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Feeding habits and prey consumption of Antarctic minke whales, *Balaenoptera bonaerensis* in JARPA research area

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ABSTRACT

The purpose of this study is to understand the feeding habits of Antarctic minke whale *Balaenoptera bonaerensis* in JARPA research area of Antarctic. All 6,338 samples were taken by JARPA (the Japanese Whale Research Program under Special Permit in the Antarctic) from 1987/88 to 2003/04 survey years. This study showed that Antarctic krill *Euphausia superba* was the most important prey species for the Antarctic minke whales over the survey period. In coastal area (swallow area) such as Ross Sea and Prydz Bay, *E. crystarollophias* was also important prey species for the Antarctic minke whales. Amphipods and fish were minor prey, which were often observed together with abundant krill in the stomach contents. The analyses of prey digestion showed that Antarctic minke whales tended to feed on prey in the early morning and late evening. Prey intake had decreased gradually from early morning to daytime and then increased at late evening. Daily prey consumption by Antarctic minke whale was estimated using two methods, direct method from diurnal changes of stomach contents mass and indirectly method from energy requirement. The results of daily consumption estimate were similar between the two methods ranged from 3.6 to 5.3 % of body weight (immature male: 107-142 kg, immature female: 141-201 kg, mature male: 245-292 kg, mature female: 300-366 kg). From 1999/00 to 2002/03 seasons, the annual consumption of Antarctic krill were calculated as 1.3 and 5.2 million tonnes, equivalent to 4 and 26 % of the krill biomass in Area IV and V, respectively. These results indicate Antarctic minke whales are the dominant top-predator species in Area IV and V.

INTRODUCTION

The abundance of Antarctic minke whales (*Balaenoptera bonaerensis*) in the Antarctic (south of 60 ° S) has been estimated to be as high as 760,396 animals during the austral summer (IWC, 1991). Several researchers have examined the stomach contents of Antarctic minke whales, and showed Antarctic krill (*Euphausia superba*) is the most important prey species (Kawamura 1980, Bushuev 1986, Ichii and Kato, 1991). In coastal (shallow) area such as Ross Sea and Prydz Bay, they fed mainly on *E. crystarollophias* and some fishes (Bushuev 1986, Tamura 1998).

Some studies have estimated the prey consumption of Antarctic minke whales on the basis of energy-requirements calculations (Hinga, 1979; Lockyer, 1981). Antarctic krill, which is the main prey species of Antarctic minke whales, is the key species in the Antarctic marine ecosystem. Seals, birds, fishes and squids as well as baleen whales consume Antarctic krill (Laws 1977). Armstrong and Siegfried (1991) estimated that Antarctic minke whales were reached to consume 95 % of the total consumption of Antarctic krill consumed by whales in the Antarctic. Thus, the Antarctic minke whale is considered one of the key species and plays an important role during the austral summer in the Antarctic Ecosystem.

In recent year, it was closed up the global climate change such as global warming and an increase in radiation of ultraviolet light due to destroy of ozone layer. Atkinson *et al*. (2004) analyzed the krill biomass around

Antarctic, and reported their density had declined since the 1970s. Especially near the Antarctic Peninsula, their biomass sharply decreased. On the other hand, salps appear to have increased in the Antarctic. These changes have had profound effects within the Antarctic ecosystem.

Data such as stomach contents, sexual maturity, body mass, abundance estimates of Antarctic minke whale and krill biomass estimates from the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA) provided us to understand the feeding ecology of Antarctic minke whales. The four main objectives of the JARPA are (1) elucidation of the stock structure of Antarctic minke whales to improve the stock management, (2) estimation of biological parameters of the Antarctic minke whales, (3) elucidation of the role of whales in the Antarctic marine ecosystem through the study of whale feeding ecology and (4) elucidation of the effect of environmental changes on cetaceans. To achieve the study objectives, sighting survey for cetaceans, biological research has been conducted from the beginning of JARPA since the 1987/88 season.

In this paper, we investigated the feeding habits (prey species, distribution of prey, diurnal feeding pattern, stomach contents mass and their prey consumption) of Antarctic minke whales in the Antarctic based on data obtained from JARPA. And, we estimated the feeding impact on krill resources by Antarctic minke whales in JARPA research area during 1999/00 and 2002/03 seasons.

MATERIALS AND METHODS

Research area, periods, sample size and sighting position of whales sampled

A total of 549, 2,864, 2,535 and 390 Antarctic minke whales were randomly sampled in Area III-East (35°E to 70°E), Areas IV (70°E to 130°E), V (130°E to 170°W) and VI-West (170°W to 145°W) of Antarctic between 1987/88 and 2003/04 seasons, respectively (Table 1).

The whales were sampled according to sampling procedures described by Nishiwaki *et al* (2005). Sampled whales were immediately transported to a research base vessel, where biological measurements and sampling were carried out. Body length was measured to the nearest 10 cm from the tip of the upper jaw to the deepest part of the fluke notch. Body weight was measured using the special large weighing machine on the flensing deck of the research base vessel. The JARPA survey used ship time, which was converted into local time. As result, our study covered from 3:00 to 21:00 hrs.

Sampling and analyses of stomach contents

Antarctic minke whales have some chambered stomach system (Hosokawa and Kamiya, 1971; Olsen *et al.*, 1994). Each stomach contents were weighed to the nearest 0.1 kg. The freshness of forestomach (1st. stomach) contents was categorized into four classes (F = fresh, fff = lightly digested, ff = moderately digested, f = heavily digested). Then, some individuals of all whales sampled, a sub-sample (300 g) of forestomach contents from each whale with relatively fresh prey in its stomach contents was removed and fixed in 10% formalin solution water for later analyses. In the laboratory, prey species in the sub-samples were identified to the lowest taxonomic level as possible (Barnard 1932, Fischer and Hureau, 1985a; 1985b, Baker *et al*., 1990).

The daily prey consumption by Antarctic minke whales

The amount of krill consumed by Antarctic minke whales was estimated directly from information on the masses of stomach contents (Forestomach and fundus (2nd. stomach)) (method-1), and indirectly by calculating the whale's energy requirements (method-2).

Method-1 Estimation of daily consumption of krill from diurnal change in stomach content mass

Miura (1969) proposed a method for estimating daily prey consumption from diurnal changes in stomach content mass (Vi) with the passage of time based on a known digestion rate in the stomach. If the proportion of prey digested during an interval is d, and the proportion of undigested prey (S) is $1\text{-}d$, the amount of prey consumed (Ci) is given by the following equations:

$$t_1\text{: } C_1=V_1$$
$$t_2\text{: } C_2=V_2\text{-}SV_1$$
$$t_3\text{: } C_3=V_3\text{-}SV_2\text{-}S^2V_1$$
$$t_i\text{: } C_i=V_i\text{-}SV_{i\text{-}1}\text{-}S^2V_{i\text{-}2}\cdots S^{i\text{-}1}V_1$$

Therefore, the daily prey consumption ($\sum_{i=1}^{k} C_i$) is given by:

$$\sum_{i=1}^{k} C_i = V_1 \frac{(1-2S+S^k)}{1-S} + V_2 \frac{(1-2S+S^{k-1})}{1-S} + \cdot\cdot + V_{k-1}(1-S) + \cdot\cdot + V_k$$

In this study, we calculated the mean stomach content mass as % of body mass (*Vi*) at 1 hour intervals. Assuming that prey takes 8 hours to digest the stomach contents of whales (Tobayama, 1974, Bushuev, 1986) and that *d* is exponential (Elliott and Persson, 1978), we estimated *S* to be 0.69 and 0.75, if the proportion of undigested prey in the stomach after 8 hours is 5 % and 10 %, respectively.

We assumed that Antarctic minke whales did not feed during 21:00 to 03:00 hrs, because *E. superba* disperses at night in the late summer (Ichii, 1987).

Method-2 Estimation of daily consumption of krill from the standard metabolism

The Antarctic minke whales are thought to undertake seasonal migrations between winter breeding areas in tropical or subtropical waters and summer feeding areas in the Southern Ocean.

We calculated the daily prey consumption (*F*) during the austral summer by different maturity stages of Antarctic minke whale from the field metabolic rate and energy deposit according to following equations:

Immature male or female : F (kg day^{-1})=(FMR × 1.575 + ED) / E / A
Mature male: F (kg day^{-1})= (FMR + ED) / E / A
Mature female: F (kg day^{-1})= (FMR + ED +R) / E / A

FMR :Field metabolic rate (kJ day^{-1})
ED :Energy deposit (Blubber and muscle) (kJ day^{-1})
E :Caloric value of *E. superba* (kJ kg^{-1})
R :Reproduction cost (kJ day^{-1})
A :Assimilation efficiency

We made the following additional assumptions:

(1) Mean body mass (*W*)

We calculated mean body masses of 2,900 kg and 3,800 kg for immature males and females, and 6,800 kg and 8,100 kg for mature males and females from JARPA data.

