THIS PAPER CAN NOT BE CITED WITHOUT WRITTEN PERMISSION FROM THE AUTHORS

Food habit and prey consumption of Antarctic minke whale Balaenoptera bonaerensis in JARPA research area

TSUTOMU TAMURA AND KENJI KONISHI

The Institute of Cetacean Research, 4-18, Toyomi-cho, Chuo-ku, Tokyo 104-0055, Japan.

KEYWORDS: ANTARCTIC MINKE WHALE; ANTARCTIC KRILL; ANTARCTIC; MONITORING; ENERGETICS; FOOD/PREY; SCIENTIFIC PERMITS

ABSTRACT

We analyzed the stomach contents of Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean. The Antarctic minke whales fed mostly on Antarctic krill (*Euphausia superba*) in offshore area, and ice krill (*E. crystallorophias*) in coastal (shallow) area on continental shelf such as Ross Sea and Prydz Bay. The average of fresh stomach contents per capita has decreased year after year. Daily prey consumption was estimated using two independent methods, which were from theoretical energy requirement calculations and from diurnal changes of stomach contents mass. The results showed that estimated daily prey consumptions were similar between the above two methods and ranged from 2.67 to 4.95 % of body weight (immature male: 84-144 kg, immature female: 120-188 kg, mature male: 182-337 kg, mature female: 283-401 kg). These estimates almost corresponded with the results of maximum weight of stomach contents. The prey consumption during feeding season was 7.5-12.9 and 16.4-30.3 tons for immature and mature male, 10.8-16.9 and 33.9-48.1 tons for immature male and mature pregnant female, respectively. Our results seems useful to assess the Antarctic minke whale's feeding impact on krill resources and the level of interspecific competition among other baleen whales, seals and sea birds.

INTRODUCTION

Recently, the consumption of krill by baleen whales is getting important for the ecosystem in the Southern Ocean. Although the Antarctic krill (*Euphausia superba*) is preyed upon by many predators such as baleen whales, seals, sea birds, fish and squid. The prey consumption by whales can not disregard to understand the ecosystem because of their large biomass (Miller and Hampton, 1989).

The Antarctic minke whale (*Balaenoptera bonaerensis*) is most abundant baleen whale species in the Southern Ocean (south of 60° S) estimated to be as high as at 760,396 animals with 95 % confidence interval (510,000 – 1,140,000) in the austral summer of 1980s (IWC 1991). It breeds in austral winter at lower latitude and migrate to the Antarctic Ocean for feeding in austral summer (Horwood 1990, Kasamatsu *et al.* 1995). In Southern Ocean, the Antarctic minke whale feed mostly on Antarctic krill in offshore (*e.g.* Kawamura 1980, Bushuev 1986, Ichii and Kato 1991), and ice krill (*E. crystallorophias*) in coastal (shallow) area on the continental shelf such as Ross Sea and Prydz Bay (Bushuev 1986, Tamura 1998).

Some studies already estimated the daily prey consumption of the whales on the basis of energy-requirement calculations (Hinga 1979, Lockyer 1981a, 1981b, Armstrong and Siegfried 1991, Reilly *et al.* 2004). However, these methods were based on estimates and some assumptions regarding basal metabolic rate, growth, reproduction, migration and energy deposition in austral winter. So this, the estimates have some uncertain information such as body weight of the whale. The quantitative data of stomach contents were few until now.

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 and sample size

The research area covers Areas III-East (35°E to 70°E), IV (70°E to 130°E), V (130°E to 170°W) and VI-West (170°W to 145°W) which were designated by the IWC (Fig. 1). The surveys were conducted mainly from December to March between 1987/88 and 2004/05 seasons (Table 1). A total of 6,778 minke whales were sampled by the JARPA between 1987/88 and 2004/05 seasons. This study used the data of 6,777 minke whales, because one individual was lost before the landing on the flensing deck of the research base vessel (Table 1).

Research activity

The whales were randomly sampled using three sighting and sampling vessels and brought to a research base vessel, where biological measurements and sampling were carried out.

Sex, sexual maturity, body length, body weight, stomach contents mass, freshness category of stomach contents and prey species were used in this paper. 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 was weighed using the special large weighing machine on the flensing deck of the research base vessel. All whales were sampled during daylight hours, between 03:00 and 21:00 local time.

Sampling and analyses of stomach contents

All Balaenopterid species have four chambered stomach system (Hosokawa and Kamiya 1971, Olsen *et al.* 1994). Each stomach contents mass 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, See Appendix. 1). Then, sub samples (approx. 300 g) from forestomach contents with relatively fresh prey was removed and fixed in 10% formalin solution water for later analyses. At 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 estimation of daily prey consumption by Antarctic minke whale

The amount of krill consumed by Antarctic minke whales was estimated using two independent methods, which were from theoretical energy requirements calculations (method-1) and from diurnal changes of stomach contents (Forestomach and fundus (2nd. stomach)) (method-2).

