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Food and daily food consumption of southern minke whales in the Antarctic*

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Summary. The stomach contents of 273 southern minke whales (*Balaenoptera acutorostrata*) taken in the region 55°S to the ice-edge and between 105°E and 115°E by a Japanese survey during 1987/88 were examined. The minke whales' dominant feeding ground coincided with a distinctive hydrographic front in the vicinity of the ice-edge at the mouth of Vincennes Bay. Krill (*Euphausia superba*) were the dominant food species comprising 100% and 94% by weight of stomach contents in the ice-edge and offshore zones, respectively. In the offshore zone, minke whales tend to feed on *E. superba* rather than *Thysanoessa macrura*, which is found more frequently than the former in net samples. Total food consumption by minke whales per day was estimated to be 1170 t (22.1 kg/km^2) and 596 t (2.0 kg/km^2) in the ice-edge and offshore zones, respectively. Feeding activity peaked in the early morning in the ice-edge zone, whereas it occurred irregularly throughout the day in the offshore zone. Two size modes of krill (25–28 mm in body length (1 year-old) and 41–48 mm (3–4 year-old)) dominated the diet. Although the former was numerically more abundant, the latter dominated the diet by weight, suggesting that larger krill are more important food for minke whales. Observed spatial pattern of krill populations in the study region suggests that movement of the subsurface cold water mass tended to carry krill offshore from the ice-edge.

Introduction

Several authors (Ohsumi et al. 1970; Kawamura 1980; Kawamura and Kikuno 1980; Bushuev 1986) have examined the stomach contents of the southern minke whale (*Balaenoptera acutorostrata*) and found that krill (*Euphausia superba*) is the most important food species. These studies, however, were based on samples obtained from commercial whaling operations which were essentially limited to the ice-edge zone.

In 1988 Japan conducted "research take" of minke whales under the auspices of a scientific permit issued by the Japanese government (Kato et al. 1989). This survey adopted a random sampling strategy in a wide latitudinal area (from 55°S to the ice-edge between 105°E and 115°E), thus resulting in information on whale feeding being collected from a larger geographical area than previously sampled. Furthermore it was possible to estimate food consumption by minke whales quantitatively from abundance information.

In an attempt to improve the definition of the oceanographic structure of minke whale feeding grounds, oceanographic data (i.e. water temperature) were collected throughout the cruise. Information on ice-edge position was also routinely recorded.

This paper presents the results of analyses of stomach samples and data collected during the above cruise and attempts to examine some aspects of minke whale feeding ecology.

Materials and methods

A total of 273 minke whales, including one dwarf form minke whale, were collected at random during the cruise between January 17 and March 26, 1988. (The dwarf form minke whale is a different type of the typical minke whale in body size, characters of the baleen plates and the dorsal fin (Best 1985; Arnold et al. 1987).) The cruise trackline was designed so as to cover the whole area uniformly using the reflection method (Kato et al. 1989; Kishino et al., in press). The density of minke whales, DI (density index), is expressed as the number of whales seen per 100 n. miles steamed. The sampling scheme for minke whales were varied with school size, i.e. all solitary animals detected were sampled, and two whales were sampled at random from a school of more than two animals. Body length was measured to the nearest 10 cm from the tip of the upper jaw to the deepest part of the fluke notch along a straight line parallel to the body axis. Figure 1 illustrates the positions where whales were collected. Following Kasamatsu et al. (1990a), the survey area was divided into two zones; an ice-edge zone (within 60 n. miles from ice-edge line) and an offshore zone (south of 60°S excluding the ice-edge zone). As for a zone between 60°S and 55°S, a reliable estimate (from

