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Feeding Habits and Prey Consumption of Antarctic Minke Whale (*Balaenoptera bonaerensis*) in the Southern Ocean

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Abstract

The Antarctic minke whale (*Balaenoptera bonaerensis*) is the most abundant baleen whale species in the Southern Ocean. Quantitative information on prey consumption of whales is useful to understand their feeding ecology and role in the ecosystem. The purposes of this study are 1) to investigate the feeding habit of Antarctic minke whales based on information on prey species, freshness and diurnal change in stomach contents, and 2) to estimate the amount of prey consumed by whales. Estimates are made for whales of different sexual maturity classes as it is expected that the energy requirements vary among them. The analysis is based on the data from whales taken by JARPA (Japanese Whale Research Program under Special Permit in the Antarctic) in a longitudinal sector between 35º E and 145º W, and south of 60º S. Sampling was conducted in the austral summer seasons from 1987/1988 to 2004/2005, mainly in the months from December to March. Daily prey consumption by the whales in each sexual maturity class was estimated using energy-requirement and energy deposition. The whales feed mainly before 05:00 h, which suggest that they cease to feed early in the day. Daily prey consumptions were estimated to be 83.7–325.5 kg, equivalent to 2.7–4.0% of body weight. The mean prey consumptions per capita during feeding season were 7.5 and 16.4 t for immature and mature male, 12.5 and 39.1 t for immature and mature female, respectively. In Area IV (70°–130°E), total prey consumptions of krill by Antarctic minke whales in 1999/2000 and 2001/2002 seasons were estimated to be 0.9 and 1.1 million t, respectively. In Area V (130° E–170° W including the Ross Sea), these estimates in 2000/2001 and 2002/2003 seasons were 3.9 and 4.1 million t, respectively. The estimations of feeding impact on krill resources by Antarctic minke whales in Areas IV and V were from 2.7 to 3.2%, and from 18.2 to 18.9% of krill biomasses, respectively. These results on prey consumption are important input data for the development of ecosystem modeling in the Southern Ocean.

Keywords: Antarctic minke whale, feeding habit, krill, prey consumption

Introduction

Determining the extent of the impact of predators on the ecosystem is an important factor to consider for the development of ecosystem models, which in turn could assist in the elaboration of multi-species management policies. The Southern Ocean has a simple food web with the Antarctic krill (*Euphausia superba*) as the key species. The consumption by some penguin and seal species on krill has been estimated (Doidge and Croxall, 1985; Boyd, 2002). For example, the prey consumption during austral summer of Antarctic fur seal (*Arctocephalus gazella*) around South Georgia was estimated to be 1.1 million t (Doidge and Croxall, 1985). However quantitative information on consumption by baleen whales, the largest consumer group, is quite limited (Miller and Hampton, 1989).

The Antarctic minke whale (*Balaenoptera bonaerensis*) is the most abundant balaenopterid species in the Southern Ocean (IWC, 1991). Like other balaenopterid species (except the Bryde's whale *B. edeni*) the Antarctic minke whale spends its breeding season at lower latitude in austral winter and migrates to the Southern Ocean to feed in austral summer (Horwood, 1990; Kasamatsu *et al.*, 1995). The Antarctic minke whale feeds mainly on Antarctic krill in offshore waters (Kawamura, 1980; Bushuev, 1986; Ichii and Kato, 1991), and on ice krill (*E. crystallorophias*) on the coastal shelf, such as Ross Sea and Prydz Bay (Bushuev, 1986; Tamura, MS 1998).

Previous studies estimated the daily prey consumption of the Antarctic minke whales in the Southern Ocean on the basis of energy-requirement calculations (Lockyer, 1981a; Armstrong and Siegfried, 1991; Reilly *et al.*, 2004). None of these studies considered the fact that whales condition change with the progression of the feeding season. It is known that baleen whales store energy in their blubber and internal fat in the feeding season. Nordoy *et al.* (1995) estimated the food requirements of Northeast Atlantic minke whales based on energy stores. Therefore for the estimation of prey consumption it is important to assess the energy storage directly during feeding season of the minke whales.

In this study, the feeding habit and daily prey consumption of the Antarctic minke whales is examined based on a large data set obtained during the research surveys of the JARPA (Japanese Whale Research Program under Special Permit in the Antarctic) between the austral summer season 1987/1988 and 2004/2005. The JARPA survey procedure was described by Nishiwaki *et al.* (MS 2006). It is expected that the output of this study will assist the understanding of the role of the Antarctic minke whale in the ecosystem and the development of ecosystem models for management purposes.

Methods

Research area, period and number of samples

Data used in the present study were collected during the surveys of the JARPA in the International Whaling Commission's (IWC) Antarctic management Areas III-East (35°–70° E), IV (70°–130° E), V (130° E–170° W including the Ross Sea) and VI-West (170°–145° W), and south of 60° S (Fig. 1). The surveys were conducted in the austral summer seasons (December–March) from 1987/1988 to 2004/2005 seasons. During the surveys a total of 6 777 Antarctic minke whales were sampled. Table 1 shows the number of samples by area and sex. After sampling whales were brought to the research base vessel where animals were examined by biologists on-board. All whales were sampled during daylight hours, between 03:00 and 21:00 h.

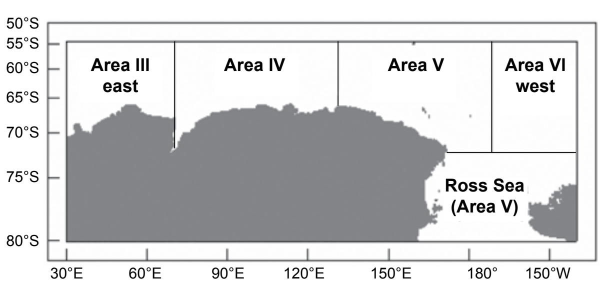

Fig. 1. Research area in the Antarctic.

