	0.001	0.96										

*See Fig. 7

western Indian Ocean (possible boundary at about 80–90°E) and two others in eastern and western South Pacific waters (possible boundary at around 130°W) have been suggested (Kasamatsu 1993), no clear boundaries were evident in the Antarctic. This is probably due to substantial mixing of stocks in the feeding area of Antarctic waters.

Long-finned pilot whales and hourglass dolphins

Long-finned pilot whales mainly occurred in northernmost areas of the Antarctic waters from the eastern Indian Ocean to western South Pacific (Fig. 4d). Fig. 5d shows that an apparent distribution gap at 54–58°S in the South Atlantic–Indian Ocean sector, but no such gap in the South Pacific sector. The southernmost sighting was at 64°S. Longitudinal peaks in the encounter rates (Fig. 6d) were at 90–100°E on the eastern side of the Indian Ocean sector and at 170–160°W in the South Pacific sector, with smaller peaks at 120–130°E, 110–120°W and 40–50°W.

Hourglass dolphins mainly occurred in northernmost areas of the Antarctic, especially in the Indian Ocean and South Atlantic sector. This species penetrated farthest south between 150°E and 150°W (Fig. 4e) with the southernmost sighting 67°S in the South Pacific. Hourglass dolphins were not seen in waters south of 66°S in the South Atlantic and Indian Ocean sector, but were frequently observed south of that

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Table IV. Uncorrected abundance estimates of Odontocetes in Antarctic waters during December–February.

Area	Division	Stratum	Sperm whale Abund.	Sperm whale CV	Beaked whales Abund.	Beaked whales CV	Killer whale Abund.	Killer whale CV	Pilot whale Abund.	Pilot whale CV	Hourglass dolphin Abund.	Hourglass dolphin CV
I	West	WS			463	0.48	261	0.70				
		WM	92	0.95	1077	0.51	4069	0.53			939	0.98
	East	ES			1847	0.34	1469	0.42				
		EM			6030	0.41	3021	0.75			9296	0.56
	North	N	1456	0.55	4247	0.57			43013	0.85	11847	1.09
II	West	WS			2170	0.22	423	0.46				
		WM			8121	0.67	1227	0.79				
	East	ES	130	0.46	2517	0.42	1672	0.46				
		EMS	216	0.58	3471	0.32	1311	0.76				
		EMN	392	0.37	9874	0.29	3110	0.96				
	North	NS			13131	0.35	8690	0.47	18205	1.14	15042	0.45
		NN	426	1.00			5631	1.06				
III	West	WS	510	0.67	6983	0.66	822	0.68				
		WN	224	0.48	14808	0.32						
	East	ES	350	0.59	6510	0.48	500	0.88				
		EM	339	0.76	5201	0.47	2241	0.68				
	North	NS	411	0.46	7723	0.27	5922	0.44				
		NN	99	0.93	9120	0.44	2608	0.96				
IV	West	WS	407	0.56	3514	0.26	655	0.70	1877	1.09		
		WMS	259	0.31	5964	0.23	1236	0.51				
		WMN	364	0.37	10972	0.31	2231	0.59	6205	1.12	14526	0.39
	East	ES	46	0.42	287	0.63	2093	0.43	1125	1.09		
		EM	78	0.87	2036	0.46	2066	0.72	8658	0.83	2385	0.67
	North	NS	192	0.49	6319	0.21	846	1.00	28349	0.75	9760	0.37
		NN	269	0.43	2597	0.34	1583	0.72	53070	0.80	10049	0.51
V	West	WS	561	0.38	368	0.79	4968	0.55				
		WMS			3369	0.45	1366	0.99				
		WMN	35	0.91	2752	0.32	931	0.88			2149	0.65
	East	ES			71	0.97	2112	0.59				
		EMS	828	0.49	8900	0.54	2585	0.50				
		EMN	654	0.66	7782	0.32					37233	0.37
	North	NS	59	0.73	275	0.99	777	1.00	13027	0.85	4485	0.72
		NN			682	0.77	1990	0.74			4594	0.63
VI	West	WS	318	0.41	760	0.84	2047	0.82				
		WM			1660	1.96	3070	0.72	12864	1.09	3543	0.62
	East	ES	93	0.56	2019	0.47	2004	0.83				
		EM	72	0.91	593	1.04	1905	0.98				