(2) Field metabolic rate (*FMR*)

The average *FMR* used in these calculations was proposed by Blix and Folkow (1995). The value of 80 kJ kg^{-1} per day is based on indirect determination of oxygen consumption from studies of the respiratory rates. However, young and sexually immature animals have higher metabolic rates (Kleiber, 1975; Innes *et al*., 1986). We applied this higher metabolic tare for young and sexually immature animals by multiplying with a factor AWF. This AWF was given a definition by Markussen *et al*. (1992). We calculated field metabolic rate by multiplying with an average AWF (1.575) for immature animals.

FMR=80 × W (kJ day^{-1}) ; W is body mass (W)

(3) Energy deposited during feeding season in Antarctic (*ED*)

The total muscle, internal organs fat and blubber masses of Antarctic minke whales, which were sampled during December and March were weighed in JARPA surveys, in order to calculate seasonal growth and fat deposition. These depositions were converted to energy deposition by measuring the energy density of samples of muscle and blubber of some whales sampled in the early and late seasons during austral summer, by Bomb calorimeter.

(4) Caloric value of *E. superba* (*E*)

Antarctic minke whales feed mainly on *E. superba*. The mean caloric value of *E. superba* is 4,473 kJ kg^{-1} (= 1,070 kcal kg^{-1}). This value was calculated using the energy density of *E. superba* samples of JARPA surveys by Bomb calorimeter.

(5) Residence time in the Antarctic (*D*)

The encounter rate (as a simple index of density) of Antarctic minke whales in the Antarctic increased from early November to late December and peaked in January, followed by a steady decrease through February (Kasamatsu *et al.*, 1996). We assumed that Antarctic minke whales spend about 100 days during the austral summer in the Antarctic.

(6) Reproduction cost (*R*)
The total reproductive cost for a female Antarctic minke whales was re-calculated from the analysis by Lockyer (1981a) to be 1.89×10^7 kJ (=0.45×10^7 kcal), assuming a length at birth fetus of 273 cm (Best, 1982). We assumed that all reproduction costs of Antarctic minke whales were stored during residence time in the Antarctic (*D*).

(7) Assimilation efficiency (*A*)
We assumed that Antarctic minke whales have an assimilation efficiency of 84 % (Lockyer, 1981a).

The total prey consumption by Antarctic minke whales in Area IV and V
We estimated the total prey consumption of krill consumed by different maturity stages of Antarctic minke whales in Areas IV and V based on the abundance data of Antarctic minke whale (Hakamada *et al*., 2005) and composition of maturity stages of Antarctic minke whales sampled during JARPA surveys. Furthermore, we compared between the prey consumption by Antarctic minke whale and the standing stock of krill in Area IV and V, and the feeding impact on standing stock of krill (the percentage of krill consumption in total krill biomass) by Antarctic minke whales in Area IV and V were estimated. The resources of krill in Area IV and V were calculated using echo sounder by JARPA surveys (Murase *et al*., 2005).

RESULTS

Prey items
A total of ten prey species, including one amphipod and four euphausiids and five fish species were identified (Table 2). Major prey item was krill. The ratio of empty stomach has no yearly trend (Table 3). Antarctic minke whales fed mainly on *Euphausia superba* (Table 4). The occurrence and distribution of amphipod and fishes showed in Fig. 1. Amphipod was found in offshore of eastern Area IV and Area V. Fishes were found in coastal (shallow) area of Prydz Bay and Ross Sea, especially. The occurrence and distribution of krill species showed in Fig. 2. Antarctic minke whales fed mainly on *E. superba* excluding in coastal area. In coastal (shallow) area of Prydz Bay and Ross Sea, they fed mainly on *E. crystarollophias*.

The diurnal changes in feeding activity
The relationship between freshness categories and the diurnal change in the mean stomach content mass as % of body mass was showed in Figs. 3 and 4. These figures show the proportion of undigested category of F and fff and the rate of the mean stomach content mass have decreased with time periods. After 19:00 hrs, F of freshness categories and the rate of the mean stomach content mass have increased.

Daily prey consumption of Antarctic minke whales
To clear the daily prey consumption, the average of fresh stomach contents (category: F and fff) was calculated for mature male and female in each survey year (Fig. 5). In area IV, Fig. 5 shows that the average of fresh stomach contents for mature male and female has decreased significantly year after year excluding 1989/90 JARPA (Mature male: F=0.008, Mature female F=0.007). In area V, there was same trend in that of mature female (Mature male: F=0.59, Mature female F=0.03).

Method-1
These estimate rates of daily prey consumption diurnal changes in stomach content mass (Fig. 4) were 3.7 and 4.3 % of body mass.

If the proportion of undigested prey in the stomach after 8 hours is 5 %, estimates of prey consumption were 124.7 kg and 163.4 kg for immature male and female, 292.4 kg and 348.3 kg for mature male and female, respectively (Table 5).

If the proportion of undigested prey in the stomach after 8 hours is 10 %, Estimates of prey consumption were 107.3 kg and 140.6 kg for immature male and female, 251.6 kg and 299.7 kg for mature male and female, respectively (Table 5).

Method-2
FMR
The mean body length was calculated of 6.2 and 6.7 m for immature males and females, and 8.4 and 8.9 m for mature males and females from JARPA data. We calculated mean body masses of 2,900 and 3,800 kg for

immature males and females, and 6,800 and 8,100 kg for mature males and females from JARPA data. Using these body mass and the value for the energy requirement of minke whale proposed by Folkow and Blix (1995), field metabolic rate of immature and mature males were 365,400 and 544,000 kJ day^{-1}, respectively. And, field metabolic rate of immature and mature females were 478,800 and 648,000 kJ day^{-1}, respectively (Table 6).

Blubber deposition

An immature male of 6.2 m with a mid-December blubber mass of 608 kg deposits 96 kg of blubber between mid-December (average capture date, 19 December) and mid-March (average capture date, 10 March) (Fig.6). The energy density of blubber increased from 14,435 to 20,711 kJ kg^{-1} during feed residence time in the Antarctic. Thus, it can be calculated that 70 781 KJ day^{-1} was deposited as blubber during residence time in the Antarctic (100 days). If a similar calculation is made for mature male of 8.4 m, a value of 164,064 kJ day^{-1} was obtained (Table 6).

An immature female of 6.7 m with blubber mass of 791 kg in mid-December deposits 103 kg of blubber between mid-December (average capture date, 19 December) and mid-March (average capture date, 8 March) (Fig.6). The energy density of blubber increased from 16,443 to 28,075 kJ kg^{-1}. Thus, it can be calculated that 164,064 kJ day^{-1} was deposited as blubber during residence time in the Antarctic (100days). If a similar calculation is made for mature female of 8.9 m, a value of 326,204 kJ day $^{-1}$ was obtained (Table 6).

Growth and/or deposition of muscle

An immature male of 6.2 m with muscle mass of 1,484 kg in mid-December deposits 194 kg of muscle between mid-December (average capture date, 19 December) and mid-March (average capture date, 10 March) (Fig.7). The energy density of muscle increased from 5,858 to 6,234 kJ kg^{-1} during feed residence time in the Antarctic. Thus, it can be calculated that 21,553 KJ day^{-1} was deposited as muscle during residence time in the Antarctic (100 days). If a similar calculation is made for mature male of 8.4 m, a value of 43,046 kJ day^{-1} was obtained (Table 6).

An immature female of 6.7 m with muscle mass of 1,973 kg in mid-December deposits 100 kg of muscle between mid-December (average capture date, 19 December) and mid-March (average capture date, 8 March) (Fig.7). The energy density of muscle increased from 5,941 to 6,192 kJ kg^{-1}. Thus, it can be calculated that 13,930 kJ day^{-1} was deposited as muscle during residence time in the Antarctic (100days). If a similar calculation is made for mature female of 8.9 m, a value of 37,102 kJ day^{-1} was obtained (Table 6).

Internal organs fat deposition

We estimated the mass of internal organs fat deposition to deduct the blubber deposition and growth and/or deposition of muscle from total body mass. Total body mass shows in Fig. 8. The energy density of internal organs fat assumed as same as blubber's value.

An immature male of 6.2 m can be calculated that 75,955 kJ day^{-1} was deposited as internal organs fat during residence time in the Antarctic (100 days). If a similar calculation is made for mature male of 8.4 m, a value of 168,901 kJ day^{-1} was obtained (Table 6).

An immature female of 6.7 m can be calculated that 112,529 kJ day^{-1} was deposited as internal organs fat during residence time in the Antarctic (100days). If a similar calculation is made for mature female of 8.9 m, a value of 173,280 kJ day^{-1} was obtained (Table 6).

Daily prey consumption during residence time in the Antarctic

We calculated the daily prey consumption during residence time in the Antarctic of 100 days. The field metabolic rate, blubber deposition, growth and/or deposition of muscle and internal organs fat rate were assumed to obtain the same deposition day by day during feed residence time in the Antarctic.

These estimate rates of daily prey consumption using method-2 were 4.9 and 5.3 % of body weight for immature male and female, 3.6 and 4.5 % for mature male and female, respectively. Estimates were 142.0 and 201.3 kg for immature male and female, 244.9 and 365.6 kg for mature male and female, respectively (Table 6).