Treatments of stomach contents

All balaenopterid species have four chambered stomach compartments (Hosokawa and Kamiya, 1971; Olsen *et al.*, 1994). Stomach contents were removed from each compartments and weighed to the nearest 0.1 kg. The analysis of prey consumption in this study was based on data collected from the first compartment (forestomach) and second compartment (fundus). To examine the daily feeding rhythms of the minke whale the freshness of preys in the forestomach were categorized into four digestion levels

F = fresh (prey not affected by digestion,
fff = lightly digested (prey slightly affected by digestion),
ff = moderately digested (prey moderately to highly fragmented), and
f = heavily digested (unidentifiable remains or indigestible parts only).

Because of uniformity of prey within the stomachs of almost all whales, after checking the stomach contents, some fresh prey (200 g) in the forestomach or fundus were collected and stored in 10% formalin for species identification at the laboratory. Prey species were identified to the lowest taxonomic level as possible using external morphology (Barnard, 1932; Fischer and Hureau, 1985a, b; Baker *et al.*, 1990).

Biological data

An estimate of the daily prey consumption requires the use of some additional biological and morphometric data. Body length of the whales was measured to the nearest 10 cm from the tip of the upper jaw to the deepest part of the fluke notch in a straight line. The whole body of whales was weighed using a large scale installed on the flensing deck. For some individuals muscle, blubber and internal organs were weighted for calculating the

TABLE 1. Sample size used in this study.

Area	Area III-East		Area IV		Area V		Area VI-West		Total	
Sex	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Number	322	227	1 565	1 298	1 419	1 446	320	180	3 626	3 151

energy deposited during the feeding season. A correction factor for blood loss was not calculated in this study.

Energy requirements are different for different sexual maturity classes, therefore estimations of the daily prey consumption in this study took into consideration information on sexual maturity. Sexual maturity of Antarctic minke whales was defined in accordance with Kato *et al.* (1990). Males with a single testis weight of 400 g or more was defined as sexually mature. Females with at least one corpus luteum or albicans in their ovaries were defined sexually mature.

Analytical procedure for the daily prey consumption

The daily prey consumption in each sexual maturity class was estimated from the standard metabolic rate and energy deposit according to the following equations:

Male or Immature female:

$$D_{kg} = (SMR_{kJ} + ED_{kJ}) / E_{KJ}$$

Mature female:

$$D_{kg} = (SMR_{kJ} + ED_{kJ} + R_{kJ}) / E_{KJ}$$

Where D_{kg} is daily prey consumption (kg d^{-1}), SMR_{kJ} is standard metabolic rate (kJ d^{-1}), ED_{KJ} is Energy deposition (kJ d^{-1}), R is Reproduction cost (kJ kg^{-1}) and E_{kJ} is caloric value of prey species (kJ kg^{-1}). The details of these items are described as follow:

Standard metabolic rate (SMR_{kJ}). To account for energy spent on activities such as foraging, moving between food patches and migration the standard metabolic rate (SMR_{kJ}, kJ d^{-1}) was calculated using the following equation (Markussen *et al.*, 1992):

$$SMR_{kJ} = 1.45 \times BMR \times 4.184$$

The basal metabolic rate (BMR, kcal d^{-1}) was calculated following Kleiber's equation (Kleiber, 1961):

$$BMR = 70M^{0.75}$$

where M is the Antarctic minke whale body weight (kg). The value of 1.45 is the coefficient for energy spent on activities such as foraging, moving between food patches and migration. The value of 4.184 is the conversion factor from Kcal to KJ.

Energy deposited during feeding season in Antarctic (ED_{kJ}). The total muscle, blubber and internal organs weight of some Antarctic minke whales were weighed to calculate seasonal growth and fat deposition. In this study the deposition were converted to energy deposition by measuring the energy density of muscle and blubber of some whales sampled in the early and late seasons during austral summer by bomb calorimeter (n = 1 in each sexual category).

The weight of others fat deposition (*e.g.* internal organs) was estimated to deduct the weight of blubber deposition and the weight of muscle deposition from total body weight.

Reproduction cost (R_{KJ}). The R_{KJ} for a female Antarctic minke whale was calculated by Lockyer (1981a) to be 1.89×10^6 kJ, assuming that the length at birth is 273 cm (Best, 1982). We assumed that almost all mature female were pregnant, and that all reproduction cost took during feeding season (120 days). The R_{KJ} for a female Antarctic minke whale was calculated to be 158×10^3 kJ d^{-1}.

Energy value of *Euphausia superba* (E_{KJ}). Antarctic minke whales feed mainly on *E. superba*. The energy value is 4 473 kJ kg^{-1}. In this study this value was measured by bomb calorimeter (n = 1). We assumed the same value for other prey items such as *E. crystallorophias*. Lockyer (1981a) estimated that Antarctic minke whales had an assimilation efficiency of 84%. We used same value as assimilation efficiency for calculating of daily prey consumption. Therefore energy value of prey items of whales was estimated to be 3 757 kJ kg^{-1}.

Feeding period. The encounter rate (as a simple index of distribution density) of Antarctic minke whales in the Antarctic increased from early November to late December and peak in January, followed by a steady decrease through February (Kasamatsu *et al.*, 1996). Immature animals and mature males spend 90 days in the feeding grounds, mature females spend 120 days (Lockyer, 1981a, b). We also assumed that immature animals and mature male spend 90 days, mature female spend 120 days, respectively. The total prey consumption during feeding season (SD_{kg}) was applied as following:

Immature animals and mature male:

$$SD_{kg} = 90\, D_{kg}$$

Mature female:

$$SD_{kg} = 120\, D_{kg}$$

Estimation of total prey consumption in Areas IV and V

The total prey consumption by Antarctic minke whales in Areas IV and V from 1999/2000 to 2002/2003 seasons was estimated using information on abundance in these Areas (Hakamada *et al.*, MS 2006) and the composition of the Antarctic minke whales by sex and sexual maturity status based on JARPA data.

Furthermore, we also estimated the feeding impact on krill resources by the minke whales in Area IV and V of the Antarctic from 1999/2000 to 2002/2003 seasons.