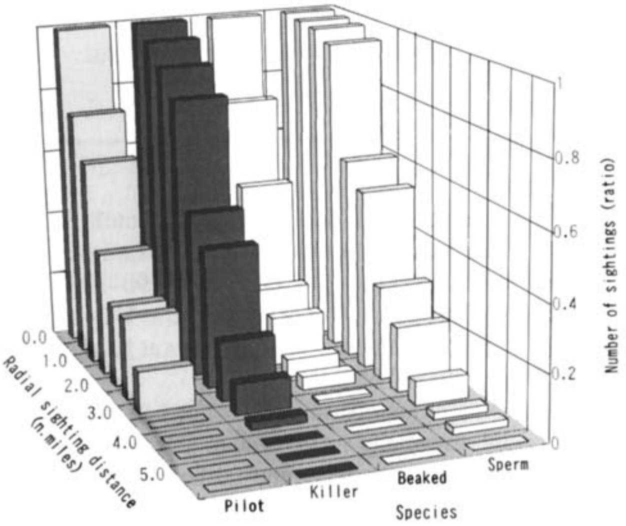

Fig. 9. Frequency distribution of radial sighting distance between 10° from the trackline observed and used for estimation of the detection function.

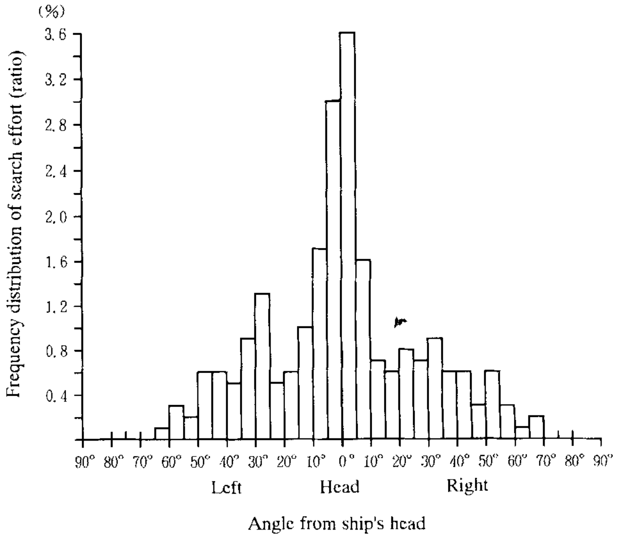

Fig. 10. Search effort distribution (pooled) of observers used in the sighting simulation.

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Table V. Dive cycles observed and used in the sighting simulations.

Species	Dive time (min)	Surfacing frequency max.	min.	mean	Mean surface duration (sec.)	No. of observations	Mean school size
Sperm	48, 55, 33, 41, 26, 61, 24, 64, 47	25	9	15.6	4.6	9	1.0
Beaked	16, 33, 25, 11, 41, 29, 46, 17, 21, 27, 16, 21	18	6	8.8	3.7	12	3.3
Killer	5, 4, 6, 3, 3, 8, 4, 5	7	3	4.4	2.8	8	5.3
Pilot	4, 3, 7	9	4	7.2	2.0	3	13.0

latitude in the South Pacific sector (Fig. 5e). Longitudinal gaps appear at 80–150°W and 0–40°W (Fig. 6e). The distribution pattern of the hourglass dolphin is apparently similar to that of the long-finned pilot whale.

Abundance estimates

Geographical areas and strata used to estimate abundance are shown in Fig. 7. As search effort (search distance) was not distributed homogeneously we checked but found no significant relationship between any species for the relationship between search distance and relative density (encounter rate) in each stratum. Consequently, it is assumed that an unstratified estimate of density should be unbiased in this respect.