Method-1 Estimation of daily consumption of krill from the standard metabolism

We calculated the prey consumption (F) during the austral summer in each different maturity stages of Antarctic minke whale from the standard metabolic rate (SMR) and energy deposit according to following equations:

Male or Immature female : $F(\text{kg day}^{-1}) = (SMR + ED) / E / A$

Mature female: $F(\text{kg day}^{-1}) = (SMR + ED + R) / E / A$

SMR :Standard metabolic rate (kJ day⁻¹)

- *ED* :Energy deposition (muscle, internal organs fat and blubber masses) (kJ day⁻¹)
- *E* :Caloric value of prey (*E. superba*) (kJ kg⁻¹)
- *R* :Reproduction cost (kJ day⁻¹)
- A :Assimilation efficiency

We made the following additional assumptions:

(1) Mean body length and mass during feeding season (W)

We calculated mean body lengths of 6.2 m and 6.7 m for immature males and females, and 8.4 m and 8.9 m for mature males and females from the data of JARPA surveys. The body mass values were obtained by use of weighing machine which was able to measure body mass of an Antarctic minke whale directly. All Balaenopterid species become fat by storing large amount of fat inside their body in feeding season, and become slim conversely by consuming the stored fat in breeding season. The body length – mass relationship for Antarctic minke whales, which were caught in December and March showed in Fig. 2. Immature and mature male of 6.2 m and 8.4 m were estimated to have an increase in body mass of 305 kg and 703 kg, respectively. A similar calculation was made for immature and mature female of 6.7 m and 8.9 m, and an increase in body mass of 308 kg and 595 kg were obtained, respectively. We also calculated mean body masses during feeding season 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 the data of JARPA surveys.

(2) Standard metabolic rate (SMR)

We calculated the basal metabolic rate (*M*) according to Kleiber's equation (Kleiber 1961):

 $M = 70W^{0.75}$ (kcal day⁻¹)

where *W* is the Antarctic minke whale body mass during feeding season (kg).

To account for energy spent on activities such as foraging, moving between food patches and migration, we calculated the standard metabolic rate (*SMR*) using the following equation (Markussen *et al.* 1992):

 $SMR = 1.45 \times M \times 4.184 \text{ (kJ day}^{-1)}$

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

The total muscle and blubber masses of Antarctic minke whales 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.

Blubber mass (tons) as a function of the body length (m) in Antarctic minke whales, which were caught in December and March showed in Fig. 3. Immature and mature male of 6.2 m and 8.4 m were estimated to have an increase in blubber mass of 105 kg and 271 kg, respectively. A similar calculation was made for immature and mature female of 6.7 m and 8.9 m, and an increase in blubber mass of 120 kg and 214 kg were obtained, respectively. There was a significant increase in the energy density of blubber, from 14,435 kJ kg -1 to 20,711 kJ kg -1 (wet mass) from December to March in feeding season.

Muscle mass (tons) as a function of the body length (m) in Antarctic minke whales, which were caught in December and March showed in Fig. 4. Immature and mature male of 6.2 m and 8.4 m were estimated to have an increase in muscle mass of 242 kg and 448 kg, respectively. A similar calculation was made for immature and mature female of 6.7 m and 8.9 m, and an increase in muscle mass of 189 kg and 271 kg were obtained, respectively. The energy density of muscle increased from 5,858 kJ kg -1 to 6,234 kJ kg -1 (wet mass) from December to March in feeding season.

The mass of internal organs fat deposition was estimated to deduct the blubber deposition and growth and/or deposition of muscle from total body mass. The energy density of internal organs fat is assumed as same as blubber's value.

(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) Feeding season (F)

Many baleen whale generally known to migrate between the feeding ground in high latitudinal waters in summer and the breeding ground in low latitudinal waters in winter. The encounter rate (as a simple index of distribution density) of Antarctic minke whales in the Antarctic as feeding ground increased from early November to late December and peak in January, followed by a steady decrease through February (Kasamatsu *et al.* 1996). There is a segregation pattern of Antarctic minke whales in the Antarctic. The proportion of males tends to decrease with latitude; maturity rate of males are related to the school sizes and mature males tend to make larger schools. Females, especially mature females, tend to be distributed in southern part of the research area (Kato 1982, Horwood 1990). Lockyer (1981a, b) estimated the feeding season that immature animals and mature male spend 90days, mature female spend 120 days, respectively. We assumed that they moved southward in austral summer and northward in austral winter at the same time. We also assumed that immature animals and mature male spend 90days, mature female spend 120 days, respectively.

(6) Reproduction cost (R)

The total reproductive cost for a female Antarctic minke whales was calculated by Lockyer (1981a) to be 1.89 $\times 10^7$ kJ (= 0.45 $\times 10^7$ kcal), assuming that the length at birth is 273 cm (Best 1982). We assumed that almost mature female were pregnant, and all reproduction cost took during feeding season (120 days).

(7) Assimilation efficiency (*A*)

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

Method-2 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-d, the amount of prey consumed (Ci) is given by the following equations:

 $t_{1}: C_{1}=V_{1}$ $t_{2}: C_{2}=V_{2}-SV_{1}$ $t_{3}: C_{3}=V_{3}-SV_{2}-S^{2}V_{1}$ $t_{i}: C_{i}=V_{i}-SV_{i-1}-S^{2}V_{i-2}\cdots S^{i-1}V_{1}$

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

$$\sum_{i=1}^{k} C_{i} = V_{1} \frac{(1-2S+S^{k})}{1-S} + V_{2} \frac{(1-2S+S^{k-1})}{1-S} + \dots + V_{k-1}(1-S) + \dots + V_{k}$$

In this study, we calculated the mean stomach content (forestomach and fundus stomach) mass as % of body mass (Vi) at 1 hour intervals based on the stomach content mass (kg) and body mass (kg). Nordøy *et al.* (1993) showed that krill were digested by bacterial fermentation, and that this digestion process was very rapid. Assuming that it takes 4 hours that prey is digested in the stomach of Antarctic minke whales (Bushuev 1986) and that d is exponential (Elliott and Persson 1978), we estimated *S* to be 0.67 and 0.74, if the proportion of undigested prey in the stomach after 4 hours is 20 % and 30 %, respectively.