The biomass of krill resources were estimated by acoustic survey as described in Murase *et al.* (MS 2006).

Results

Prey species composition

A total of ten prey species, one amphipod (*Parathemisto gaudichaudi*), four euphausiids (*Euphausia superba*, *E. crystallorophias*, *E. frigida*, *Thysanoessa macrura*) and five fishes (*Pleragramma antarcticum*, *Notolepis coatsi*, *Electona antarctica*, *Chinodraco* sp. and *Notothenis* sp.), were identified from the stomachs of the Antarctic minke whales. The Antarctic krill was dominant prey species, occurring in 85–100% by weight composition of the whales examined in each area (Table 2, Figs. 2a, b), followed by ice krill, two euphausiids (*E. frigida*, *T. macrura*), one amphipod (*P. gaudichaudi*) and one fish species (*P. antarcticum*).

Diurnal changes in feeding activity

The composition of freshness categories and the diurnal change in the mean of the ratio of stomach contents weight to body weight, expressed as a percentage (RSC), is shown in Figs. 3 and 4. These figures show that the

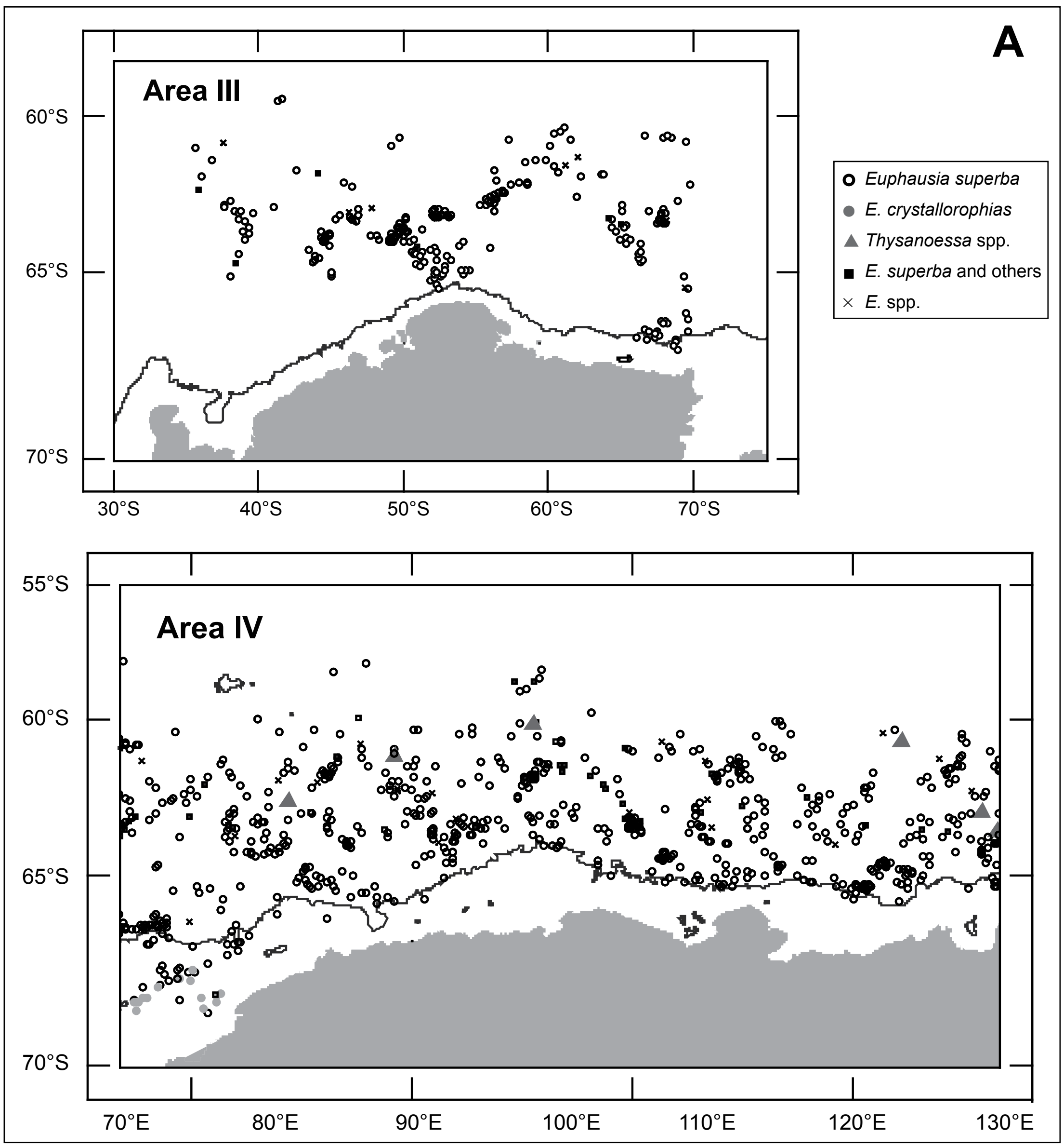

Fig. 2. (**A**) Sampling position of Antarctic minke whales and their dominant prey species in Areas III-East and IV. Line shows water depth contour of 1 000 m.