Frequency distribution of pooled perpendicular sighting distances by species and by school size are presented in Fig. 8. Estimated search half-widths by species and by school size Table II indicated that the search half-widths for smaller school sizes were smaller than those for larger schools. Table III shows the number of schools seen, mean school sizes and encounter rates by stratum. Table IV shows uncorrected abundance estimates by stratum in each Area.

The probability of the observer being able to detect the sighting cue for a whale (the blow when it surfaces) were obtained for species from a least squares regression of the number of sightings against radial distances in the 1978/79–1987/88 cruises (Fig. 9). Only sightings made within 10 degrees of either side of the vessel's course were used, as this was the most frequently, and presumably the most efficiently searched area. The angular distribution of search effort by

Table VI. Parameters used in the sighting simulation.

Vessel speed	12 kns
Observation period	10 h
No. of observers	3
Track length	120 n miles
Angle of sighting sector	180°
No. of schools generated	1000 schools
Binoculars field of view	7°
Scanning angle velocity	2.7°sec^{-1}
Diving intervals	3-64 min (by species, see Table V)
No. of surfacings	3-25 per whale (by species, see Table V)
Surfacing interval	2-5 sec (by species, see Table V)
Observer detection function	$G(r)=^{-ar^2}$ a: (by species, see Fig.9)
Generated school size composition by species (see Fig. 11).	

observers was derived from the video record of observers during the 1985/86 IWC/IDCR cruise (Fig. 10). In the sighting cruises, about two-thirds of the primary sightings were made by the two primary observers in the barrel and the remainder by other observers. We therefore used three primary observers in the simulations, although the original model by Doi *et al.* (1982, 1983) used two observers. School size compositions observed during the 1978–88 IDCR cruises and used in the simulations are shown in Fig. 11. A total of 25 dive cycles for sperm whales, beaked whales, killer whales and long-finned pilot whales were recorded from direct observations during 1983–90 (Table V). The simulations were conducted each dive cycle of each species with other parameters as shown in Table VI.

The value of $\hat{g}(0)$ (strictly speaking, here $\hat{g}(0)$ means the probability of seeing an animal within the perpendicular distance range of 0–0.09 n mile) was calculated as the total number of animals seen/total animals generated. We estimated the variance of $\hat{g}(0)$ using the boot-strap resampling procedure (Efron 1979, Kasamatsu *et al.* 1990, Kishino *et al.* 1991). In estimating the variance, the data from the simulation trials were resampled with replacements, and the bootstrap procedure was replicated 100 times.

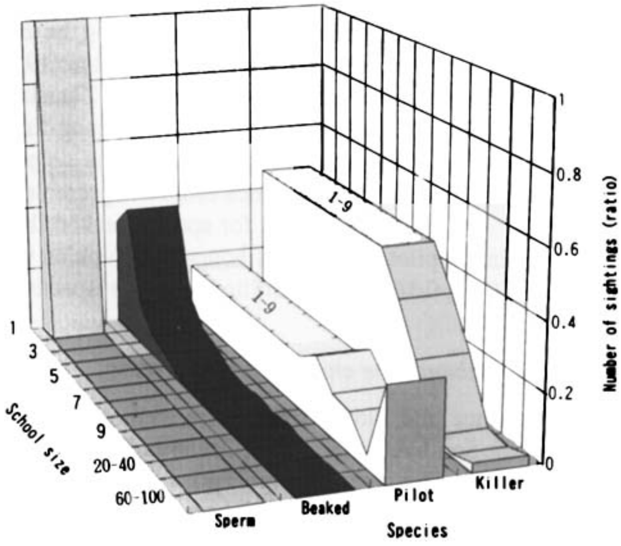

Fig. 11. School size compositions observed and used in the sighting simulations.

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Table VII. Estimated $\hat{g}(0)$ and corrected abundance estimates of Odontocetes.