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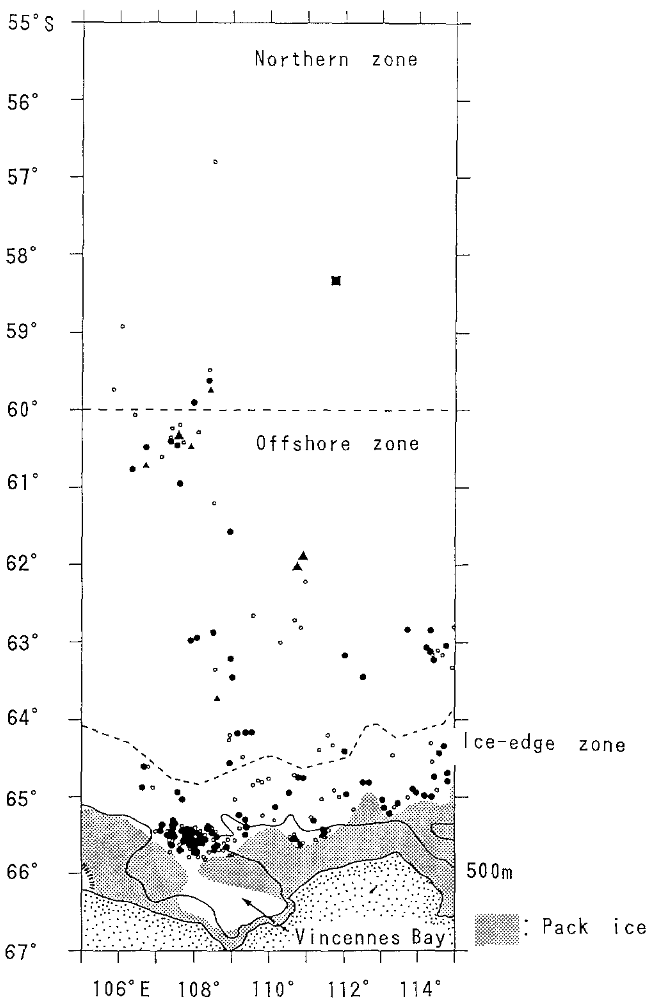


Fig. 1. Occurrence and distriubution of food organisms in the stomachs of minke whales. ●: *Euphausia superba* only ▲: Dominant occurrence of *Thysanoessa* spp. ▴: Subordinate occurrence of *Thysanoessa* spp. among *E. superba* ■: Fish (*Myctophid* sp.) only (fed on by a dwarf form minke whale) o: No collection of stomach contents because of empty stomach or heavy digestion of contents

sightings) of the minke whale population present was not available due to unfavorable weather conditions. Hence this zone was excluded from subsequent quantitative analyses of stomach contents.

Between 50 and 200 individuals of krill were randomly sampled from each whale with relatively fresh food in its stomach, and preserved in 10% formalin solution for examination. Krill were measured and their maturities were determined using the Makarov and Denys (1981) system of the classification. Body length (BL) was measured to the nearest 1 mm from the anterior tip of the rostrum to the posterior end of the telson. When krill were heavily digested, BL was calculated from a regression function for BL on carapace length ((CL) tip of rostrum to mid-dorsal posterior edge of carapace). When CL could not be used due to digestion or for other reasons, BL was estimated from the regression of BL on uropod length ((UL) total length of uropod, excluding setae). Regression formulae for BL on CL were calculated for each class by sex and maturity stage (Table 1). For the purpose of obtaining a formula for BL on UL, all maturity stages were combined (Table 1).

The length composition of krill consumed per day by the entire minke whale population for each zone was estimated as follows:

$$F_i = \sum_{j=1}^{J} f_{ij} \cdot \frac{WM_j}{WK_j} \cdot \frac{NT}{NS} \qquad (1)$$

where F_i = estimated number of krill consumed per day by the entire minke whale population in the ith ($i = 1, 2, \ldots, I$) length class,
f_{ij} = number of krill measured in the ith length class in the jth ($j = 1, 2, \ldots, J$) sample,
WM_j = estimated weight of krill consumed by the jth whale per day,
WK_j = weight of krill in the jth sample,
NT = estimated number of minke whales in the population,

and

NS = number of minke whales sampled by the study.

WM_j was estimated assuming that minke whales eat 4% of their body weight per day (Sergeant 1969; Lockyer 1981; Markussen et al. 1990). Whale body weight was estimated from the weight-length relationship:

$$W = 0.0110\ L^3 \text{ (Doi 1978)} \qquad (2)$$

where W is the weight in t and L the length in m. WK_j was estimated using the weight-length relationship:

$$W = 2.36 \times 10^{-6}\ L^{3.37} \text{ (Ikeda et al. 1986)} \qquad (3)$$

where W is the weight in g and L the length in mm.

Oceanographic information on vertical thermal distributions was obtained using XBTs (Expendable Bathythermographs). Information on the pack-ice edge was collected from catcher boat observations and based on data published by Zwally et al. (1983)

Results

Hydrography of minke whale feeding grounds

The Polar Front in the area 105°–115°E is reported to be located between 55°S and 56°S (e.g. Edwards and Emery 1982; Nakai et al. 1986). This means that the survey area covered almost the entire Antarctic latitudinal zone.

Surface water (0–50 m) temperature ranged from 0.0°C to − 1.5°C at the ice-edge and increased with decreasing latitude to ca. 3.0°C near the Polar Front (Fig. 2). A distinctive front (between oceanic waters and cold shelf water) was observed near the ice-edge around the mouth of Vincennes Bay, where minke whales were highly abundant, the ID being 71–490 (Fig. 2a,b). Conversely no distinctive front was recognized near the eastern ice-edge, where whales were not so abundant, the ID reaching 42 (Fig. 2c).