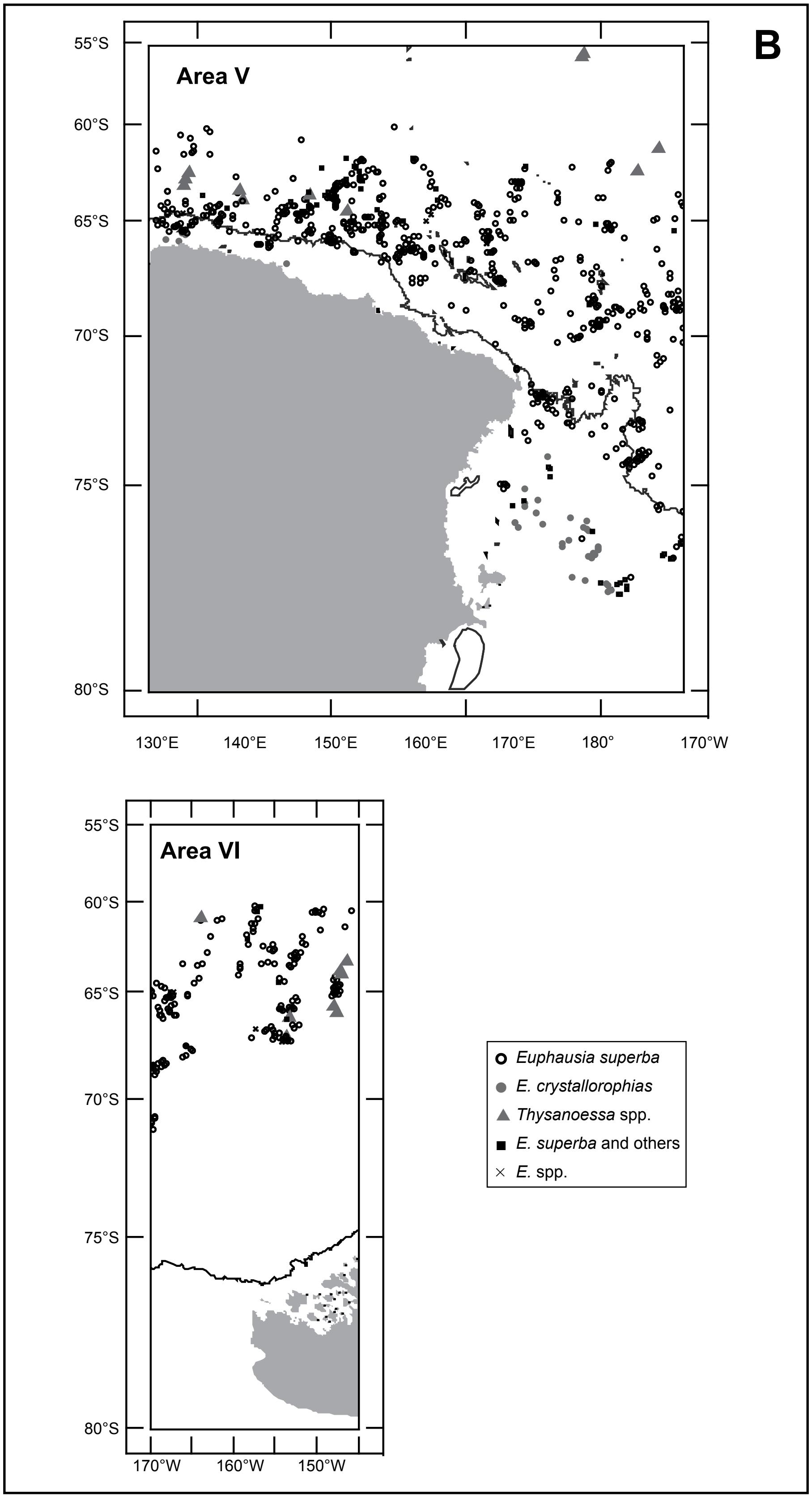

Fig. 2. (**B**) Sampling position of Antarctic minke whales and their dominant prey species in Areas V and VI-West. Line shows water depth contour of 1 000 m.

TABLE 2. Occurrence (% by weight composition) of main prey species found in the stomachs of Antarctic minke whales sampled by JARPA surveys.

Species		Area III-E	Area IV	Area V	Area VI-W
Krill	*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	*Parathemisto gaudichaudi*	0.0	0.1	0.1	0.0
Fish	*Pleuragramma antarcticum*	0.0	0.0	0.2	0.0

proportion of fresh and lightly digested categories and the rate of the mean stomach content weight had gradually decreased from early morning to afternoon. After 19:00 h, the fresh categories and the weight of the mean stomach content weight showed a slight increase.

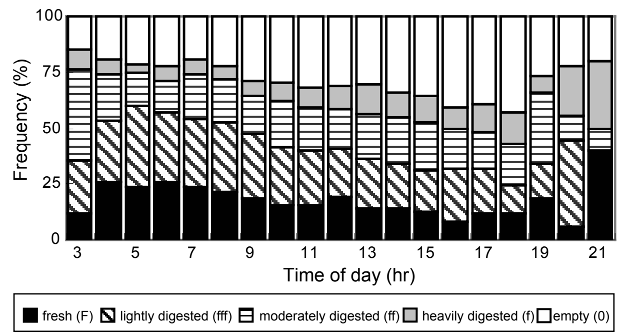

Fig. 3. Composition of prey freshness categories throughout the day in the Antarctic minke whale.

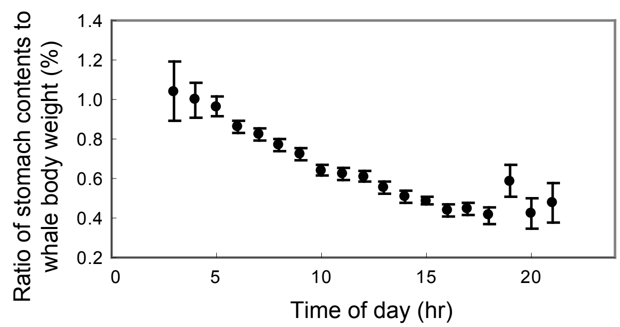

Fig. 4. Change in the ratio of stomach contents to whale body weight (RSC) throughout the day. Error bars are ± 1 S.E.

Stomach contents weight

The mean and maximum weight of stomach contents of different reproductive classes are shown in Table 3. The mean weight of fresh or lightly digested stomach contents (freshness category F and fff) were 30.9 ± 23.5 kg (RSC: 1.0%) and 43.0 ± 31.5 kg (RSC: 1.0%) for immature males and females, respectively and 74.2 ± 50.1 kg (RSC: 1.1%) and 76.3 ± 54.6 kg (RSC: 1.0%) for mature males and females, respectively.