RESULTS

Prey items

A total of ten prey species, including one amphipod, four euphausiids and five fishes were identified in the stomachs of Antarctic minke whales (Table 2). *Euphausia superba* and were the dominant prey species, occurring in 85-100 % of the stomach examined in each area (Table 3, Fig. 5), followed by *E. crystallorophias*, *E. frigida*, *Thysanoessa macrura*, an amphipod *Parathemisto gaudichaudi* and one fish species *Pleragramma antarcticum*. In offshore area, *E. superba* was the most dominant prey species, follwed by *T. macrura*. In inshore area such as Ross Sea in Area V, *E. crystallorophias* was the most dominant prey species.

The diurnal changes in feeding activity

The composition of freshness categories and the diurnal change in the mean stomach content mass as % of body mass of Antarctic minke whale was showed in Figs. 6 and 7. These figures show that the proportion of undigested category of F (fresh) and fff (lightly digested) and the rate of the mean stomach content mass have gradually decreased with time periods. After 19:00 hrs, F of freshness categories and the rate of the mean stomach content mass showed a slight increase.

Stomach contents weight

The mean and maximum weight of stomach contents were shown in table. 4. The mean weight of undigested stomach contents (freshness category F and fff) were 30.9 ± 23.5 kg (1.0 % of body weight) and 43.0 ± 31.5 kg (1.0 % of body weight) for immature male and female, respectively and 74.2 ± 50.1 kg (1.1 % of body weight) and 76.3 ± 54.6 kg (1.0 % of body weight) for mature male and female, respectively.

The maximum weight of stomach contents (category F and fff) were 125.7 kg (3.1 % of body weight) and 156.0 kg (3.4 % of body weight) for immature male and female, respectively and 343.8 kg (4.2 % of body weight) and 321.2 kg (3.6 % of body weight) for mature male and female, respectively.

The trend of stomach contents

To clear the daily prey consumption, the average of undigested stomach contents (category: F and fff) was calculated for mature male and female in each survey year (Fig. 8). In area IV, Fig. 8 shows that the average of undigested stomach contents for mature male and female has decreased year after year (Mature male: F=0.25, Mature female F=0.11). In area V, there was same trend. Especially, the trend of decrease for mature female was significant (Mature male: F=0.59, Mature female F=0.009).

Daily prey consumption of Antarctic minke whales

Method-1 Energy-requirements calculations

Standard metabolic rate (SMR)

The mean body lengths of Antarctic minke whales were 6.2 and 6.7 m for immature males and females and 8.4 and 8.9 m for mature males and females, respectively in JARPA surveys. The mean body masses during feeding season were 2,900 and 3,800 kg for immature males and females, and 6,800 and 8,100 kg for mature males and females in JARPA surveys.

Standard metabolic rate per day of immature and mature males were 16.8×10^4 and 31.8×10^4 kJ, respectively. And, standard metabolic rate per year of immature and mature females were 20.6×10^4 and 36.3×10^4 kJ, respectively (Table 5).

Energy deposition during feeding season in the Southern Ocean

We estimated the energy deposition as blubber deposition, growth and/or deposition of muscle and internal organ's fat deposition during feeding season.

Deposited energy intakes as blubber during feeding season of immature and mature males were 7.0×10^4 and 16.3×10^4 kJ per day, respectively. And, deposited energy intakes as blubber during feeding season of immature and mature females were 14.5×10^4 and 30.2×10^4 kJ per day, respectively (Table 5).

Deposited energy intakes as muscle during feeding season of immature and mature males were 2.5×10^4 and 5.0×10^4 kJ per day, respectively. And, deposited energy intakes as muscle during feeding season of immature and mature females were 2.0×10^4 and 3.3×10^4 kJ per day, respectively (Table 5).

Deposited energy intakes as fat (internal organ's fat) during feeding season of immature and mature males were 5.3×10^4 and 15.2×10^4 kJ per day, respectively. And, deposited energy intakes as fat during feeding season of immature and mature females were 8.1×10^4 and 20.7×10^4 kJ per day, respectively (Table 5).

Daily prey consumption during feeding season

The daily prey consumptions during feeding season were 37.5×10^4 and 81.3×10^4 kJ for immature and mature male, 53.8×10^4 and 126.5×10^4 kJ for immature and mature female, respectively (Table 5).

When the mean energy value of prey (*E. superba*) was 4,473 kJ kg⁻¹ (= 1,070 kcal kg⁻¹), the daily prey consumptions during feeding season were 83.7 and 181.7 kg for immature and mature male, 120.2 and 282.9 kg for immature and mature female, respectively (Table 5).

Method-2 Diurnal changes of stomach content mass

Estimated rates of daily prey consumption were 4.36 and 4.95 % of body mass of Antarctic minke whales. The estimated prey consumption weights were 126.4-143.6 kg and 165.7-188.1 kg for immature male and female, respectively and 296.5-336.6 kg and 353.2-401.1 kg for mature male and female, respectively (Table 6).

Prey consumption during feeding season and annual consumption

We estimated the prey consumption during feeding season based on methods 1 and 2.

Based on method 1, the prey consumption were 7.5 and 16.4 tons for immature and mature male, 10.8 and 33.9 tons for immature and mature female, respectively (Table 7). Based on method 2, the total prey consumption were 11.4-12.9 and 26.7-30.3 tons for immature and mature male, 14.9-16.9 and 42.4-48.1 tons for immature and mature female, respectively (Table 7).