Species	Estimate $\hat{g}(0)$	CV of $\hat{g}(0)$	χ^2	d.f.	Corrected abundance animals	CV
Sperm	0.32	0.11	5.2561	5	28 100	0.18
Beaked	0.27	0.04	7.6885	4	599 300	0.15
Killer	0.96	0.07	5.2846	4	80 400	0.15
Pilot	0.93	0.03	2.3617	4	200 000	0.35
Hourglass	-	-	-	-	144 300	0.17

Table VIII. Abundance and biomass of major Odontocetes (sperm, beaked and killer whales) by sector.

Sector	Abundance (10^3 animals)	Biomass (10^3 tonnes)	Biomass/ n mile^2
S. Atlantic	273.7	1373.3	0.49
Indian Ocean	230.6	1214.0	0.43
S. Pacific	203.6	1201.1	0.39

Estimated $\hat{g}(0)$ values from the simulations for sperm, beaked, killer and pilot whales were 0.32 (CV 0.11), 0.27 (0.04), 0.96 (0.07) and 0.93 (0.03), respectively. The frequency distributions of the perpendicular distances of the sightings from the cruises and those from the simulations are not significantly different (at the 5% level) (χ^2 values 2.3617–7.6885 df=4–5) for any species (Table VII). The sighting simulation trials for each species therefore appear to perform well. Abundance estimates corrected by $\hat{g}(0)$ and their coefficients of variation are shown in Table VII. Since the majority of the cruises were conducted between late December and early February, the abundance estimates obtained here are taken to be approximately representative of the month of January.

The biomass of each species was estimated using the mean body weight of sperm whales (27.4 tonnes, Lockyer 1981), beaked whales–southern bottlenose whales (4.5, Zemskii & Budylenko 1970), killer whales (4.0, Evans 1987), long-finned pilot whales (0.8, Sergeant 1962) and hourglass dolphins (0.1, Evans 1987) and the abundance estimates presented in this paper. Estimated biomasses for sperm, beaked, killer and long-finned pilot whales and hourglass dolphins were 0.77, 2.70, 0.32, 0.16 and 0.01 million tonnes, respectively.

Variation of abundance and biomass by sector

The abundance and biomass estimates were summed by sector for the South Atlantic, Indian Ocean and South Pacific (Table VIII). The three sectors had a broadly similar abundance and biomass, but the highest values were in the South Atlantic. The small magnitude of the variation in abundance and biomass of Odontocetes is interesting because the variation in baleen whale abundance and biomass between the sectors is large (Kasamatsu 1993).

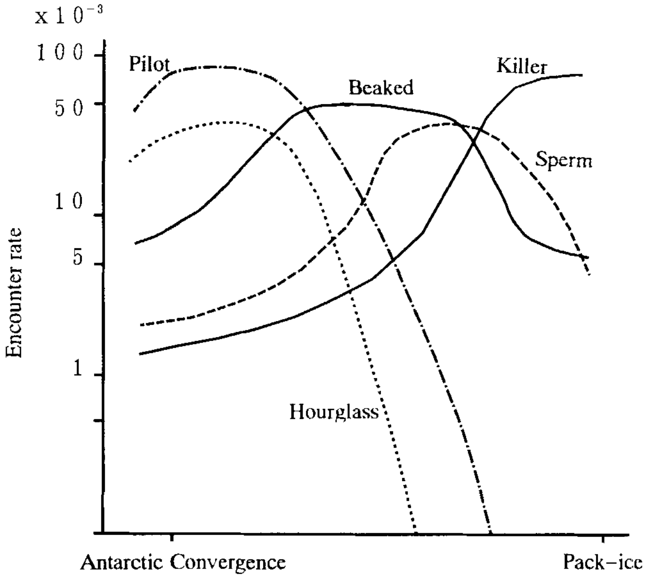

Fig. 12. Outline of latitudinal occurrence of Odontocetes in Antarctic waters, based on encounter rate from the ice edge.