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

Daily prey consumption

Body weight of whales. The average body lengths were 6.1 ± 0.7 (Average ± S.D) and 8.4 ± 0.4 m for immature and mature males, and 6.7 ± 1.0 and 8.9 ± 0.4 m for immature and mature females, respectively. The mean body weight was 2 900 ± 1 000 and 6 800 ± 1 100 kg for immature and mature males, and 3 800 ± 1 600 and 8 100 ± 1 200 kg for immature and mature females, respectively. SMR_{kJ} of immature and mature males were 168×10^3 and 318×10^3 kJ, respectively. SMR_{kJ} of immature and mature females were 206×10^3 and 363×10^3 kJ, respectively (Table 4).

Energy deposited during feeding season. There was an increase in the energy density of blubber of males from 14 435 to 20 711 kJ kg^{-1} (wet weight) and of females from 16 443 to 28 075 kJ kg^{-1} (wet weight) between December and March. There was also an increase in the energy density of muscle of males from 5 858 to 6 234 kJ kg^{-1} (wet weight) and of females from 5 941 to 6 192 kJ kg^{-1} (wet weight) between December and March (Table 5).

Fig. 5 shows the relationship between blubber weight (t) and body length (m), by sex and maturity class. Immature and mature males had an increase in blubber energy contents per day of 69 610 kJ and 162 664 kJ, respectively. Immature and mature females had an increase in blubber energy contents per day of 144 620 kJ and 303 619 kJ, respectively (Table 4).

TABLE 3. Stomach contents weight (kg) of Antarctic minke whales. RSC is ratio of stomach contents weight to body weight expressed as a percentage.

			Contents weight (F+fff)		
Sex	Maturity	Number	Average	S.D.	Maximum
Male	Immature	182	30.9	23.5	125.7
			(RSC: 1.0%)		(RSC: 3.1%)
	Mature	1 180	74.2	50.1	343.8
			(RSC: 1.1%)		(RSC: 4.2%)
Female	Immature	321	43.0	31.5	156.0
			(RSC: 1.0%)		(RSC: 3.4%)
	Mature	756	76.3	54.6	321.2
			(RSC: 1.0%)		(RSC: 3.6%)

TABLE 4. Required energy contents (KJ d^{-1}) of Antarctic minke whales.

Sex	Maturity	Body length (m)	Mean body weight (kg)	SMR (KJ d^{-1})	Blubber deposition (KJ d^{-1})	Muscle deposition (KJ d^{-1})	Others fat deposition (KJ d^{-1})	Reproduction cost (KJ d^{-1})
Male	Immature	6.1	2 900	167 825	69 610	24 698	52 535	
	Mature	8.4	6 800	318 009	162 664	50 245	151 704	
Female	Immature	6.7	3 800	205 540	144 620	20 088	150 950	
	Pregnant	8.9	8 100	362 595	303 619	31 175	368 105	157 500

Fig. 6 shows the relationship between muscle weight (t) and body length (m), by sex and maturity class. Immature and mature males had an increase in muscle energy contents per day of 24 698 kJ and 50 245 kJ, respectively. Immature and mature female had an increase in muscle energy contents per day of 20 088 kJ and 31 175 kJ, respectively (Table 4).

The weight of others fat deposition (*e.g.* internal organs) was estimated to deduct the weight of blubber deposition and the weight of muscle deposition from total body weight (Figs. 5, 6 and 7). Immature and mature male had an increase in others fat energy contents per day of 52 535 kJ and 151 704 kJ, respectively. Immature and mature female had an increase in muscle energy contents per day of 150 950 kJ and 368 105 kJ, respectively (Table 4).

Daily and seasonal prey consumption. The calculated daily energy requirements during feeding season were 315×10^3 and 683×10^3 kJ for immature and mature male, and 521×10^3 and $1\,223\times10^3$ kJ for immature and mature female, respectively (Table 6).

TABLE 5. Energy value of blubber and muscle (KJ kg^{-1}) of Antarctic minke whales.

	Blubber (KJ kg^{-1})		Muscle (KJ kg^{-1})	
Sex	December	March	December	March
Male	14 435	20 711	5 858	6 234
Female	16 443	28 075	5 941	6 192

When the mean energy value of prey of 4 473 kJ kg^{-1} and the assimilation efficiency of 84% were assumed, the daily prey consumptions during feeding season were 83.7 and 181.7 kg for immature and mature male, and 138.7 and 325.5 kg for immature and mature female, respectively. These values were equivalent to 2.9 and 2.7% of mean body weight for immature and mature male, and 3.7 and 4.0% of mean body weight for immature and mature female, respectively (Table 6).

The seasonal prey consumptions per capita during feeding season were 7.5 and 16.4 t for immature and mature male, and 12.5 and 39.1 t for immature and mature female, respectively (Table 6).