It has been shown that subsurface (50–150 m depth) cold water penetrates northward beneath the surface water from higher latitudes (Fig. 2) as observed in other regions of Antarctic (Gordon 1967, 1975; Deacon 1984; Middleton and Humphries 1989). Subsurface water with temperatures lower than − 1.0°C, originating from cold shelf water in Vincennes Bay, was extensive in the western/central region (105°–112°E), but rarely occurred in the eastern region (112°–115°E) (Fig. 2).

Circumpolar Deep Water was observed below the subsurface cold water and formed a sharp transition zone with colder shelf water around the mouth of Vincennes Bay (Fig. 2a,b).

Food composition of minke whales

Of the 202 and 52 whales taken in the ice-edge and offshore zones, respectively, (excluding 7 and 4 whales whose

Table 1. Formulae for the conversion of body length (BL) from carapace length (CL) and uropod length (UL) for krill. Formulae are linear and of the forms: BL = intercept + (slope × measured length). Maturity stages are after Makarov and Denys (1981)

Conversion	Maturity stage	Intercept (mm)	Slope	*n*	Correlation coefficient	Range (BL, mm)
BL from CL	Juvenile	2.339	2.847	540	0.917	18–42
	Subadult and adult male (2A1,2A2,2A3,3A)	8.968	2.497	216	0.823	33–54
	Ripe adult male (3B)	7.925	2.841	172	0.828	40–54
	Subadult and adult female (2A,3A,3BC)	12.191	2.060	293	0.919	28–56
	Ripe/spent female (3D,3E)	7.717	2.350	108	0.830	41–58
	All	3.466	2.763	1599	0.957	18–58
BL from UL	All	2.861	6.948	606	0.980	19–57

stomachs were damaged by the harpoon in the respective zones), 165 (82% of whales taken) and 42 (81%) had food in their stomachs in the respective zones (Table 2). Relatively fresh food were found and sampled from 100 and 30 whales in the respective zones. *E. superba* was dominant in 100 (100% of samples) and 27 (90%) stomachs in the ice-edge and offshore zones, respectively. Three juvenile (one-year-olds) whales (10%) from the latter zone had consumed almost solely on *Thysanoessa* spp. No mature whales were observed to fed predominantly on these euphausiids.

Assuming that whales consume food at a constant rate with body weight, food composition (% by weight in the diet) can be calculated for each zone as follows:

$$C_i = \frac{\sum_{j=1}^{J} P_{ij} W_j}{\sum_{j=1}^{J} W_j} 100$$

where C_i = estimated percentage of food species i (i = 1,2) by weight in the diet of minke whale population,

P_{ij} = percentage of food species i by weight in the jth (j = 1, 2, . . . , J) stomach sample,

and

W_j = body weight of the jth minke whale.

From these calculations, *E. superba* comprised 100% and 94% of the diet by weight in the ice-edge and offshore zones, respectively, and *Thysanoessa* spp. 6% in the latter zone.