Conclusions

Distribution

Although segregation and different migration patterns have been suggested for baleen whales (e.g. Mackintosh 1965), there has been little information on the seasonality and segregation of Odontocetes, except the sperm whale. Different migration patterns have now been identified, especially between the sperm and killer whales. Possible latitudinal segregation between species in Antarctic waters was indicated (Fig. 12). In general, killer whales occur in the southernmost waters, sperm whales mostly south of 60°S, beaked whales over a wide range of latitudes, and long-finned pilot whales and hourglass dolphins in the more northerly Antarctic waters. Such seasonality and segregation could have evolved to reduce competition for food.

Possible biases on density and abundance estimates

Several potential biases or problems were identified. Sample sizes of pilot whales in areas other than Area IV and those of hourglass dolphins in Areas I, IV and V may be too few to obtain reliable abundance. Any bias in abundance estimates for these species, however, would have little impact in the overall examination of the role of Odontocetes in the Antarctic ecosystem, as these species probably contribute <5% of total Odontocetes biomass.

Another problem may be an assumption that the probability of sighting is not affected by area or is constant over the entire area. Surveys covered most of Antarctic waters, including West Wind Drift area, in which strong winds can be experienced, and the relatively calm sea area in the southernmost part of Antarctic waters. Searches were conducted only

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in Beaufort 5 or less in order to reduce weather effects on the probability of sighting a whale. These criteria were applied for all species except small cetaceans such as hourglass dolphins. This may produce some negative bias in the probability of sighting, with a subsequent effect on the calculation of the encounter rate and search half-width of hourglass dolphins, but the magnitude of the biases is not known. Although there was no direct information on effect of area or sighting conditions on density estimates for toothed whales in the Antarctic to support this conjecture, Buckland *et al.* (1993) did show that there was no significant difference in the search half-width among areas for long-finned pilot whales in the North Atlantic cruises. In addition, having found no significant difference in the search half-width between the southern-most area of Antarctic waters (Kasamatsu 1993) and the area between 10–60°S (mainly West Wind Drift area; Kasamatsu & Miyashita 1983, 1984) for medium-sized whales (southern minke whales), the effect of area on the probability of sighting pilot, killer, beaked and sperm whales, may not be substantial. Therefore, encounter rate as an index of density should be representative of the density of whales free from any significant effect from area or the sighting conditions.

The estimation of mean school size was also susceptible to several potential biases. For example, pilot whales and killer whales sometimes form loose aggregations. In this situation, mean school size will be overestimated if all individual sub-groups were considered as part of a single school, because a large aggregation, spread over a large area, is more likely to be detected than the smaller individual groups (Buckland *et al.* 1993). In these cruises, the school size of the first detected group of the aggregation was recorded, and the other groups were recorded as secondary sightings. However, if a sighting was made far from the vessel, it was often difficult to identify which group was first detected. Under this circumstance, researchers sometimes recorded the aggregation as a single school while noting that it was an aggregation of several groups. There is no information on how this will effect the mean school size. The mean school size of long-finned pilot whales could not be calculated due to the small sample size and consequently observed mean school sizes were used which may lead to some overestimation.

Another source of potential problem is the estimation of $\hat{g}(0)$. There were no previous estimates of $\hat{g}(0)$ for these species in the Southern Ocean. The value of $\hat{g}(0)$ is an important component in the estimation of abundance, especially for these long-diving species. The distance travelled by a sighting vessel during the average 25 min dive of beaked whale is *c.* 5 n miles. Because the average sighting distance of beaked whales is *c.* 1.5 n miles it seems very likely that an important portion of beaked whales on or near trackline will be missed. Therefore, it becomes essential for us to evaluate $\hat{g}(0)$ if we are to understand the ecological role or population status of these animals. While other methods to estimate $\hat{g}(0)$ have not succeeded, the simulation method appears to produce reasonable estimates. Although this method lacks robustness due to the nature of the assumption required to conduct the simulations, the assumption is based on data derived from long-term sighting surveys. Most of the basic parameters were derived from large databases gathered during the research cruises. However, the dive profiles (one of the major parameters) are from a very small database. Although these dive profiles are very similar to the typical dive patterns reported by other researchers (Leatherwood *et al.* 1982), the total database is inadequate to permit an evaluation of the robustness of the simulation. Therefore, more data on dive behaviour is required to identify variations in $\hat{g}(0)$ estimate. In addition, the assumption that the parameters are constant values throughout the area and season is not likely to hold. This assumption may lead to smaller variances for $\hat{g}(0)$ estimates.