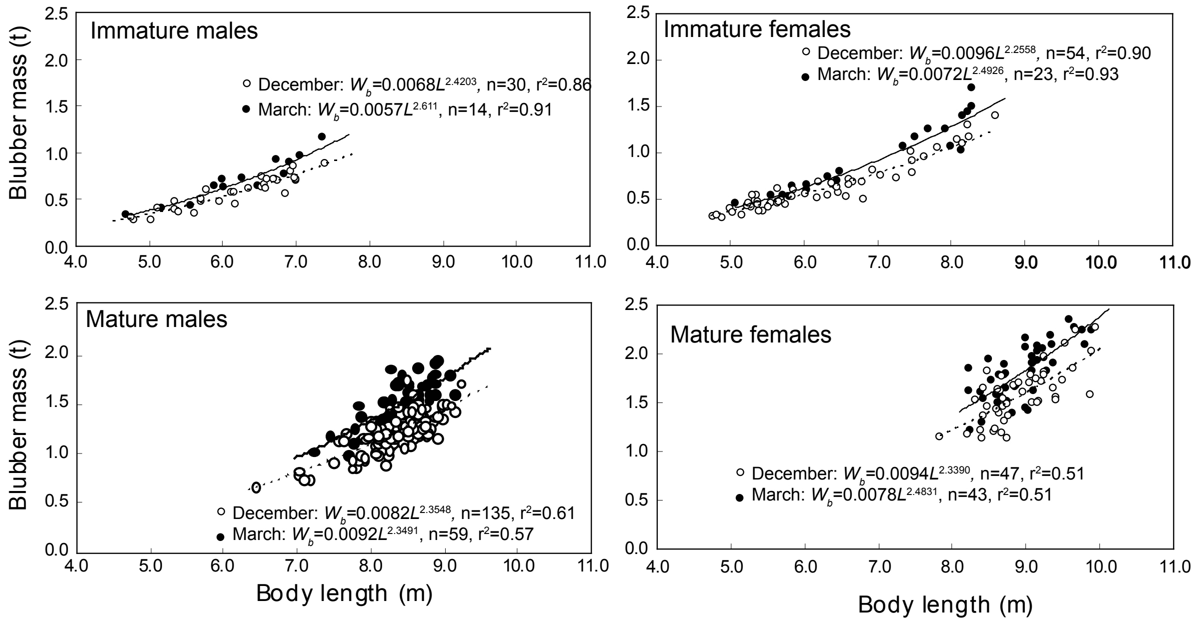

Fig. 5. The blubber weight (W_b, t) as a function of body length (L, m) for Antarctic minke whale sampled in December and March.

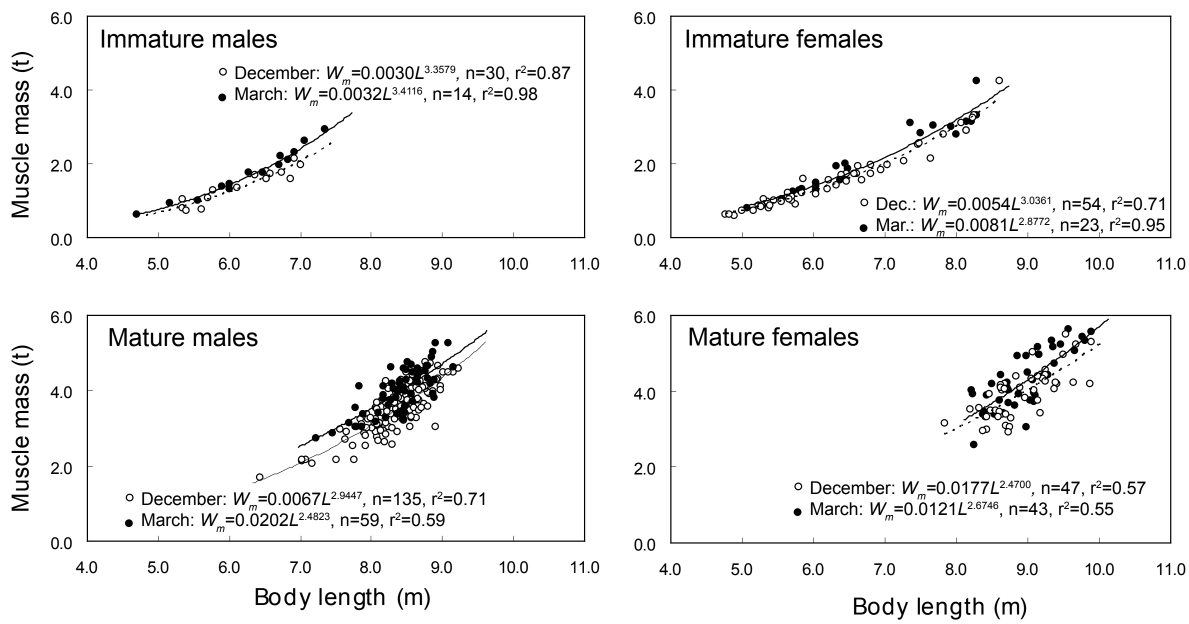

Fig. 6. The muscle weight (W_m, t) as a function of body length (L, m) for Antarctic minke whales sampled in December and March.

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

Abundance of Antarctic minke whales in Areas IV and V. The abundance of Antarctic minke whales in Areas IV and V was estimated based on sighting data collected during the JARPA as described in Hakamada *et al.* (MS 2006). In Area IV in 1999/2000 and 2001/2002 seasons, the abundance was estimated to be 44 931 and 48 280, respectively. In Area V in 2000/2001 and 2002/2003 seasons, the abundance was estimated to be 160 997 and 175 985, respectively (Table 7).

Biomass of Antarctic krill in Areas IV and V. The krill biomass was estimated by acoustic survey conducted under the JARPA as described in Murase *et al.* (MS