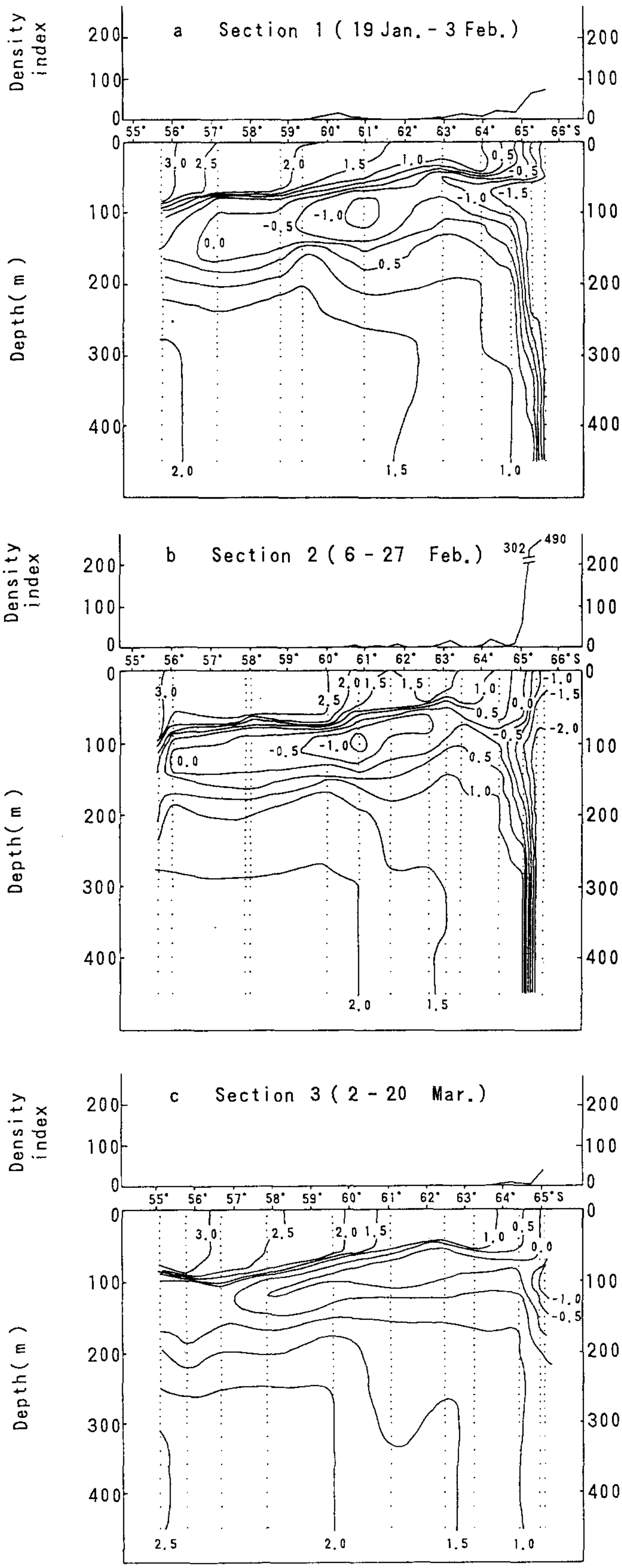
It was not possible to identify the *Thysanoessa* spp. to species (i.e. *T. macrura* or *T. vicina*), since identification keys were not applicable due to immaturity or heavy digestion of the specimens.

Fish were rarely found in the stomachs in any quantity. One exception was a dwarf form minke whale that appeared to have fed exclusively on *Myctophid* spp. far north at 58°S (Fig. 1), as reported by Kato et al. (1989).

Daily food consumption by whales in ice-edge and offshore zones

Using the length-weight relationship for minke whales (equation 2), mean body weights of animals were calculated to be 6.23 t and 4.43 t for the ice-edge and offshore zones, respectively, from dividing the total weight of whales taken by the number of whales taken in the respective zone. This difference in weight between the zones is mainly caused by the segregation of female whales (i.e. sexually matured females are dominant in the ice-edge zone, while younger immature in offshore zone.) (Kato et al. 1990). Kasamatsu estimated the numbers of minke whales in the ice-edge and offshore zones to be 4,696 and 3,366, respectively (unpublished data) (Table 3). (The methodology used by him was described in Kasamatsu et al. (1990a).) Multiplying the population estimates by the mean body weights, the total biomass of minke whales were calculated as 29,256 t and 14,911 t for the ice-edge and offshore zones, respectively (Table 3). Assuming a daily food intake rate is 4% of the body weight, the total amounts of food consumed by whales were estimated to be 1,170 t (22.1 kg/km^2) and 596 t (2.0 kg/km^2) per day in the ice-edge and offshore zones, respectively. Consequently, by food species in each region, 1,170 t (100%) of krill were consumed in the ice-edge zone, whereas 560 t (94%) of krill and 36 t (6%) of *Thysanoessa* spp. were consumed in the offshore zone. Minke whales therefore consumed 1730 t (98%) of *E. superba* and 36 t (2%) of *Thysanoessa* spp. per day throughout the survey area.

From the examination of daily changes in relative stomach fullness, minke whales tend to feed earlier in the day in the ice-edge zone, whereas in the offshore zone no



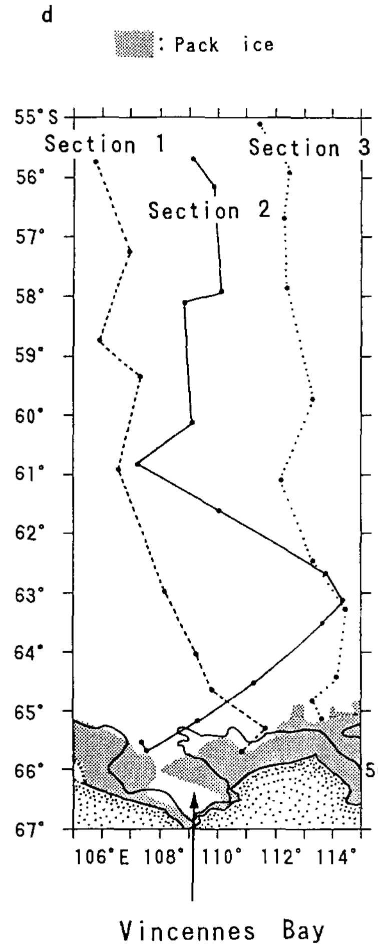


Fig. 2. a–c Whale densities and water temperature profiles along the latitudinal sections, 1,2 and 3. Density index is expressed as the number of whales seen per 100 n. miles steamed. **d** Geographical distribution of each section

clear trend in the timing of feeding was discernible (Fig. 3). Bushuev (1986) has suggested that the former feeding pattern is typical of regions where there is abundant and stable food supply, whereas the latter characterizes regions of low or unstable food supply.