Table IX. Estimated food consumption by Odontocetes in the Antarctic waters.

Species	This paper: Abundance[1]	This paper: Biomass (10³ tons)	This paper: Food consumption (10³ tons)	Laws 1977: Abundance	Laws 1977: Biomass (10³ tons)	Laws 1977: Food consumption (10³ tons)
Sperm	28100	769.9	3100[2]	43000	1161	4900
Beaked	599300	2696.9	9700[3]			
Killer	80400	321.6	900[4]			
Pilot	200000	160.0	500[5]			
Hourglass	144300	14.4	100[6]			
Total		3952.8	14300			

[1]Abundance in peak month of occurrence (see Table VII).
[2]Same assumption as Laws (1977) used was adopted.
[3]Assume that daily food consumption was 4% of body weight and mean duration days in the Antarctic waters 90 days (Kasamatsu 1993).
[4]Daily food consumption 4% and mean duration 70 days (Kasamatsu 1993).
[5]Daily food consumption 4.7 % (Sergeant, 1969) and mean duration 70 days (Kasamatsu 1993).
[6]Daily food consumption 8% as same as other dolphin (Sergeant 1969) and mean duration 60 days (Kasamatsu 1993).

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Role of beaked whales in the Antarctic marine ecosystem

Several authors have discussed the Antarctic ecosystem in terms of estimates of consumption by top predators (e.g. Gulland 1970, Laws 1977a, b, Bengston 1984, Everson 1984). The most extensive estimates of krill consumption have been for whales. Laws (1977a) indicated that Antarctic whales initially (in pre-whaling times) removed about 190 million tonnes of krill annually but that they currently (i.e. mid-1970s) removed about 43 million tonnes. The difference of *c.* 150 million tonnes has been termed the "krill surplus" which if consumed by other predator groups such as the crabeater seal, could result in major changes in their demography (Beddington & de la Mare 1984, Bengston & Laws 1985).

Laws's (1977a) figures took into account only sperm whales among the Odontocetes. However, the results of this study clearly indicate that other Odontocetes, especially the southern bottlenose whale, play a significant role in the Antarctic ecosystem. On the basis of results obtained in this study, we have made preliminary estimates of food consumption by Odontocetes in Antarctic waters (Table IX). The estimated total amount of food consumption is 14.4 million tonnes, of which 67% is by beaked whales and 22% by sperm whales. This total can be compared with the estimate of 4.9 million tonnes (sperm whales only) by Laws (1977a, 1977b).

Medium-sized Odontocetes such as beaked whales prey primarily on cephalopods (squid) (Leatherwood & Reeves 1983, Mead 1989, Goodall & Galeazzi 1985, Sekiguchi *et al.* 1993) which are major predators of large plankton and small nekton, particularly krill (Nemoto *et al.* 1985). The large annual consumption of squid (*c.* 11 million tonnes) by beaked whales has never been considered for production estimates. Furthermore, if the conversion efficiency of krill biomass to squid biomass of 40% (Everson 1984) can be adopted, the indirect annual consumption of krill and other organisms by beaked whales is estimated at *c.* 24 million tonnes, which is close to the annual consumption of 33 million tonnes estimated for penguins (Everson 1984). Therefore, it is critically important for us to include medium-sized Odontocetes, especially the southern bottlenose whale, in any study of the Antarctic ecosystem. Moreover, it is important to include the medium-sized Odontocetes into the discussion of the marine ecosystem, not only in Antarctic water, but in all seas.