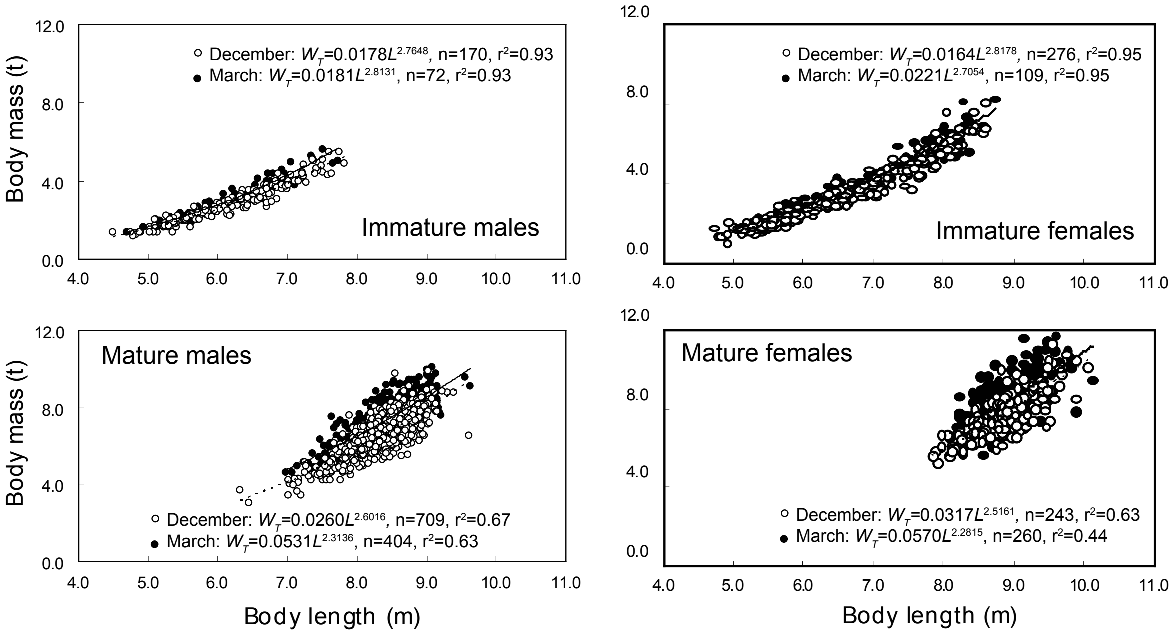

Fig. 7. Total body weight (W_T, t) as a function of body length (L, m) for Antarctic minke whales sampled in December and March.

TABLE 6. The daily and seasonal prey consumption of Antarctic minke whales.

Sex	Maturity	Body length (m)	Mean body weight (B.W., kg)	Daily prey consumption during feeding season (KJ d^{-1})	(kg d^{-1})	(% of B.W.)	Seasonal consumption (t)
Male	Immature	6.1	2 900	314 668	83.7	2.9	7.5
	Mature	8.4	6 800	682 622	181.7	2.7	16.4
Female	Immature	6.7	3 800	521 198	138.7	3.7	12.5
	Pregnant	8.9	8 100	1 222 994	325.5	4.0	39.1

2006). In Area IV in 1999/2000 and 2001/2002 seasons, the biomass was estimated to be 34.2 and 34.1 million t, respectively. In Area V in 2000/2001 and 2002/2003 seasons, the biomass was estimated to be 20.7 and 22.6 million t, respectively (Table 8).

Total prey consumption and feeding impact. In Area IV, total prey consumptions of krill by Antarctic minke whales of 1999/2000 and 2001/2002 season were estimated to be 0.9 and 1.1 million t, respectively. On the other hand, in Area V, total prey consumptions of krill by Antarctic minke whales of 2000/2001 and 2002/2003 season were estimated to be between 3.9 and 4.1 million t, respectively (Table 7).

The estimations of feeding impact on krill resources by Antarctic minke whales in Areas IV and V were from 2.7 to 3.2%, and from 18.2 to 18.9% of krill biomass, respectively (Table 8).

Discussion

Diversity of prey species

The main prey species of Antarctic minke whales during austral summer were two krill species. Consumption of these species depended on the distributional difference of the krill species. The Antarctic minke whales fed mostly on Antarctic krill in offshore area, and ice krill in coastal (shallow) area on continental shelf such as Ross Sea and Prydz Bay. It is strongly suggested that Antarctic minke whale feed on local predominant prey species. Ice krill is a dominant euphausiid on the continental shelf (Water depth <1 000 m), the occurrence of Antarctic krill

TABLE 7. The seasonal prey consumption of Antarctic minke whales in Areas IV and V. The abundance of whales was estimated by Hakamada *et al*. (MS 2006).

Stratum	Year	Abundance (inds.)	Composition (%)				Abundance (inds.)				Seasonal consumption in Antarctic (million t)				
			IM	MM	IF	MF	IM	MM	IF	MF	IM	MM	IF	MF	Total
Area IV															
Total	1999/00	44 931	11.9	41.2	21.4	25.5	5 347	18 512	9 615	11 457	0.04	0.30	0.12	0.45	0.91
	2001/02	48 280	9.6	36.1	20.2	34.1	4 635	17 429	9 753	16 463	0.03	0.29	0.12	0.64	1.08
Area V															
West	2000/01	19 608	17.1	50.7	13.6	18.6	3 361	9 944	2 661	3 641	0.03	0.16	0.03	0.14	0.36
	2002/03	100 775	6.0	48.0	10.0	36.0	6 047	48 372	10 078	36 279	0.05	0.79	0.13	1.42	2.38
East	2000/01	141 389	10.5	37.4	7.9	44.2	14 883	52 835	11 163	62 509	0.11	0.86	0.14	2.44	3.56
	2002/03	75 210	13.5	36.1	13.9	36.5	10 137	27 141	10 464	27 468	0.08	0.44	0.13	1.07	1.72
Total	2000/01	160 997					18 244	62 779	13 824	66 150	0.14	1.03	0.17	2.58	3.92
	2002/03	175 985					16 184	75 513	20 542	63 747	0.12	1.23	0.26	2.49	4.10

IM: Immature males, MM: Mature male, IF: Immature female, MF: Mature female

TABLE 8. Seasonal prey consumption and feeding impact on the krill resource of Antarctic minke whales in Areas IV and V (Murase *et al*., MS 2006).

Area	Year	Abundance (inds.)	Prey consumption (million t)	Krill biomass (million t)	Krill biomass (% of whale's feeding)
IV	1999/00	44 931	0.9	34.2	2.7
	2001/02	48 280	1.1	34.1	3.2
V	2000/01	160 997	3.9	20.7	18.9
	2002/03	175 985	4.1	22.6	18.2

increases close to the continental shelf break and further off the shelf (Thomas and Green, 1988). Regional differences of the prey species of the minke whales might reflect changes in the distribution of these prey species in the research area. Direct comparison between stomach contents and prey availability in small areas is necessary for future research.

The diurnal feeding rhythm

Our results suggested that Antarctic minke whales have a diurnal feeding rhythm, with a primary peak early in the morning. This coincided with results of previous reports (Ohsumi, 1979; Bushuev, 1986). Other studies on common minke whales (*B. acutrostrata*) in the Northern Hemisphere have shown a tendency for a diurnal feeding activity (Haug *et al.*, 1997; Lindstrøm *et al.*, 1998). In the eastern North Atlantic and western North Pacific, they might not feed at night (Folkow and Blix, 1993; Haug *et al.*, 1997; Tamura, MS 1998). The diurnal pattern seems to be similar to that found in North Atlantic fin whales (Vikingsson 1997). Our result indicates that Antarctic minke whales ceased to feed at earlier time in the day due to the satisfaction with feeding. The maximum amounts of prey found in the stomachs indicate that daily energy-requirement can be met with a single stomach fill. For fin whale off Iceland, Vikingsson (1997) estimated that the mean passage time from the forestomach to fundus was 3–6 h, and that from the forestomach to the anus around 15–18 h. Our result support his estimation.