Length composition of krill consumed by minke whales

For analyses of krill length composition, stomach samples from the ice-edge zone were divided into three groups. These comprised the western (WIA), central (CIA) and eastern ice-edge area (EIA) groups. Samples in the offshore zone were divided into three groups being the central (COA), eastern (EOA) and northern offshore area (NOA) groups (Fig. 4). There were distinctive regional differences in the length compositions. Krill with a modal length of 25–28 mm were dominant (with a secondary minor mode at 41–44 mm) in the western/central region (WIA, CIA and COA), whereas krill with a mode at 45–48 mm and a minor mode at 25–28 mm dominated the eastern region (EIA and EOA). In the most northern region (NOA), 25–28 mm and 41–48 mm modes were present in nearly equal proportions.

Using the equation (1), the length composition of krill consumed per day by the minke whale population was constructed for each of ice-edge and offshore zones. For

Table 2. A summary of information on stomach contents. Figures without parentheses indicate the number of minke whales

Stomach contents	Occurrence (%)	
	Ice-edge	Offshore
Euphausia superba	100 (100.0)[b]	24 (80.0)
E. superba/Thysanoessa spp.[a]	0 (0.0)	3 (10.0)
Thysanoessa spp.	0 (0.0)	2 (6.7)
Thysanoessa spp./*E. superba*	0 (0.0)	1 (3.3)
No collection due to heavy digestion	65	12
Empty	37	10
Lost due to damage by the harpoon	7	4
Total	209	56

[a] By the order of dominancy
[b] Percentage to the total collected stomach samples

Table 3. Estimates of number, mean body weight and biomass of minke whales in the ice-edge and offshore zones. *from Kasamatsu (unpublished data)

Zone	Area $10^3 km^2$ (%)	Number *n* (%)	Mean body weight t	Biomass t (%)
Ice-edge	53 (15)	4696* (58)	6.23	29256 (66)
Offshore	298 (85)	3366* (42)	4.43	14911 (34)
Total	351 (100)	8062* (100)		44167 (100)

obtaining the overall length composition consumed by the total minke whale population ("Ice-edge" + "Offshore"), we summed the two length compositions with weighing the corresponded absolute value of minke whale population size in the each zone (Fig. 5a). This overall length composition largely reflected characteristics of the length composition of the dominant feeding ground (i.e. WIA), namely a 25–28 mode combination with a smaller 41–44 mm peak.

Using the length-weight relationship for krill (equation 3), the length composition by numbers was converted to weight. As shown in Fig. 5b, krill in the 41–48 mm mode, which comprised only 31% of the total krill consumed by numbers, amounted to as much as 71% by weight. This is because krill with a modal length of 41–48 mm has 5.7 times as much weight as krill with a mode at 25–28 mm.

Discussion

The mouth of Vincennes Bay used to be an important minke whale whaling ground (Bushuev 1986; Ichii 1990). Vincennes Bay is a continental shelf, topographically deep bay (deeper than 1000 m at the inner part of the bay) caused by glacial incision, and filled with cold shelf water (Vanney and Johnson 1985) (Fig. 1). The distinctive surface front caused by meeting of the cold shelf water and oceanic waters may accompany horizontal convergence, because oceanic surface flow in the East Wind Drift is southward under the influence of the Ekman transport (Deacon 1982; Smith et al. 1984). This convergent effect appeared to concentrate krill to this specific area, consequently this area became an important feeding ground of minke whales.

Satellite image shows that eddies are generated near the continental shelf break off Adelie Land (Swithinbank 1988), i.e. a frontal region between the shelf water and oceanic waters, and a common krill fishing ground (Ichii 1990). Eddies may be therefore an additional factor accumulating krill near the front in the study area.