Seasonal prey consumption of Antarctic minke whales in Area IV and V of the Antarctic

We estimated the total prey consumption of krill consumed by Antarctic minke whales in Area IV and V based on the abundance of whales, the average of daily prey consumption using method-1 and 2, and the composition of maturity stages of Antarctic minke whales sampled during JARPA. These average estimate rates of daily prey consumption were 4.3 and 4.4 % of body weight for immature male and female, 3.9 and 4.2 % for mature male and female, respectively. Estimates were 124.7 and 168.4 kg for immature male and female, 263.0 and 337.9 kg for mature male and female, respectively.

In Area IV, total prey consumptions of krill by Antarctic minke whales of 1999/00 and 2001/02 season were estimated to be 1.3 and 1.9 million tonnes, respectively. On the other hand, in Area V, total prey consumptions of krill by Antarctic minke whales of 2000/01 and 2002/03 season were estimated to be 4.8 and 5.2 million tonnes, respectively (Appendix 1, Table 7).

The estimations of feeding impact on krill resources by Antarctic minke whales in Area IV and V were ranged from 4 to 5 % of krill standing stock, and from 25 to 26 %, respectively. The average estimations of feeding impact on krill resources by Antarctic minke whales in Area IV and V were 4 and 25 % of krill standing stock a year, respectively (Table 7).

DISCUSSION

Prey items

The Antarctic minke whales in the Antarctic during austral summer from 1987/88 to 2003/04 seasons were stenophagous. We confirmed that they fed mainly on Antarctic krill *Euphausia superba* in offshore. Prey species varied geographically. In coastal area (swallow area) such as Ross Sea and Prydz Bay, they fed mainly on *E. crystarollophias* and some fishes. The results were coincided with previous reports (*e.g*. Bushuev 1986). *E. crystarollophia* distribute in coastal/ swallow area (Thomas and Green 1988, Hosie 1991).

In Northern Hemisphere, prey switching of minke whales *B. acutorostrata* has been observed in some regions (the Barents Sea in the North Atlantic (Haug *et al*. 2002); the western North Pacific (Tamura and Fujise 2002)). In Antarctic, Antarctic krill and salps (mainly *Salpa thompsoni*) are major zooplankton (Pakhomov *et al*. 2002).

In recent years, it has reported that krill densities have decreased, and salps densities appear to have increased in the Southern Ocean (Loeb *et al.* 1997; Atkinson *et al.* 2004). However, there was no evidence the prey switching of Antarctic minke whale from krill to salps in the Antarctic. This result shows that salps are not fit to eat for Antarctic minke whales.

The diurnal changes in feeding activity

Our results suggested that Antarctic minke whales seem to have a bimodal durnal feeding rhythm, with a primary peak in the early morning and a secondary one in the late evening. Our results were coincided with previous reports (Ohsumi 1979, Bushuev 1986). Unfortunately, no information is available from 21:00 hours to 03:00 hours. Although, they might not feed on prey during night due to *E. superba* disperses at night in the austral summer (Ichii 1987). Other studies of minke whales in Northern Hemisphere have shown tendency for a diurnal feeding activity (Haug *et al*. 1997, Lindstrom *et al*. 1998). In feeding areas of abundant and stable prey, Antarctic minke whales are not hungry and might ceased to feed at earlier time in the day due to be satisfied with feeding. It takes 8 hours to digest the stomach contents of whales (Tobayama 1974, Bushuev 1986). After digestion of prey, they might feed on prey again.

The average mass of fresh stomach contents for mature male and female has decreased significantly year after year in Area IV excluding 1989/90 season. In area V, there was same trend in that of mature female. We did not identify that krill densities have decreased, and salps densities appear to have increased in our survey area. This phenomenon may show that the krill availability has been decreased year after year.

Daily prey consumption of Antarctic minke whales

Using method 1, the daily prey consumption rates were calculated to be 3.7 and 4.3 % of body weight if the proportion of undigested prey after 8 hours was 5 and 10 %, respectively. If feeding also occurred at night, these rates would underestimate the actual prey consumption rates. Thus, the daily consumption rate was estimated to be at least 3.7 %.

The estimated prey consumption rates using method-2 were 4.9 and 5.3 % of body weight for immature males and females, respectively, and 3.6 and 4.5 % for mature males and females, respectively. All estimates of daily prey consumption rate obtained from the two methods ranged from 4 to 5%. These values were similar to estimates by Lockyer (1981b) and Bushuev (1986).

Armstrong and Siegfried (1991) estimated the mean daily prey consumption rates from respiratory allometry methods of male and female minke whales during the austral summer to be 6.7 and 6.2 %, respectively. Since JARPA data indicate that the maximum stomach contents mass (Forestomach and fundus) was 343.8 kg and 4.2 %, Armstrong and Siegfried's prey consumption rates may be overestimates.

Reilly *et al*. (2004) considered the question of energy budget studies of baleen whales in the Antarctic. They estimated the prey consumption of Antarctic minke whale from Tamura *et al*. (1997). Tamura *et al*. (1997) compared the daily prey consumption using three methods. One method was a direct approach based on diurnal change in stomach contents mass, the others were energetic-based approaches. The average of three estimates ranged from 3.4 % to 3.8 % of body weight. Our present study was improved from these previous methods of Tamura *et al*. (1997). The present authors regard the present estimates to be more reliable. These estimates could be used with confidence for the estimation of total prey consumption of Antarctic minke whales.

Consumption of krill during austral summer by Antarctic minke whales in Areas IV and V

In the Antarctic, large baleen whale species were depleted rapidly in the 20th century. Laws (1977) suggested that before the 1970's, blue whale and humpback whale were the most harvested and were reduced to about 3 and 5 % of their estimated initial biomasses. This rapidly decreasing of baleen whales provided the annual surplus of krill as much as 150 million tonnes. This surplus became available for other krill predators, such as Antarctic minke whale, crabeater seals (*Lobodon carcinophagus*), Antarctic fur seals (*Arctocephalus gazella*), some penguins and sea birds.

Some researchers estimated the total prey consumption of baleen whales using energy budget models in the Antarctic. Armstrong and Siegfried (1991) indicated that the Antarctic minke whales consume 95 % of the total biomass of krill that is consumed by baleen whales in the Antarctic. This prey consumption of Antarctic minke whale was equal to be 35.5 million tonnes using 760,396 of the estimated population. Tamura (2003) showed that the annual crustacean consumption by Antarctic minke whales was 42-64 million tonnes, and that this amounted to 40-54 % of total annual crustacean consumption by cetaceans in the Southern Hemisphere.

We estimated the total prey consumption of krill consumed by Antarctic minke whales in Area IV and V based on the abundance, the average of daily prey consumption using direct method and energy requirement method, and the composition of maturity stages of Antarctic minke whales sampled during JARPA.

In Area IV, total prey consumption of krill by Antarctic minke whales of 1999/00 and 2001/02 seasons were estimated to be 1.3 and 1.9 million tonnes, respectively. In Area V, total prey consumption of krill by Antarctic minke whales of 2000/01 and 2002/03 seasons were estimated to be 4.8 and 5.2 million tonnes, respectively. The average estimations of feeding impact on krill resources by Antarctic minke whales in Area IV and V were 4 and 25 % of krill biomass, respectively.

Tamura *et al*. (1997) estimated the prey consumption of krill by Antarctic minke whales around the Ross Sea in the Antarctic to be an order of magnitude greater than the estimated consumption by Adelie penguins (*Phgoscelis adeliae*) and crabeater seals.

Reilly *et al*. (2004) estimated the prey consumption and energy transfer of baleen whales in the South Atlantic sector of the Antarctic (about 30W – 70W). The estimations of feeding impact on krill resources by baleen whales were ranged from 4 to 6 %. They estimated that the prey consumption of baleen whales in this region was approximately 1.6 million tonnes, possibly up to as much as 2.7 million tonnes in the Antarctic. However, the abundance of Antarctic minke whale was only 18,000 animals in their study.

Mori and Butterworth (2004) tried to build up the Multi-species type ecosystem modeling in the Antarctic. They treated Antarctic minke whale, blue whale (*B. musculus*) and Antarctic krill. Antarctic minke whales and blue whales feed mainly on Antarctic krill, their distributions are similar, near the ice edge in the Antarctic. They noted two interesting features of the dynamics of these species using simple ecosystem model. First, a decrease of krill biomass from the 1970s to the 1990s due to the rapid increasing abundance of Antarctic minke whales. Second, a recovery of blue whales despite the impact of Antarctic minke whales on krill resources and its resultant decrease the abundance of Antarctic minke whale. Finally, their model's result showed that the Antarctic minke whale population decreases gradually, on the other hand, blue whale population increases gradually, both populations returning to their original population level.