JARPA has not conducted research activity at night. Whether or not the minke whales feed on prey at night needs to be confirmed using methodology such as the depth data logger system in future.

Daily prey consumption of Antarctic minke whales

Previous estimates of daily prey consumption rates using respiratory allometry of male and female Antarctic minke whales during the austral summer were 6.7 and 6.2% of body weight, respectively (Armstrong and Siegfried, 1991). These may be overestimates because those values would require a maximum of two feeding times per day for daily energy requirement. However the results of this study indicated a range of maximum weight of stomach contents from 3.1 to 4.2% of their body weight. Furthermore our study detected only one peak of the diurnal feeding rhythm.

In this study estimates of the daily prey consumption rate (% of body weight) ranged from 2.7 to 4.0% of their body weight (Table 7). These values were similar to the estimates by Lockyer (1981b), Bushuev (1986) and Mori and Butterworth (2004). Using modeling approach, Mori and Butterworth (2004) indicated that the daily prey consumption rate of Antarctic minke whale ranged from 3.0 to 5.0% of body weight. The estimates from our energy requirements calculations almost corresponded with the results of maximum weight of stomach content in the field data. Therefore these results can be used with confidence as the estimation of daily prey consumption by Antarctic minke whales.

The issue of seasonal energy deposition and body condition of North Atlantic fin and sei whales were discussed by Vikingsson (1995) and Lockyer (1987). As next step the assessment of geographical, monthly and yearly change in the energy requirements of Antarctic minke whales should be investigated. The output from these analyses will be important for the development of ecosystem models.

Some uncertainties in the prey consumption estimates

The important parameters used for estimating prey consumption in this study are the energy contents of prey, muscle and blubber. However, in this study these values were calculated on the basis of very few samples. To account for differences within the season a large number of samples should be examined in the future.

Regarding residence time of Antarctic minke whale in the feeding ground in this study we assumed a period of 120 days for mature females. Baleen whales are generally known to migrate between feeding grounds in high latitudinal waters in summer and the breeding grounds in low latitudinal waters in winter. The ratio of high to low feeding seasons and the proportion of the energy intake per year during the high feeding season are assumed without actual data. This could bring some uncertainty to the estimations. It might be possible in the near future to provide information on residence time using satellite tagging.

There are several models available to estimate whale consumption (see review by Leaper and Lavigne, 2007). Future analyses should evaluate the extent of change in prey consumption estimate derived from using different models.

Prey consumption as an input parameter for ecosystem modeling

In the Southern Ocean, large baleen whale species were depleted drastically in the 20th century. Laws (1977) suggested that before the 1970s, blue (*B. musculus*) and humpback (*Megaptera novaeangliae*) whales were the most harvested and were reduced to about 3 and 5% of their initial biomasses, respectively. Fin (*B. physalus*) was reduced to about 20% of their initial biomasses. This rapid decreasing of large baleen whale species provided the annual surplus of krill as much as 150 million t (Laws, 1977). This surplus became available for other krill predators, such as Antarctic minke whale, crabeater seal (*Lobodon carcinophagus*), Antarctic fur seal (*A. gazella*), some penguins and sea birds. This phenomenon is called "krill surplus from the depletion of baleen whales".

In the South Atlantic sector of the Southern Ocean, Reilly *et al.* (2004) estimated the total prey consumption by baleen whales and the feeding impact on krill resources in 2000. The total prey consumption was estimated between 1.6 and 2.7 million t. This range is approximately 4–6% of the krill resources. The total prey consumption by other krill predators such as seabirds and pinnipeds was estimated 16 million t in this region (Croxall *et al.*, 1985). This consumption was ten times greater than that estimates by baleen whales.

In our study region, the total prey consumption by baleen whales was estimated between 0.9 and 4.1 million t. This range is approximately 2.7–18.9% of the krill resources. At present there is little information about the consumption of other krill predators such as seabirds and pinnipeds in our study region for comparison with our results.

Mori and Butterworth (2004) indicated that trend of abundance of Antarctic minke whale had declined after the 1980s using multispecies interaction model including Antarctic minke whale, blue whale and krill in the Southern Oceans. The causes of the decrease in abundance of Antarctic minke whale seem to be abundance over carrying capacity of Antarctic minke whales, competition among Antarctic minke whales, some baleen whales such as blue, fin and humpback whales and some predators such as seals and sea birds, or decreasing of krill biomass due to environment changes.

In a recent study, regression analyses clearly showed that blubber thickness, girth and fat weight have been decreasing for nearly two decades using catch data from all 18 survey years in the JARPA (Konishi *et al.*, 2008). This phenomenon shows that an increase in the abundance of other krill feeders than minke whales and a resulting decrease in the krill population must be considered as a likely explanation.

In the future it is important to investigate the trend of population dynamics among krill and krill predators such as baleen whales, seals and sea birds in the Southern Ocean for management of Antarctic ecosystem. For consideration of ecosystem interaction, many data sets such as natural mortality, birth rate, abundance, per capita of consumption, prey biomass are required.

Therefore, estimates of many parameters for applying in the multi-species ecosystem modeling should be improved in the future. To improve estimates of the daily and seasonal consumption by the minke whales is also important one. Our results are useful to apply as the input data of daily consumption by the minke whales in the entire Southern Ocean for ecosystem-based management. However, our estimates do not account for geographical, monthly and yearly change of their energy requirements.

As next step, the assessment of geographical, monthly and yearly change of their energy requirements by the minke whales is needed. Furthermore, the present results should be compared with information on krill resources and other krill predator's distribution and consumption.

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