We also estimated the annual prey consumption based on methods 1 and 2. Based on method 1, we calculated the annual prey consumption using *SMR*, reproduction cost, energy value of prey and assimilation efficiency. Based on method 2, we assumed that Antarctic minke whales spend about 90 days and 120 days in the feeding areas in the feeding ground (Lockyer 1981a, 1981b). Lockyer (1981b) reported that the daily food consumption of the minke whale in winter was equivalent to 10 % of that in the summer. We adopted these assumptions for calculating annual prey consumption. Based on method 1, the prey consumption were 19.4 and 36.8 tons for immature and mature male, 23.8 and 40.0 tons for immature and mature female, respectively (Table 7). Based on method 2, the total prey consumption were 14.9-16.9 and 34.8-39.6 tons for immature and mature male, 19.5-22.1 and 51.0-57.9 tons for immature and mature female, respectively. The prey consumption during feeding season based on methods 1 and 2 accounted for 64-86 % and 77-83 % of annual prey consumption, respectively (Table 7).

Feeding impact on krill resources by Antarctic minke whales in Area IV and V of the Antarctic

In Area IV, total prey consumptions of krill by Antarctic minke whales of 1999/00 and 2001/02 season were estimated to be 1.19 and 1.33 million tons, respectively. On the other hand, in Area V, total prey consumptions of krill by Antarctic minke whales of 2000/01, 2002/03 and 2004/05 season were estimated to be between 4.48, 5.73 and 2.97 million tons, respectively (Appendix 2, Table 8). The estimations of feeding impact on krill resources by Antarctic minke whales in Area IV and V were 4 %, and from 22 to 25 % of krill standing stock, respectively (Table 8).

DISCUSSION

Prey items

The Antarctic minke whales fed mostly on Antarctic krill (*Euphausia superba*) in offshore area, and ice krill (*E. crystallorophias*) in coastal (shallow) area on continental shelf such as Ross Sea and Prydz Bay. It is strongly suggested that Antarctic minke whale has been feeding on most abundant prey species among target species. *E. crystallorophias* is dominant euphausiid on the continental shelf (< 1,000m), the occurrence of Antarctic krill increases close to the continental shelf break and further off the shelf (Thomas and Green, 1988).

The diurnal changes in feeding activity

Our results suggested that Antarctic minke whales seem to have a diurnal feeding rhythm, with a primary peak in the early morning. This coincided with previous reports (Ohsumi 1979, Bushuev 1986). Other studies in common minke whales (*B. acutrostrata*) in Northern Hemisphere have shown tendency for a diurnal feeding activity (Haug *et al.* 1997, Lindstrøm *et al.* 1998). In the eastern North Atlantic and western North Pacific, they do not feed prey at night (Folkow and Blix 1993, Haug *et al.* 1997, Tamura 1998).

Our result showed that Antarctic minke whales fed on the prey easily and might be ceased to feed at earlier time in the day due to the satisfaction with feeding. If they feed on prey fully at once, they can be satisfied with daily energy-requirement for whales.

Daily prey consumption of Antarctic minke whales

Using method 1, the daily prey consumption was little to that using method 2. However, the estimate based on method 1 may be negatively biased to some extent depending on the residence time in the Antarctic. In the case of that immature animals and mature male spend 90days in the feeding ground, the prey consumption during feeding season was estimated to be 16.3-31.6 tons and accounted for 56-63% of annual prey consumption. It was cleared that they needed to extend the stay period to fill their demand energy requirement. In the case of method 1, we estimated the daily prey consumption using energy deposition during feeding season in Antarctic. This energy deposition during feeding season was based on one assumption that they moved southward in austral summer and northward in austral winter at the same time. If their migration were multiform pattern, our body length – mass relationship for Antarctic minke whales in December and March had negatively biased to some extent.

Using method 2, the daily prey consumption would underestimate the actual prey consumption, because no information is available from 21:00 to 03:00 hrs. Thus, the daily consumption rate was estimated to be at least 4.4 % of body weight of whales. However, the estimates based on two independent methods were coincidence

well each other. These estimates based on methods 1 and 2 were supported by the maximum weight of stomach contents and the diurnal feeding rhythm obtained in the field data.

Estimates of the daily prey consumption rate obtained from the above two methods ranged from 2.67 to 4.95 %. These values were similar to estimates by Lockyer (1981b) and Bushuev (1986). Our results were reasonable estimates even from the point of energy requirement and field stomach contents data. The estimates of this study almost corresponded with the results of maximum weight of stomach contents, could be used with confidence for the estimation of daily prey consumption by Antarctic minke whales.

The estimates daily prey consumption rates using respiratory allometry of male and female Antarctic minke whales during the austral summer is to be 6.7 and 6.2 %, respectively (Armstrong and Siegfried 1991). But these estimates may be overestimates, because, it needs to be a maximum of two feeding times per day for daily energy requirement. However, the results of maximum weight of stomach contents were ranged from 3.1 to 4.2 % of their body mass. And, there was only one peak of the diurnal feeding rhythm, it was difficult to feed on prey over 6 % of their body mass in a day.

Mori and Butterworth (2004) built up the Multi-species (Antarctic minke whale, blue whale (*B. musculus*) and Antarctic krill) type ecosystem modeling in the Antarctic. Antarctic minke whales and blue whales both feed mainly on Antarctic krill near the ice edge in the Antarctic. 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. They assumed the daily prey consumption rate (% of body mass) by Antarctic minke whales were ranged from 0.6 or 2.85 or 5.1 %. And, they assumed that the body weight of Antarctic minke whales was 7 tons, the feeding days was 90 days. They indicate that the daily prey consumption rate of Antarctic minke whale was ranged from 3.0 to 5.0 % of body mass using their model. It seems plausible based on our results. It might be useful for analyzing of ecosystem modeling in the Southern Ocean.