Results in this study suggest that Antarctic minke whales play an important role within current ecosystem of the Antarctic during austral summer. Some results of JARPA suggest there are some changes of krill availability of Antarctic minke whale in recent years (Konishi and Tamura, 2005, Bando *et al*., 2005, Zenitani and Kato, 2005), the pursuit of the cause and future prediction of baleen whale stock dynamics are important in future. At the same time, the ecosystem is changing due to the change of krill availability to them. These data collected during JARPA surveys of scientific whaling were needed to understand the ecosystem of Antarctic, and should be collected continuously to follow the future ecosystem change. We should conduct comparative research on the seasonal, local and annual distribution and abundance of cetaceans and their prey and the monitoring of their feeding habits.

Further studies on these modeling and long-term monitoring researches would clarify the interaction of major predator such as baleen whales (Antarctic minke, fin, humpback, blue whale) and krill in the Antarctic.

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Table 1. Areas, years of surveys and sample size used in this study

Area III-East

	1995/96	1997/98	1999/00	2001/02	2003/04	Total
Male	69	74	63	54	62	322
Female	41	36	46	56	48	227
Total	110	110	109	110	110	549

Area IV

	1987/88	1989/90	1991/92	1993/94	1995/96
Male	153	184	165	200	204
Female	119	142	123	130	126
Total	272	326	288	330	330

	1997/99	1999/00	2001/02	2003/04	Total
Male	205	170	147	138	1,566
Female	123	160	183	192	1,298
Total	328	330	330	330	2,864

Area V

	1988/89	1990/91	1992/93	1994/95	1996/97
Male	85	164	167	200	132
Female	151	159	160	130	198
Total	236	323	327	330	330

	1998/99	2000/01	2002/03	Total
Male	207	186	168	1,309
Female	122	144	162	1,226
Total	329	330	330	2,535

Area VI-West

	1996/97	1998/99	2000/01	2002/03	Total
Male	74	40	72	67	253
Female	36	20	38	43	137
Total	110	60	110	110	390

Table 2. Prey species found in the stomachs of Antarctic minke whales sampled by the JARPA

	species
Main prey	
Amphipoda	*Parathemisto gaudichaudi*
Krill	*Euphausia superba*
	E. crystallorophias
	E. frigida
	Thysanoessa macrura
Pisces	*Pleuragramma antarcticum*
Miner prey	
Pisces	*Notolepis coatsi*
	Electona antarctica
	Chionodraco sp.
	Notothenis sp.

Table 3. Composition of main prey found in the stomachs of Antarctic minke whales sampled by JARPA surveys

Area III-East

Year	1995/96	1997/98	1999/00	2001/02	2003/04
Number	110	110	109	110	110
(Main prey)					
Krill	66	71	75	90	86
Ampipods	0	0	0	0	0
Fish	0	0	0	0	0
%					
Krill	100.0	100.0	100.0	100.0	100.0
Ampipods	0	0	0	0	0
Fish	0	0	0	0	0
Empty	28	36	18	11	12
%	29.8	33.6	19.4	10.9	12.2
Broken	16	3	16	9	12

Area IV

Year	1987/88	1989/90	1991/92	1993/94	1995/96	1997/98	1999/00	2001/02	2003/04
Number	272	326	288	330	330	328	330	330	330
(Main prey)									
Krill	210	171	208	253	173	206	206	244	186
Ampipods	0	0	0	0	0	0	0	1	1
Fish	0	0	0	0	0	0	0	0	0
%									
Krill	100.0	100.0	100.0	100.0	100.0	100.0	100.0	99.6	99.5
Ampipods	0	0	0	0	0	0	0	0.4	0.5
Fish	0	0	0	0	0	0	0	0	0
Empty	49	134	66	65	136	103	89	66	123
%	18.9	43.9	24.1	20.4	44.0	33.3	30.2	21.2	39.7
Broken	13	21	14	12	21	19	35	19	20

Table 3. Continued

Area VI-West

Year	1996/97	1998/99	2000/01	2002/03
Number	110	60	110	110
(Main prey)				
Krill	65	28	76	46
Ampipods	0	0	0	0
Fish	0	0	0	0
%				
Krill	100.0	100.0	100.0	100.0
Ampipods	0	0	0	0
Fish	0	0	0	0
Empty	37	26	23	58
%	36.3	48.1	23.2	55.8
Broken	8	6	11	6

Area V

Year	1988/89	1990/91	1992/93	1994/95	1996/97	1998/99	2000/01	2002/03
Number	236	323	327	330	330	329	330	330
(Main prey)								
Krill	159	230	214	243	193	213	256	227
Ampipods	0	1	0	1	0	0	1	0
Fish	0	3	0	0	0	0	1	0
%								
Krill	100.0	98.3	100.0	99.6	100.0	100.0	99.2	100.0
Ampipods	0	0.4	0	0.4	0	0	0.4	0
Fish	0	1.3	0	0	0	0	0.4	0
Empty	67	75	85	75	113	91	57	86
%	29.6	24.3	28.4	23.5	36.9	29.9	18.1	27.5
Broken	10	14	28	11	24	25	15	17

Table 4. Wet weight composition (%) of krill found in the stomachs of Antarctic minke whales sampled by JARPA surveys

Area III-East

Year	1995/96	1997/98	1999/00	2001/02	2003/04
Species / Number	63	80	107	28	35
Krill					
Euphausia superba	100.0	97.5	100.0	100.0	100.0
E. crystallorophias		0.6			
E. frigida		1.9			
Thysanoessa macrura					

Area IV

Year	1987/88	1989/90	1991/92	1993/94	1995/96	1997/98	1999/00	2001/02	2003/04
Species / Number		55	45	164	138	182	180	96	75
Krill									
Euphausia superba		98.0	97.8	97.6	87.7	96.0	96.1	90.7	97.5
E. crystallorophias		1.8	2.2	0.6	8.8			8.3	
E. frigida				0.01					
Thysanoessa macrura		0.2		1.8	3.5	4.0	3.9	0.9	2.5

Area V

Year	1988/89	1990/91	1992/93	1994/95	1996/97	1998/99	2000/01	2002/03
Species / Number	69	33	142	162	163	139	95	71
Krill								
Euphausia superba	88.2	86.0	81.8	88.9	85.1	97.1	69.2	97.3
E. crystallorophias	7.5	10.7	16.5	3.1	10.4	0.7	27.6	2.7
E. frigida	1.4							
Thysanoessa macrura	2.9	3.3	1.7	8.0	4.5	2.2	3.2	

Area VI-West

Year	1996/97	1998/99	2000/01	2002/03
Species / Number	80	40	56	23
Krill				
Euphausia superba	94.4	98.8	89.3	82.6
E. crystallorophias				
E. frigida				
Thysanoessa macrura	5.6	1.3	10.7	17.4

Table 5. Daily prey consumption of Antarctic minke whales using method-1

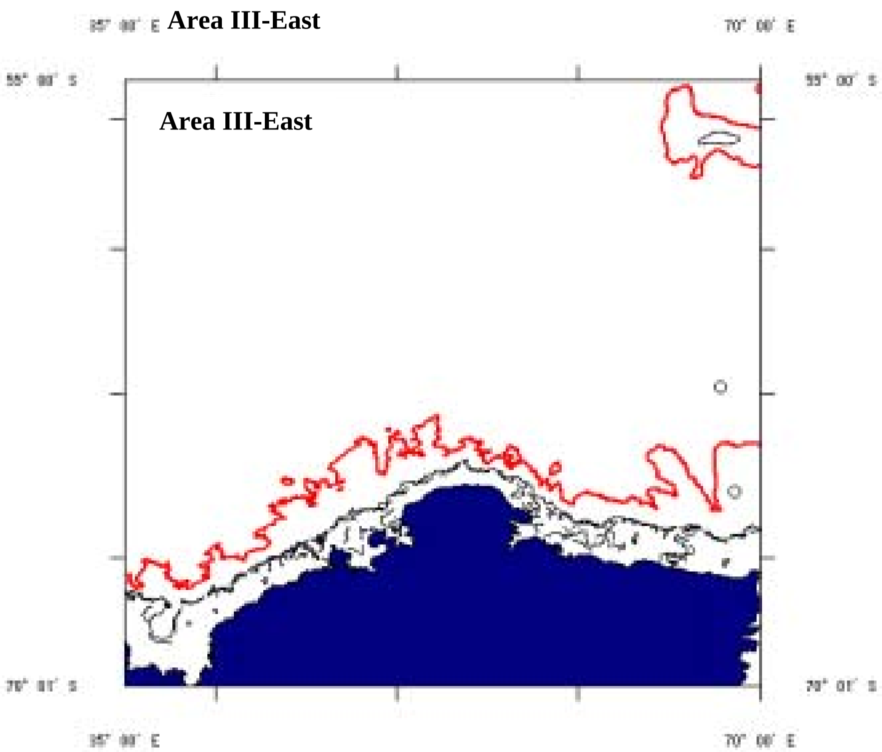
Sex	Maturity	Body weight	Method-1			
		(kg)	(kg)	(%)	(kg)	(%)
Male	Immature	2,900	107.3	3.7	124.7	4.3
	Mature	6,800	251.6	3.7	292.4	4.3
Female	Immature	3,800	140.6	3.7	163.4	4.3
	Mature	8,100	299.7	3.7	348.3	4.3