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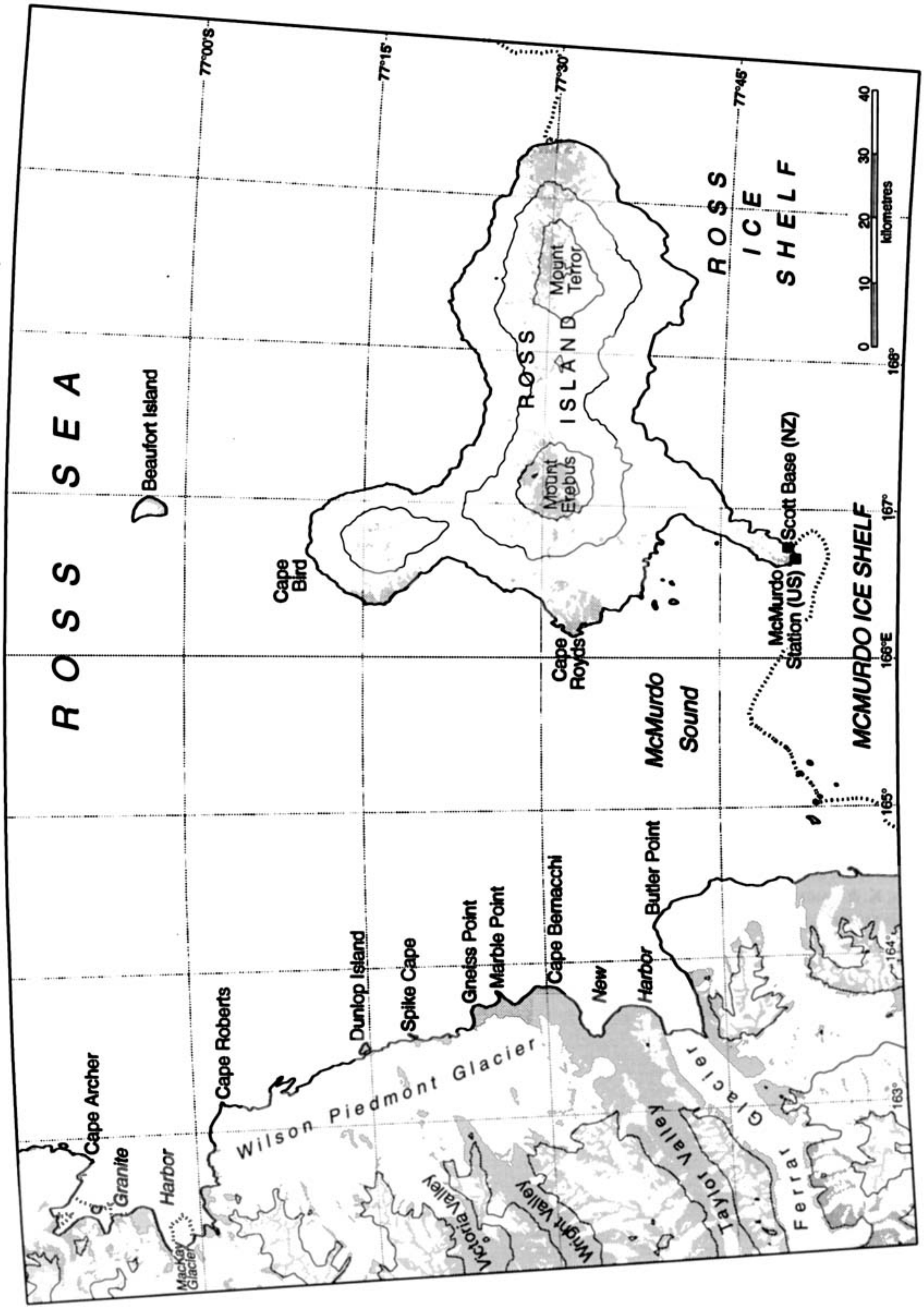
***Antarctic Science* Handy Atlas Map No. 15.**

IMW Sheets ST 57–60 Cape Roberts–Ross Island area, 1:1 000 000 scale, contour interval at 1000 m. Shaded areas represent rock outcrops.



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