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

Some studies proposed the annual prey consumption of Antarctic minke whales using energy requirement models in the Antarctic. Armstrong and Siegfried (1991) estimated that an 'average-sized' male and female of Antarctic minke whale consume 37.2 tons, 56.2 tons during feeding season, respectively. They indicated that the Antarctic minke whales consume 95 % of krill biomass that is consumed by baleen whales in the Antarctic equal to 35.5 million tons, if the estimated population of Antarctic minke whales was applied 760,396 animals. However, their annual prey consumption was more than 2.9-4.0 and 3.3-5.2 times the range of 9.2-12.8 tons and 10.9-16.9 tons for immature male and female animals by this study. The result of consumption by Antarctic minke whales seems overestimate.

In the Southern Ocean, large baleen whale species were depleted drastically 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 initial biomasses. This rapid decreasing of large baleen whale species provided the annual surplus of krill as much as 150 million tones (Laws 1977). This surplus became available for other krill predators, such as Antarctic minke whale, crabeater seal (*Lobodon carcinophagus*), Antarctic fur seal (*Arctocephalus gazella*), some penguins and sea birds.

Mori and Butterworth (2004) indicated that trend of abundance of Antarctic minke whale had been declined after 1980's using multispecies interaction model among Antarctic minke whale, blue whale and krill in the Southern Oceans. The causes of abundance of Antarctic minke whale decreasing seem to be over carrying capacity of Antarctic minke whales, competition among Antarctic minke whales, some baleen whales such as blue, fin (*B. physalus*) and humpback whales (*Megaptera novaeangliae*) and some predators such as seals and sea birds, or decreasing of krill biomass due to environment changes. It was reported that abundances of humpback whales increased 11-12 % per year in the some region of Southern Oceans (Bannister, 1994, IWC, 2000). And, it was reported that Antarctic krill biomass in the south western Atlantic reduced by 80% from the level in 1970's due to the rise in seawater temperature (Atkinson *et al.* 2004). Kato (1987) indicated that the growth rate of Antarctic minke whales such as blue whales being depleted. If the carrying capacity level of Antarctic minke whale is decreasing, the growth rate of Antarctic minke whales will increase, and the age at maturity will decrease. It must monitor the biological parameters such as the growth rate, the age at maturity and the body condition such as blueber thickness of whales for longtime.

Unfortunately, the information of abundance and biological parameters of cetaceans, seals and sea birds were limited in the Southern Oceans. It will be necessary to monitor abundance and biological parameters of cetaceans and other organisms in the Antarctic to evaluate the role of Antarctic minke whales in the Antarctic marine ecosystem in the future.

ACKNOWLEDGMENTS

We thank Dr. Hidehiro Kato, Dr. Yoshihiro Fujise, Mr. Kazuo Yamamura, late Dr. Fujio Kasamatsu, Mr. Shigetoshi Nishiwaki and Mr. Hajime Ishikawa, research leaders of these cruises for giving us the opportunity to carry out this study. The stomach contents examined in this study were collected by many researchers and crews. We also thank the captains, crews and researchers who were involved in the JARPA research cruises for their efforts. We thank Mrs. Ryoko Zenitani, Mr. Takeharu Bando and Dr. Yoshihiro Fujise for providing us maturity data of Antarctic minke whales sampled. We thank Mrs. Ikuyo Kouda for her helpful analyzing of the stomach contents. Our sincere thank to Dr. Hiroshi Hatanaka, Dr. Luis A. Pastene of the Institute of Cetacean Research (ICR) and Dr. Hidehiro Kato, Dr. Taro Ichii of the National Research Institute of Far Seas Fisheries for their valuable suggestions and useful comments on this paper.