Table 6. Daily prey consumption of Antarctic minke whales using method-2

Sex	Maturity	Body length (m)	Body weight (kg)	FMR (KJ/day)	Blubber deposition (KJ/day)	Muscle deposition (KJ/day)	Fat deposition (KJ/day)	Reproduction cost (KJ/day)	Daily prey consumption		
									(KJ/day)	(kg/day)	(%)
Male	Immature	6.2	2,900	365,400	70,781	21,553	75,955		635,345	142.0	4.9
	Mature	8.4	6,800	544,000	164,064	43,046	168,901		1,095,252	244.9	3.6
Female	Immature	6.7	3,800	478,800	151,158	13,930	112,529		900,497	201.3	5.3
	Mature	8.9	8,100	648,000	326,204	37,102	173,280	189,000	1,635,221	365.6	4.5

Table 7. Abundance and prey consumption of Antarctic minke whales and feeding impact on Antarctic krill resources estimating by JARPA data in Area IV and V between 1998/99 JARPA and 2003/04 JARPA

Stratum	Year	Abundance (inds.)	Prey consumption (million ton)	Krill biomass (million ton)	Feeding impact (%)
IV	1999/00	44,572	1.3	36.4	3.7
	2001/02	61,463	1.9	38.1	4.9
V	2000/01	148,509	4.8	18.7	25.8
	2002/03	163,593	5.2	21.0	24.8



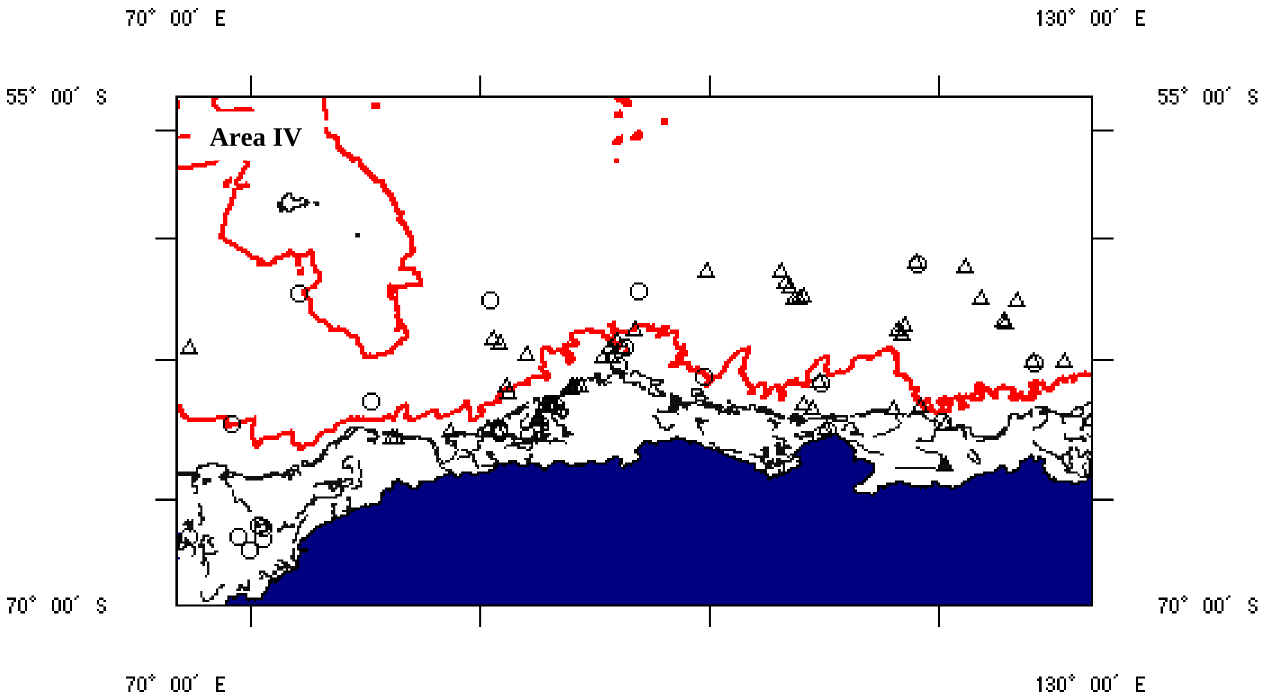


Fig.1-a. Distribution of fish and amphipods consumed by Antarctic minke whales in Area III-East and IV (● and ○ : Fish, ▲ and △ : Amphipods)

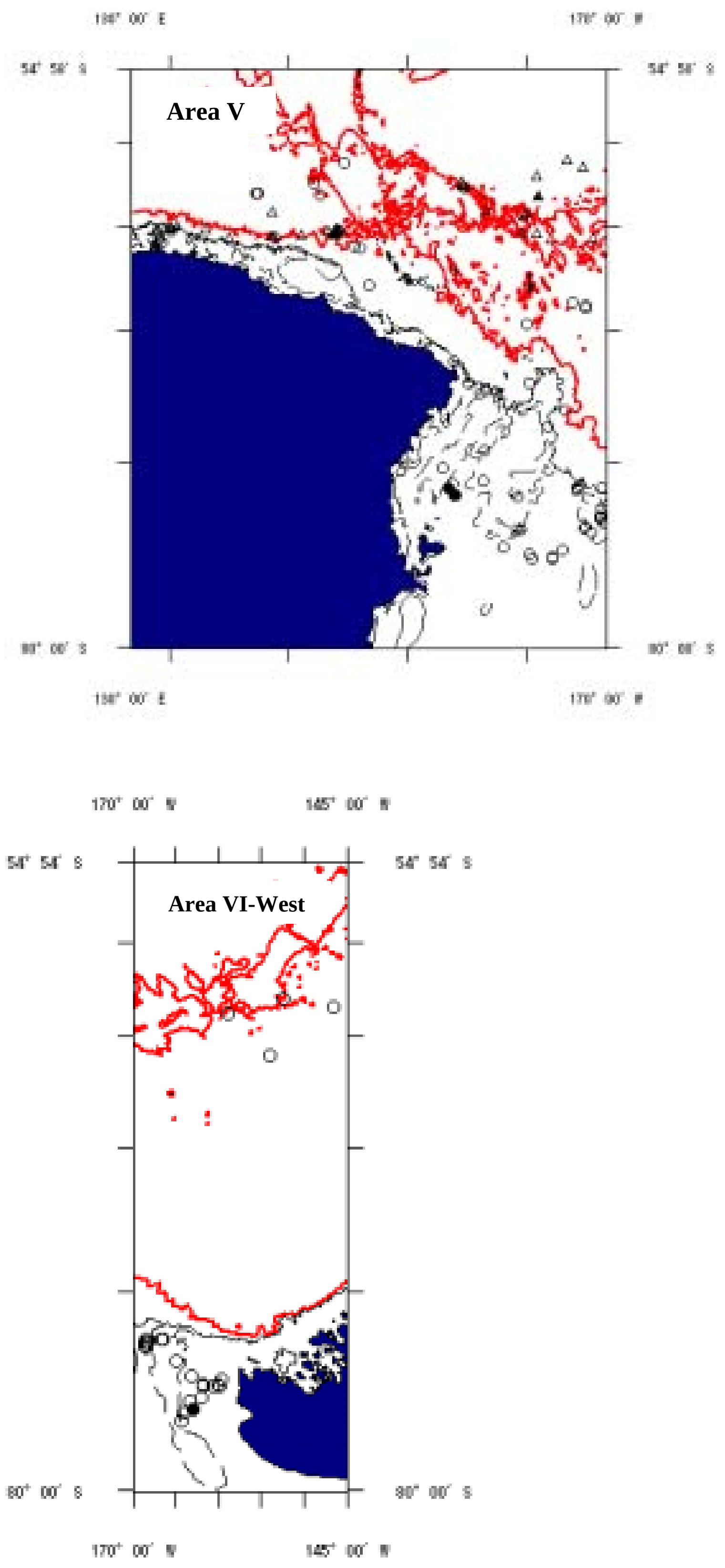


Fig.1-b. **Distribution of fish and amphipods consumed by Antarctic minke whales in Area V and VI-West (● and ○ : Fish, ▲ and △ : Amphipods)**