The strong subsurface front separating the colder shelf water and Circumpolar Deep Water, such as shown in Fig. 2a,b, is the prime site for significant hydrodynamic processes, i.e. the transformation of Circumpolar Deep Water

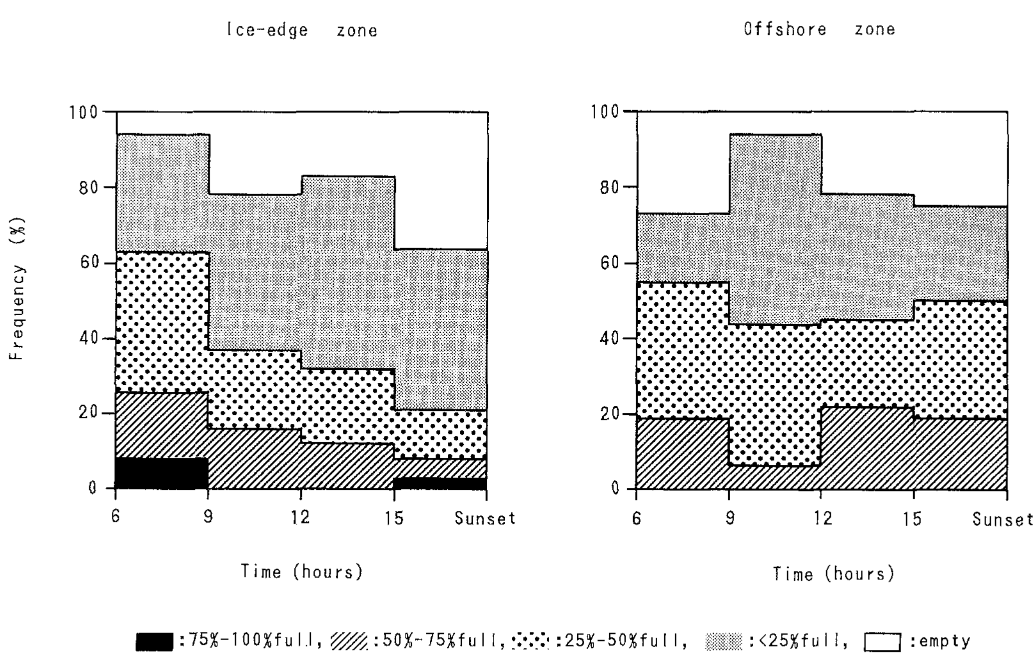


Fig. 3. Diurnal changes in relative fullness of stomach contents of minke whales in ice-edge and offshore zones