REFERENCES

- Armstrong, A.J., Siegfried, W.R. 1991. Consumption of Antarctic krill by minke whales. Antarctic Science, 3(1):13-18.
- Atkinson, A., Siegel, V., Pakhomov, E. and Rothery, P. 2004. Long-term decline in krill stock and increase in salps within the Soutern Ocean. *Nature*, 432:100-103.
- Baker, A.de.C., Boden, B.P. and Brinton, E. 1990. A practical guide to the euphausiids of the world. Natural History Museum Publications: London. 96 pp.
- Bando, T., Zenitani, R., Fujise, Y. and Kato, H. Estimation of biological parameters in the Antarctic minke whale, *Balaenoptera bonaerensis*' based on JARPA data from Areas IV and V. (JA/J05/PJR5 in this meeting)
- Barnard, K.H. 1932. Amphipoda. Discovery Rep., 5:1-326.
- Best, P.B. 1982. Seasonal abundance, feeding, reproduction, age and growth in minke whale off Durban (with incidental observations from the Antarctic). *Rep. int. Whal. Commn* 32:759-786.
- Blix, A. S. and Folkow, L. P. 1995. Daily energy expenditure in free living minke whales. *Acta Physiol. Scand.*, 153:61-66.
- Bushuev, S.G. 1986. Feeding of minke whales, *Balaenoptera acutorostrata*, in the Antarctic. *Rep. int. Whal. Commn* 36:241-245.
- Elliott, J.M., Persson, L. 1978. The estimation of daily rates of food consumption for fish. J. Animal Ecol. 47:977-991.
- Fischer, W. and Hureau, J.C. (eds). 1985a. FAO species identification sheets for fishery purposes. Southern Ocean (Fishing areas 48, 58 and 88) (CCAMLA Convention Area). Prepared and published with the support of the Comission for the Conservation of Antarctic Marine Living Resources. Rome, FAO, Vol. 1. 1-232.
- Fischer, W. and Hureau, J.C. (eds). 1985b. FAO species identification sheets for fishery purposes. Southern Ocean (Fishing areas 48, 58 and 88) (CCAMLA Convention Area). Prepared and published with the support of the Comission for the Conservation of Antarctic Marine Living Resources. Rome, FAO, Vol. 2. 233-470.
- Folkow, L.P., Haug, T., Nilsen, K.T. and Nordøy, E.S. 2000. Estimated food consumption of minke whales *Balaenoptera acutorostrata* in Northeast Atlantic waters in 1992-1995. *NAMMCO Sci. Publ.* 2.
- Hakamada, T., Matsuoka, K. and Nishiwaki, S., 2006. An update of Antarctic minke whales abundance estimate based on JARPA data (SC/D06/J6 in this meeting)
- Haug, T., Nilssen, K.T., Lindstrom, U. and Skaug, H.J. 1997. On the variation in size and composition of minke whale (*Balaenoptera acutorostrata*) forestomach contents. J. Northwest Atl. Fish. Sci. 22:105-114.
- Haug, T. Lindstrom, U. and Nilssen, K. T. 2002. Variations in minke whale (*Balaenoptera acutorostrata*) diet and body condition in response to ecosystem changes in the Barents Sea. Sarsia 87:409-422.
- Hinga, K.H. 1979. The food requirements of whales in the southern hemisphere. *Deep-Sea Research*. 26A:569-577.
- Hosie, G.W. 1991. Distribution and abundance of euphausiid larvae in the Prydz Bay region, Antarctica. *Antarctic Science* 3:167-180.
- Hosokawa, H. and Kamiya, T. 1971. Some observations on the cetacean stomachs, with special considerations on the feeding habits of whales. *Sci. Rep. Whales Res. Inst.*, 23:91-101.
- Ichii, T. 1987. Observation of fishing operation and distributional behavior of krill on a krill trawler off Wilkes Land during the 1985/86 season. *In*: Selected Scientific Papers. CCAMLR, Hobart, SC-CAMLR-SSp/4:335-368.
- Ichii, T. and Kato, H. 1991. Food and daily food consumption of southern minke whales in the Antarctic. *Polar Biol.*, 11:479-487.
- Innes S, Lavigne D.M, Eagle W. M. and Kovacs K. M., 1986. Estimating feeding rates of marine mammals from heart mass to body mass ratios. *Mar. Mamm. Sci.* 2:227-229

International Whaling Commission. 1991. Report of the Scientific Committee. Rep. int. Whal. Commn 41:51-219.

Kasamatsu, F., Joyce, G.G. Ensor, P. and Mermoz, J. 1996. Current occurrence of baleen whales in Antarctic

waters. Rep. int. Whal. Commn 46:293-304.

Kawamura A. 1980. A review of food of Balaenopterid whales. Sci Rep Whales Res Inst 32:155-197

- Kleiber, M. 1961. The fire of life. J. Wiley and Sons Inc., New York and London, 454pp.
- Konishi, K. and Tamura T. 2005. Yearly trend of blubber thickness in the Antarctic minke whale, *Balaenoptera bonaerensis* in Area IV and V. (JA/J05/PJR9 in this meeting)
- Laws, R.M. 1977. Seals and whales of the Southern Ocean. Phil. Trans. R. Soc. Lond., Ser. B279: 81-96.
- Lindstrom, U., Fujise, Y., Haug, T. and Tamura, T. 1998. Feeding habits of western North Pacific minke whales, *Balaenoptera acutorostrata*, as observed in July-September 1996. *Rep. int. Whal.Commn* 48:463-469.
- Lockyer, C. 1981a. Estimation of the energy costs of growth, maintenance and reproduction in the female minke whale, (*Balaenoptera acutorostrata*), from the southern hemisphere. *Rep. int. Whal. Commn* 31:337-343.
- Lockyer, C. 1981b. Growth and energy budgets of large baleen whales from the Southern Hemisphere. FAO Fish. Ser. (5) [*Mammals in the Sea*] 3:379-487.
- Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., Trivelpiece, S. 1997. Effects of seaice extent and krill or salp dominance on the Antarctic food web. Nature 387:897-900.
- Miura, T. 1969. Research methods of the productivity of limnological life. Koudansya. Tokyo.168-171. [in Japanese].
- Markussen, N.H., Ryg, M. and Lydersen, C. 1992. Food consumption of the NE Atlantic minke whale (*Balaenoptera acutorostrata*) population estimated with a simulation model. *ICES J. mar. Sci.*,49:317-323.
- Mori, M. and Butterworth, D.S. 2004. Consideration of multispecies interactions in the Antarctic: A preliminary model of the minke whale-Blue whale- Krill interaction. *Ecosytem Approches to Fisheries in the Southern Benguela Afr. J. mar. Sci.* 26:245-259.
- Murase, H., Tamura, T., Matsuoka, K., and Hakamada, T. 2006. First attempt of estimation on feeding impact on krill standing stock by three baleen whale species (Antarctic minke, humpback and fin whales) in Areas IV and V using JARPA data. (SC/D06/J22 in this meeting)
- Ohsumi, S. 1979. Feeding habits of the minke whale in the Antarctic. Rep. int. Whal. Commn, 29:473-476.
- Olsen, M.A., Nordøy, E.S., Blix, A.S. and Mathiesen, S.D. 1994. Functional anatomy of the gastrointestinal system of Northeastern Atlantic minke whales (*Balaenoptera acutorostrata*). J. Zool., Lond., 234:55-74.
- Pakhomov, E.A., Froneman, P.W. and Perissinotto, R. 2002. Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. *Deep-Sea Research II*. 49:1881-1907.
- Reilly, S., Hedley, S., Borberg, J., Hewitt, R., Thiele, D., Watkins, J. and Naganobu, M. 2004. Biomass and energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean. *Deep-Sea Research II*. 51A:1397-1409.
- Tamura, T., Ichii, T. and Fujise, Y. 1997. Consumption of krill by minke whales in Areas IV and V of the Antarctic. IWC Scientific Committee working paper SC/M97/17, 9p. (unpublished).
- Tamura, T. 1998. *The study of feeding ecology of minke whales in the Northwest Pacific and the Antarctic*. D.C. Thesis. Hokkaido University. 125pp [in Japanese].
- Tamura, T. and Fujise, Y. 2002. Geographical and seasonal changes of the prey species of minke whale in the western North Pacific. *ICES J. mar. Sci.* 59:516-528.
- Tamura, T. 2002. Regional assessments of prey consumption and competition by marine cetaceans in the world. In *Responsible Fisheries in the Marine Ecosystem*. Pp. 143-170. Ed. By Snclair, M. and Valdimarsson, G. 448pp. Rome. FAO and CABI Publishing.
- Tobayama, T. 1974. *Studies on the feeding habits of the little toothed whales*. D.C. Thesis. Tokyo University. 231pp. [in Japanese].
- Thomas, P.G. and Green, K. 1988. Distribution of Euphausia crystallorophias within Prydz Bay and its importance to the inshore marine ecosystem. *Polar Biol.* 8:327-331.
- Zenitani, R. and Kato, H. Long term trend of age at sexual maturity of Antarctic minke whales by counting transition phase in earplugs. (JA/J05/PJR7 in this meeting)