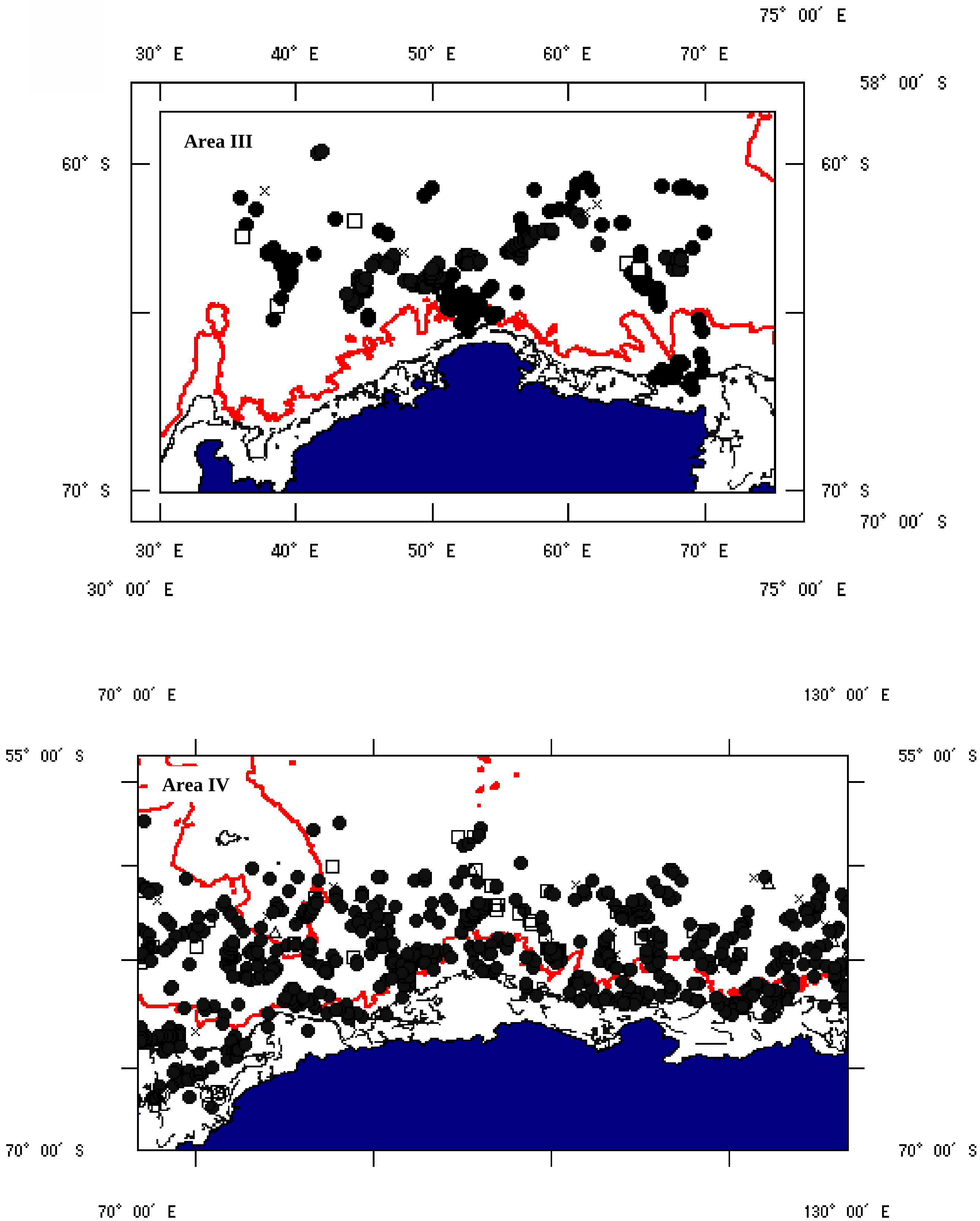


Fig.2-a. **Distribution of krill consumed by Antarctic minke whales in Area III-East and IV (●: *Euphausia. superba*, ○: *E. crystarollophias*, △: *Thysanoessa* spp., □: *E. S.* + others, ×: *E.* spp.)**

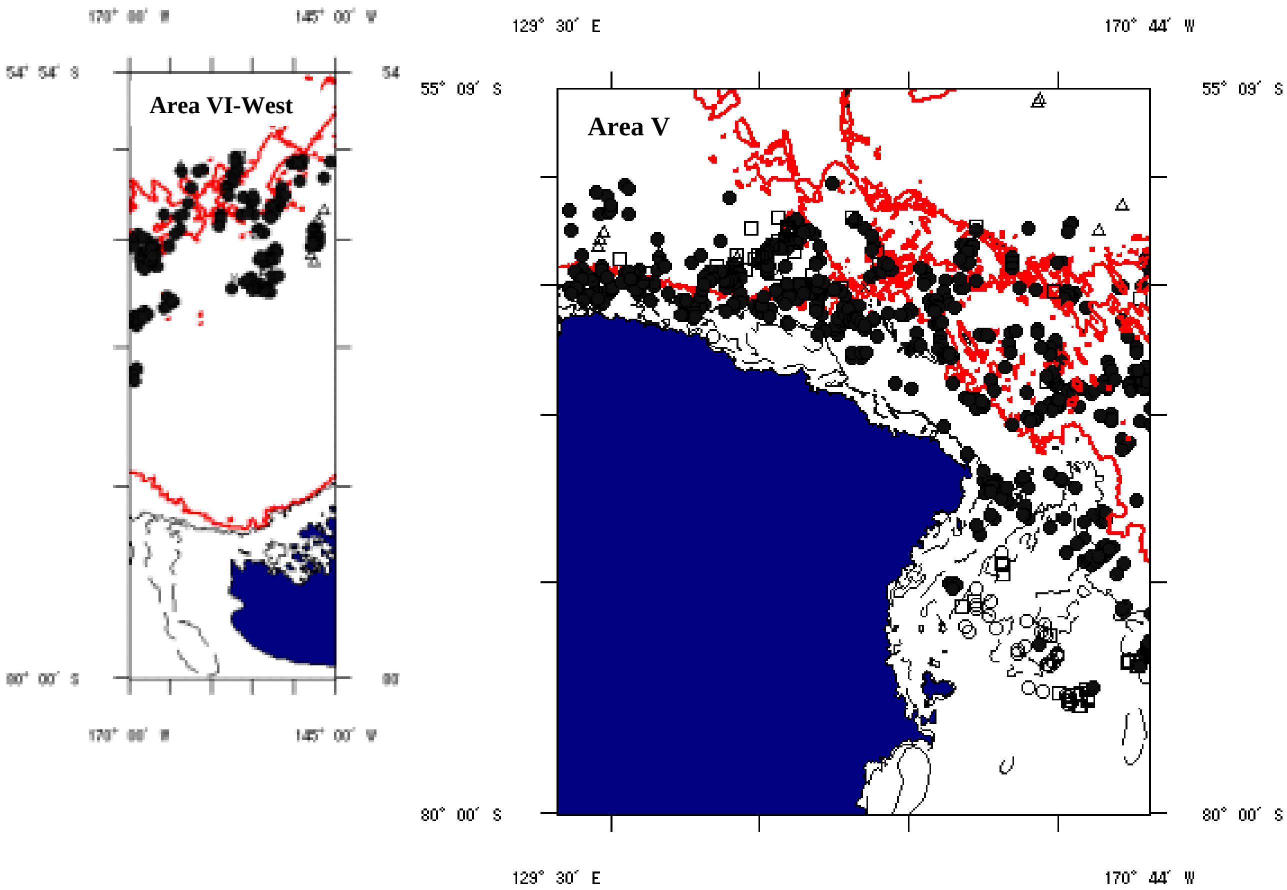


Fig.2-b. Distribution of krill consumed by Antarctic minke whales in Area V and VI-West (●: *Euphausia. superba*, ○: *E. crystarollophias*, △: *Thysanoessa* spp., □ : *E. S.* + others, ×: *E.* spp.)

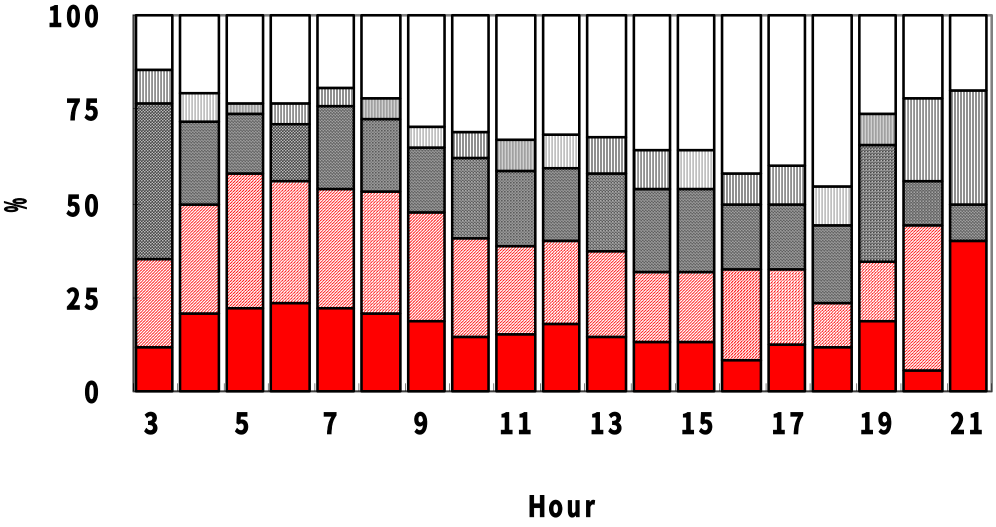


Fig. 3. Relationships between freashness categories for prey and time periods in Antarctic
(F : fresh, fff : lightly digested, ff : moderately digested, f : heavily digested, :Empty)