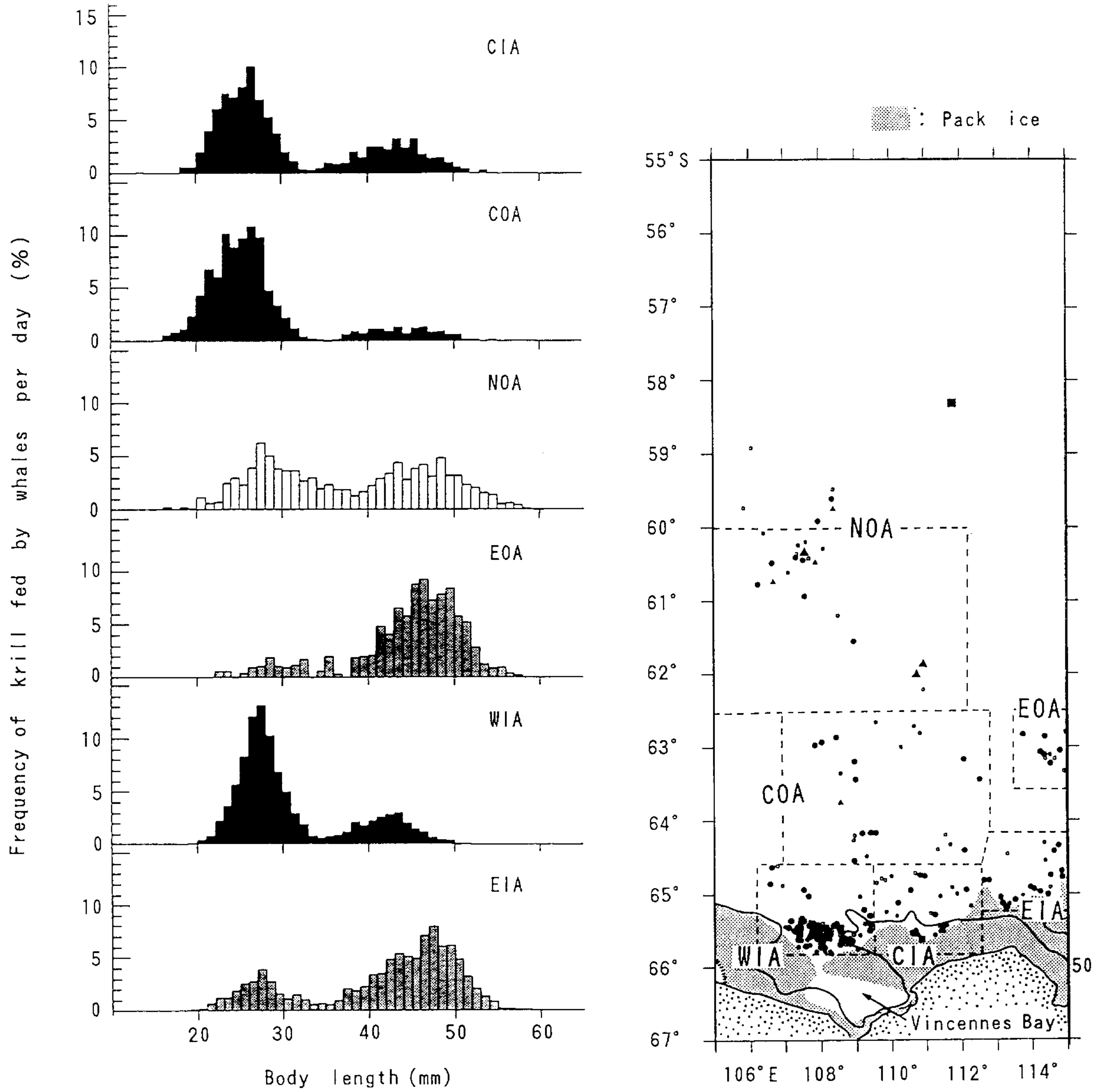


Fig. 4. Length compositions of krill by areas. These are arranged in the order in which survey was conducted. Solid histogram: the western/central group; Shaded histogram: the eastern group; Open histogram: the northern most group

into a variety of surface, slope, shelf and bottom waters (Middleton and Humphries 1989; Jacobs, in press).

Ichii (1990) has indicated that a combination of topographical features (e.g. the continental shelf break and banks/deeps on the continental shelf) and sea-ice are associated with the most prominent minke whaling grounds. The former factor causes specific hydrographic conditions which must induce krill concentrations. In addition, sea-ice is likely to be an important factor required for successful feeding (e.g. the presence of the ice-edge may reduce the effect of unfavorable weather, and contribute to krill aggregating at a water depth accessible to feeding whales (Bushuev 1990)). The present results support this conclusion.

Zwally et al. (1983) have shown that ice melts during early summer (in November) in Vincennes Bay, and hence potentially durable primary productivity is expected there. This may also support high krill abundance and subsequently high whale abundance in the general vicinity of the Bay.

According to net sampling data (Fishery Agency 1980), *E. superba* is most frequent in the ice-edge zone whereas *T. macrura* dominates the offshore zone of the study area. Surprisingly, the present stomach content analyses show that *E. superba* comprised the dominant food item in both zones. This observed difference between whale stomach and net samples in the offshore zone suggests that minke whale selectively fed on *E. superba*. However it should be noted that three juvenile whales (one-year-olds) fed almost entirely on *Thysanoessa* spp.. This can be explained by the probability that juvenile animals have less experience in foraging for active swimmers such as krill (Hamner et al.

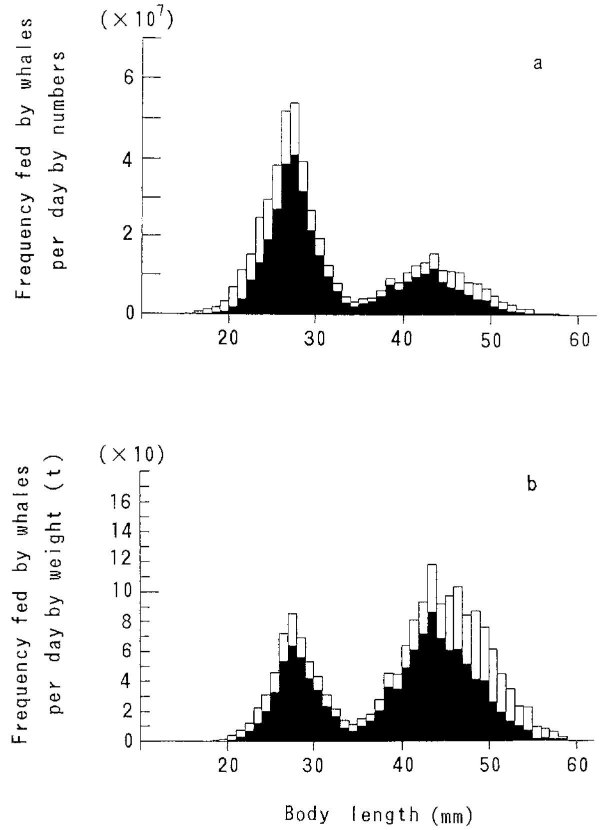


Fig. 5. Overall length composition of krill consumed per day by all the minke whales in the study area in terms of krill numbers **a** and weight **b**. Solid bars indicate numbers/weight for the ice-edge zone and open bars for the offshore zone

1983), which are normally preferred food items of mature individuals.