Area	Area	III-East	Are	a IV	Are	ea V	Area V	VI-West	То	otal
Season	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1987/88			153	119					153	119
1988/89					85	151			85	151
1989/90			184	142					184	142
1990/91					164	159			164	159
1991/92			165	123					165	123
1992/93					167	160			167	160
1993/94			200	130					200	130
1994/95					200	130			200	130
1995/96	69	41	203	126					272	167
1996/97					132	198	74	36	206	234
1997/98	74	36	205	123					279	159
1998/99					207	122	40	20	247	142
1999/2000	63	46	170	160					233	206
2000/01					186	144	72	38	258	182
2001/02	54	56	147	183					201	239
2002/03					168	162	67	43	235	205
2003/04	62	48	138	192					200	240
2004/05					110	220	67	43	177	263
Total	322	227	1,565	1,298	1,419	1,446	320	180	3,626	3,151

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

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

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

	Species	Area III-E	Area IV	Area V	Area VI-W
Krill		100.0	99.9	99.7	100.0
	Euphausia superba	99.5	95.2	85.4	93.0
	E. crystallorophias	0.1	2.7	11.5	0.0
	E. frigida	0.4	0.0	0.2	0.0
	Thysanoessa macrura	0.0	2.1	2.9	6.8
Ampipods	s Parathemisto gaudichaudi	0.0	0.1	0.1	0.0
Fish	Pleuragramma antarcticum	0.0	0.0	0.2	0.0

 Table 3. Occurrence (%) of main prey species found in the stomachs of Antarctic minke whales sampled by JARPA surveys

 Table 4. Stomach contents weight of Antarctic minke whales

Sex	Maturity	Number	Cont	ents weight	(All)	Number	Conte	ents weight ((F+fff)
			Average	S.D.	Maximum		Average	S.D.	Maximum
Male	Immature	535	18.1	20.4	125.7	182	30.9	23.5	125.7
			(0.6%)	(0.6%)	(3.1%)		(1.0%)	(0.7%)	(3.1%)
	Mature	2,532	50.0	47.6	343.8	1,180	74.2	50.1	343.8
			(0.7%)	(0.7%)	(4.2%)		(1.1%)	(0.7%)	(4.2%)
Female	Immature	978	25.4	28.1	156.0	321	43.0	31.5	156.0
			(0.7%)	(0.7%)	(4.2%)		(1.0%)	(0.7%)	(3.4%)
	Mature	1,895	49.5	50.8	321.2	756	76.3	54.6	321.2
			(0.6%)	(0.6%)	(3.6%)		(1.0%)	(0.7%)	(3.6%)

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

Sex	Maturity	Body	Body	SMR	Blubber	Muscle	Fat	Reproduction	Daily pro	ey consump	tion
		length	weight		deposition	deposition	deposition	cost	during	feeding seas	son
		(m)	(kg)	(KJ/day)	(KJ/day)	(KJ/day)	(KJ/day)	(KJ/day)	(KJ/day)	(kg/day)	(%)
Male	Immature	6.2	2,900	167,825	69,610	24,698	52,535		374,605	83.7	2.89
	Mature	8.4	6,800	318,009	162,664	50,245	151,704		812,645	181.7	2.67
Female	Immature	6.7	3,800	205,540	144,620	20,088	81,306		537,562	120.2	3.16
	Pregnant	8.9	8,100	362,595	302,215	33,265	207,344	157,500	1,265,379	282.9	3.49

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

Sex	Maturity	Body weight	S=0.	74	S=0.	67
		(kg)	(kg)	(%)	(kg)	(%)
Male	Immature	2,900	126.4	4.36	143.6	4.95
	Mature	6,800	296.5	4.36	336.6	4.95
Female	Immature	3,800	165.7	4.36	188.1	4.95
	Mature	8,100	353.2	4.36	401.0	4.95