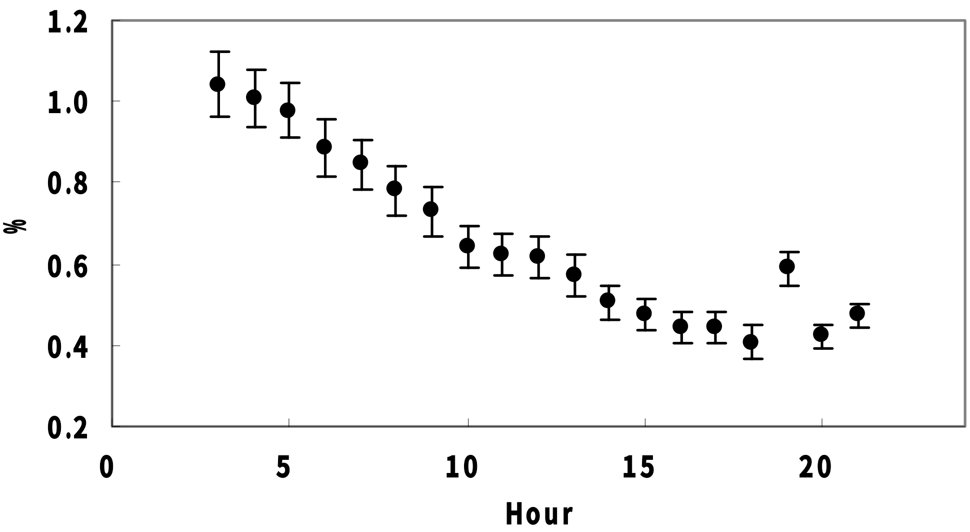
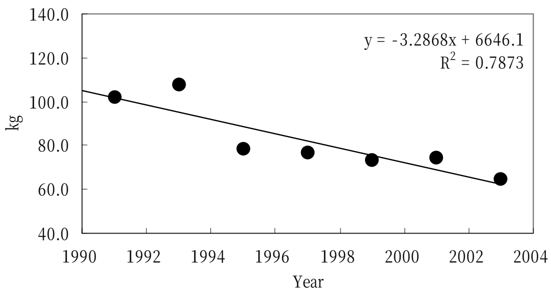


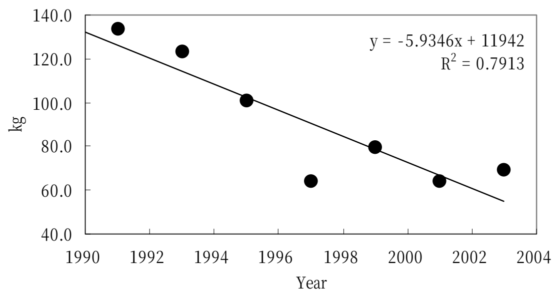
Fig. 4. Change in the mean mass ± *S.E.* of stomach content with time.
Weight expressed as percentage of Antarctic minke whale body mass.

Area IV

***Mature male**

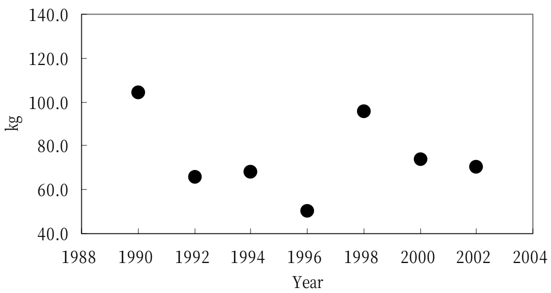


***Mature female**



Area V

***Mature male**



***Mature female**

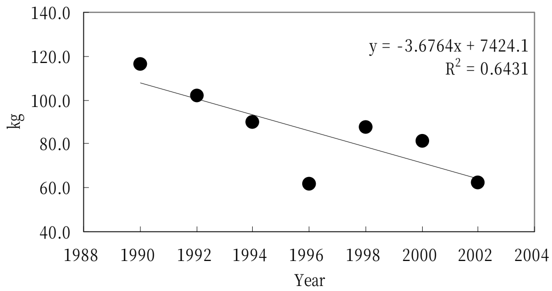
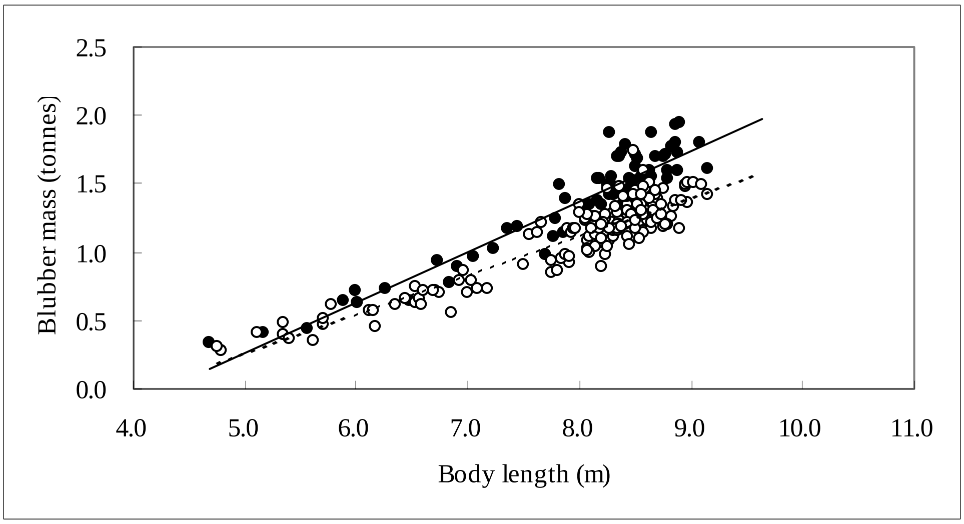


Fig. 5. Yearly changes in the mean mass of stomach content. Data used in 63-67^{o}S and January and February.

***Male**



***Female**

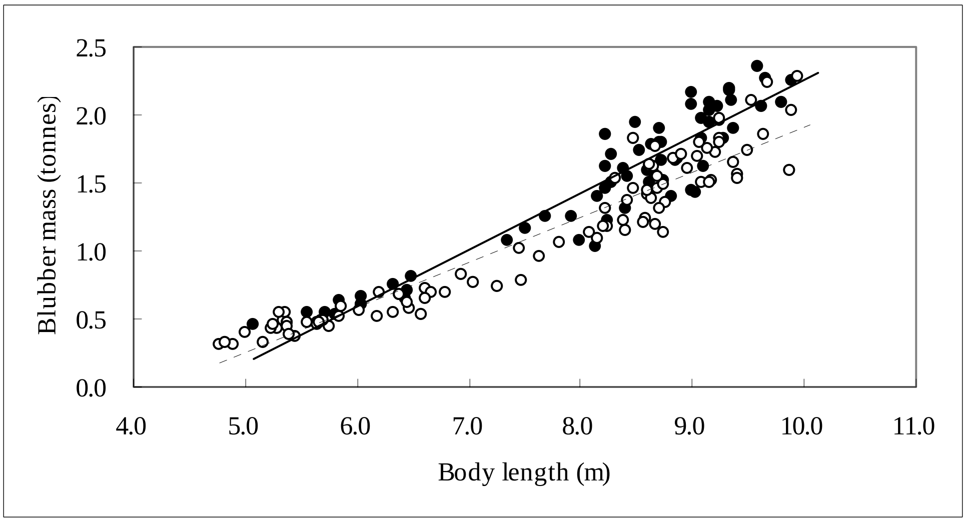
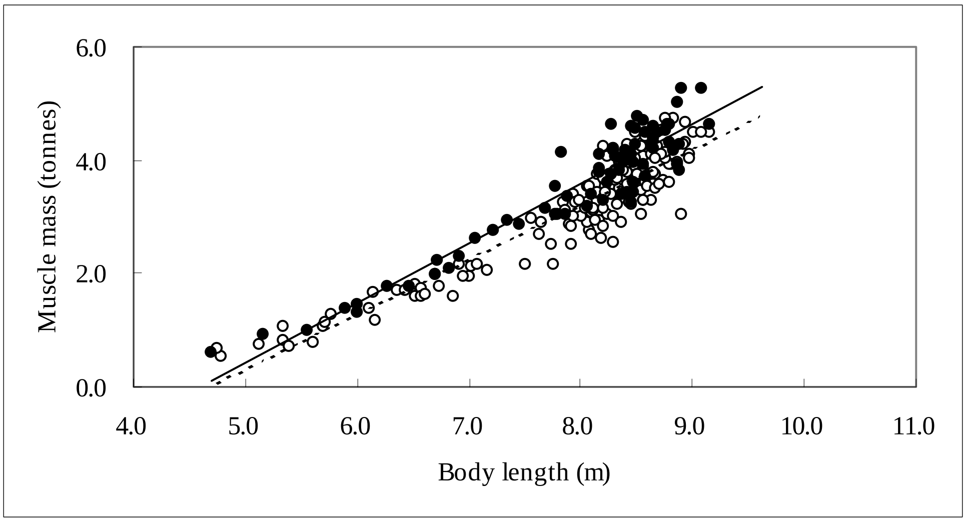


Fig. 6. The blubber mass (tonnes) as a function of body length (m) in Antarctic minke whale, which were sampled in December and March. The equations describing the linear regressions were as following. Male: (December ○, n=156: y=0.29x-1.19, r^2=0.84; March ●, n=71: y=0.37x-1.59, r^2=0.87), Female: (December ○, n=94: y=0.33x-1.42, r^2=0.91; March ●, n=66: y=0.42x-1.92, r^2=0.87).