T. macrura is reported to be an important food of baleen whales in the area from 100°–135°W (Nemoto and Nasu 1958), where *E. superba* is considered to be scarce (Marr 1962; Mackintosh 1973). This area correspond to one of low density areas of minke whales (Kasamatsu et al. 1990b).

Net samples have also shown the occurrence of less abundant euphausiids such as *E. triacantha* and *E. crystallorophias*. Since the former species does not swarm in the adult stages (Baker 1959), it is concluded that it does not comprise a suitable food for minke whales. *E. crystallorophias* swarms but only a single occurrence in net samples was recorded, suggesting that it is a minor food species in the region studied.

This study has adapted the 4% figure as the daily feeding rate for minke whales, which is based on theoretical studies (e.g. Sergeant 1969; Lockyer 1981; Markussen et al. 1990). However, as pointed out by Horwood (1990), this figure is not supported by field data (i.e. quantities of stomach content), with likely intake rate of 0.6 to 2.1%. Recently, Kato and Shimadzu (1986) weighed food contents from the first and second stomachs of 39 Antarctic minke whales, whose both stomachs were judged to be full. (Conventionally the first stomach contents have been weighed on the whales whose first stomachs are judged to be full.) They obtained the rates of 1.9 to 5.1% and considered that these values may be still conservative in the light of the proceed of digestion of the food contents. It is therefore considered that 4% figure may not be so high.

A constant feeding rate with age/size, which is assumed in this study, is unlikely, because younger/smaller whales are likely to have a higher relative food intake. Using the energetic approach described by Lockyer (1981), with the von Bertalanffy (1938) growth equations (given for area 70°–130°E in IWC (1979)) and the weight-length relationship (Doi 1978), we can predict that the feeding rate for one-year-old (2.1 t) male minke whale is 1.37 times as high as that for 10-year-old (6.0 t) male whale. As for female, assuming that sexual maturity is 7 years (Kato 1987) and pregnancy rate is 78% (Best 1982), the rate for one-year-old (2.1 t) is 1.25 times as high as that for 10-year-old (7.1 t). There is also difference by sex, i.e. matured female at 6.6 t, which requires energy for reproduction, has a higher intake rate than matured male at the same body weight by a factor of 1.18. All these ratios, however, are not applicable until we know the intake rate of which size/age or sex should be most close to the 4% value. Moreover, feeding rate may be varied depending on area (i.e. the ice-edge or offshore zones). Therefore, at this stage of conjectured knowledge on quantitative food intake, it may not be appropriate to complicate, by incorporating the variable feeding rate, the calculations for estimating food consumption for each zone.

Daily food consumption per area by minke whales in the offshore zone was about 1/10 of that in the ice-edge zone. Daily feeding patterns of minke whales also suggest that in the former zone the food supply was low or unstable (Fig. 3). Hampton (1985) has reported that in the offshore zone krill are generally uniformly spread and form widely-spaced small swarms, probably because of an absence of distinctive hydrographic features to concentrate them into any restricted area. This wide spread distributional pattern of krill in combination with low abundance may be one reason for reproductive segregation of mature female minke whales in the ice-edge zone.

Kawamura and Kikuno (1980) examined length compositions of krill consumed by minke whales from November to February in the Indian sector during three consecutive seasons. Our results agree quite well with theirs. Such agreement leads to the conclusion that larger krill (40–50 mm) are more important food for the minke whale than small ones (15–30 mm), although the latter may be numerically dominant in stomach contents depending on years. According to the theoretical growth curve for krill (Ikeda 1985), assuming that krill grow for only 4 or 5 months of the year, a length mode of 40–50 mm corresponds approximately to an age of 3 to 4 years, while 15–30 mm krill are essentially one year old.

Length compositions clearly differed between the western/central region (WIA, CIA and COA) and the eastern region (EIA and EOA). The subsurface cold water of the former region originated from the cooler shelf water mass in Vincennes Bay, whereas that of the latter region was from the warmer shelf water mass on the continental shelf (Fig. 2). The difference in the subsurface water mass may be partly responsible for the differences in the krill population between the two regions. Hampton (1985) has suggested that lateral velocity shear between surface and subsurface waters may create favorable conditions whereby krill can easily move into new water by undertaking small upward and downward migrations. Therefore, krill populations could extend their distribution offshore from the ice-edge by the movement of the subsurface water if some animals in the population resided for long periods of time in this water. This would explain the observed spatial pattern in krill length composition.

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