Table 7. The prey consumption of Antarctic minke whales during feeding season

Sex	Maturity	Prey con during fee	sumption ding season		Annual pr	ey consumption	
		Method-1	Method-2	Metl	nod-1	Method	1-2
		(t)	(t)	(t)	(%)	(t)	(%)
Male	Immature	7.5	11.4 - 12.9	19.4	64.3	14.9 - 16.9	76.6
	Mature	16.4	26.7 - 30.3	36.8	64.3	34.8 - 39.6	76.6
Female	Immature	10.8	14.9 - 16.9	23.8	64.3	19.5 - 22.1	76.6
	Mature	33.9	42.4 - 48.1	40.0	85.8	51.0 - 57.9	83.0

Table 8. 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
1999/2000 JARPA and 2002/03 JARPA (Ref. Murase *et al.* in this meeting)

Stratum	Year	Abundance (inds.)	Prey consumption (million ton)	Krill biomass (million ton)	Feeding impact (%)
IV	1999/00	44,931	1.19	34.2	3.5
	2001/02	48,960	1.33	34.1	3.9
V	2000/01	164,789	4.48	20.7	21.6
	2002/03	201,883	5.73	22.6	25.4



Fig.1. Research area in the Antarctic



*Mature male



Fig. 2. 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.

Immature male (December \bigcirc , n=170; March \bullet , n=72): (December: y=0.0178x^{2.7648}, r²=0.93; March: y=0.0181x^{2.8131}, r²=0.93) Mature male (December \bigcirc , n=709; March \bullet , n=404): (December: y=0.0260x^{2.6016}, r²=0.67; March: y=0.0531x^{2.3136}, r²=0.63) Immature female (December \bigcirc , n=276; March \bullet , n=109): (December: y=0.0164x^{2.8178}, r²=0.95; March: y=0.0221x^{2.7054}, r²=0.95) Mature female (December \bigcirc , n=243; March \bullet , n=260): (December: y=0.0317x^{2.5161}, r²=0.63; March: y=0.0570x^{2.2815}, r²=0.44)

*Immature male

*Mature male



Fig. 3. 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.

*Immature male

*Mature male



Fig. 4. 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.



Fig.5-a. Distribution of krill consumed by Antarctic minke whales in Areas III-East and IV (●:Euphausia. superba, ○:E. crystallorophias, :Thysanoessa spp., □:E. S. + others, ×: E. spp.)



Fig.5-b. Distribution of krill consumed by Antarctic minke whales in Areas V and VI-West. (•:*Euphausia. superba*, ○:*E. crystallorophias*, :*Thysanoessa* spp., □:*E.* S. + others, ×: *E.* spp.)



Fig. 6. Composition of between freashness categories for prey and time periods in Antarctic (F ■: fresh, fff ■: lightly digested, ff ■: moderately digested, f ■: heavily digested, 0 □: empty)



Fig. 7. Change in the mean mass \pm *S.E.* of stomach content with time. Weight expressed as percentage of Antarctic minke whale body mass.





Area V





*Mature female

Fig. 8. Yearly trend of the mean mass of undigested stomach content. (Data was from individuals collected from an area south of 63 degrees in January and February.)

Appendix. 1. Classification of freshness of forestomach (1st. stomach) contents.

Code	Class	Description
F	Freash	Prey not affected by digestion
fff	Lightly digested	Prey slightly affected by digestion
ff	Moderately digested	Prey moderattory to highly fragmented
f	Heavily digested	Unidentifiable remains or indigestible parts only

Appendix 2. Total prey consumption and the estimations by Antarctic minke whales in Area IV and V between 1999/2000 and 2004/05.

(Ref. Hakamada et al., in this meeting)

Area IV																						
	Abundance	æ	ody wei	ieht (ke		Sexu	al mati	urity ((%)	-	Abundanc	e (inds.)		Daily p	rey con	sumpt	ion (kg)	Annual c	consumptic	on in Anta	arctic(mil	ion ton)
year	(inds.)	IM	MM	IF	MF	IM	MIM	IF	MF	IM	MIM	IF	MF	IM	MIM	IF	MF	IM	MM	IF	MF	Total
1999/00	44,931	2,900	6,800	3,800	8,100	9.1	42.4	17.9	30.6	4,085	19,062	8,033	13,752	117.9	271.6	158.0	345.7	0.04	0.47	0.11	0.57	1.19
2001/02	48,280	2,900	6,800	3,800	8,100	11.2	45.2	10.0	33.6	5,413	21,799	4,828	16,240	117.9	271.6	158.0	345.7	90.0	0.53	0.07	0.67	1.33
Area V																						
	Abundance	æ	ody wei	ieht (ke		Sexu	al mati	urity ((%)		Abundanc	e (inds.)		Daily p	rey con	sumpt	on (kg)	Annual c	consumptic	on in Anta	arctic(mil	ion ton)
year	(inds.)	IM	MM	IF	MF	IM	MIM	IF	MF	IMI	MIM	IF	MF	IM	MIM	IF	MF	IM	MM	IF	MF	Total
2000/01	164,789	2,900	6,800	3,800	8,100	10.3	34.2	19.4	36.1	16,978	56,428	31,959	59,424	117.9	271.6	158.0	345.7	0.18	1.38	0.45	2.47	4.48
2002/03	201,883	2,900	6,800	3,800	8,100	7.0	43.9	12.7	36.4	14,071	88,706	25,694	73,412	117.9	271.6	158.0	345.7	0.15	2.17	0.37	3.05	5.73
2004/05	91,819	2,900	6,800	3,800	8,100	4	28.5	10.3	56.4	4,452	26,154	9,460	51,752	117.9	271.6	158.0	345.7	0.05	0.64	0.13	2.15	2.97