***Male**



***Female**

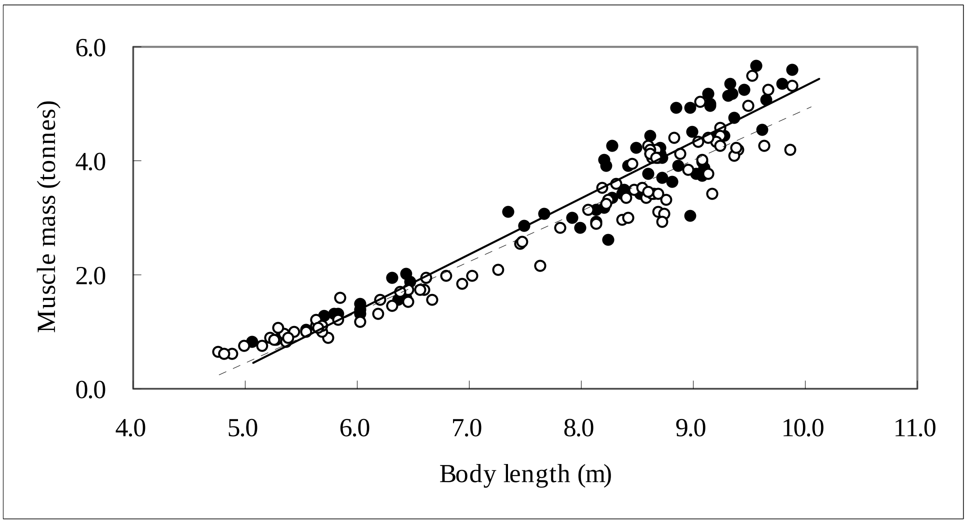
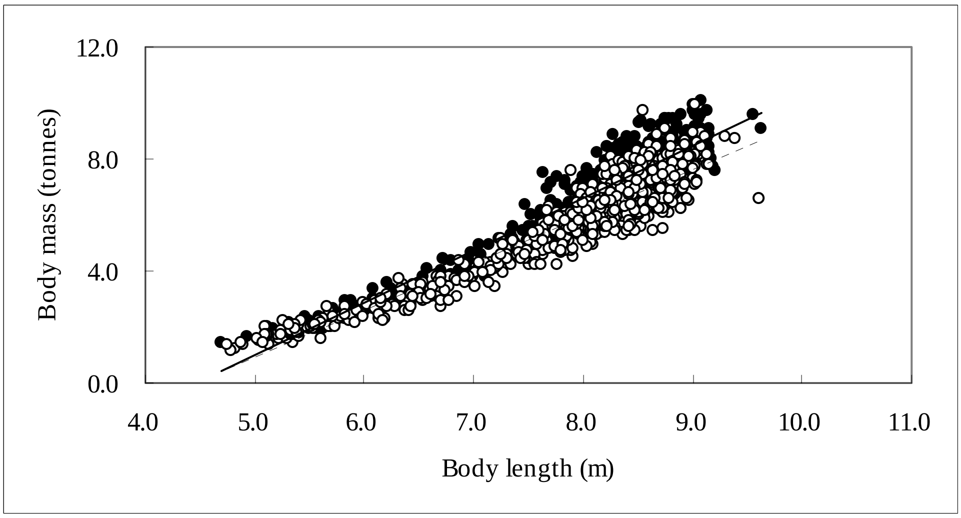


Fig. 7. The muscle mass (tonnes) as a function of body length (m) in Antarctic minke whales, which were sampled in December and March. The equations describing the linear regressions were as following. Male: (December ○, n=156: y=0.97x-4.53, r^2=0.87; March ●, n=71: y=1.04x-4.77, r^2=0.89), Female: (December ○, n=94: y=0.89x-3.99, r^2=0.93; March ●, n=66: y=0.99x-4.56, r^2=0.89).

***Male**



***Female**

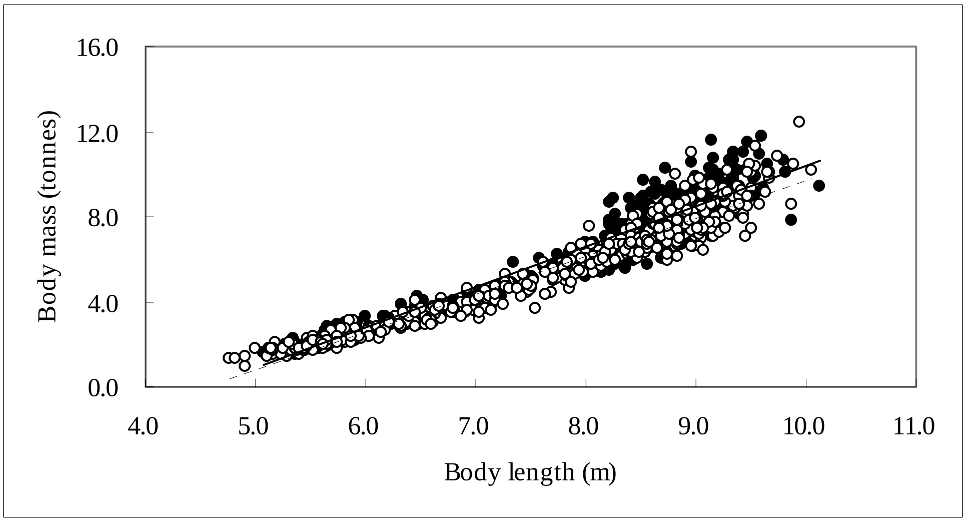


Fig. 8. Total body mass (tonnes) as a function of body length (m) in Antarctic minke whales, which were sampled in December and March. The equations describing the linear regressions were as following. Male: (December ○, n=816: y=1.68x-7.49, r^2=0.89; March ●, n=473: y=1.87x-8.33, r^2=0.89), Female: (December ○, n=503: y=1.77x-8.05, r^2=0.94; March ●, n=375: y=1.90x-8.60, r^2=0.89).

Appendix 1. Total prey consumption and the estimations of feeding impact on krill resources by Antarctic minke whales in Area IV and V between 1999/00 and 2002/03.

*** Area IV**

Stratum	Year	Abundance (inds.)	Sexual maturity (%)				Abundance (inds.)				Body weight (kg)				Daily prey consumption (kg)				Annual consumption in Antarctic (million ton)				
			IM	MM	IF	MF	IM	MM	IF	MF	IM	MM	IF	MF	IM	MM	IF	MF	IM	MM	IF	MF	Total
West	1999/00	16,182	9.0	47.0	16.0	28.0	1,456	7,606	2,589	4,531	2,900	6,800	3,800	8,100	124.7	263.0	168.4	337.9	0.02	0.24	0.05	0.18	0.50
	2001/02	35,950	14.8	34.2	22.6	28.4	5,335	12,293	8,118	10,205	2,900	6,800	3,800	8,100	124.7	263.0	168.4	337.9	0.08	0.39	0.16	0.41	1.05
East	1999/00	28,390	14.3	35.2	18.7	31.7	4,073	9,998	5,308	9,011	2,900	6,800	3,800	8,100	124.7	263.0	168.4	337.9	0.06	0.32	0.11	0.37	0.85
	2001/02	25,513	12.0	28.6	16.6	42.9	3,062	7,289	4,228	10,934	2,900	6,800	3,800	8,100	124.7	263.0	168.4	337.9	0.05	0.23	0.09	0.44	0.80

*** Area V**

Stratum	Year	Abundance (inds.)	Sexual maturity (%)				Abundance (inds.)				Body weight (kg)				Daily prey consumption (kg)				Annual consumption in Antarctic (million ton)				
			IM	MM	IF	MF	IM	MM	IF	MF	IM	MM	IF	MF	IM	MM	IF	MF	IM	MM	IF	MF	Total
West	2000/01	19,057	17.1	50.7	13.6	18.6	3,267	9,665	2,586	3,539	2,900	6,800	3,800	8,100	124.7	263.0	168.4	337.9	0.05	0.30	0.05	0.14	0.55
	2002/03	83,734	6.0	48.0	10.0	36.0	5,024	40,192	8,373	30,144	2,900	6,800	3,800	8,100	124.7	263.0	168.4	337.9	0.08	1.27	0.17	1.22	2.73
East	2000/01	129,452	10.5	37.4	7.9	44.2	13,627	48,374	10,220	57,231	2,900	6,800	3,800	8,100	124.7	263.0	168.4	337.9	0.20	1.53	0.21	2.32	4.26
	2002/03	79,859	13.5	36.1	13.9	36.5	10,764	28,819	11,111	29,166	2,900	6,800	3,800	8,100	124.7	263.0	168.4	337.9	0.16	0.91	0.22	1.18	2.48