

# Prey composition and consumption rate by Antarctic minke whales based on JARPA and JARPAII data

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## ABSTRACT

In this study, the information on the feeding habits of Antarctic minke whales (*Balaenoptera bonaerensis*) sampled during the surveys of the Japanese Whale Research under Special Permit in the Antarctic (JARPA and JARPAII), for the period of 1987/88–2010/11 are summarized. Some of the analyses considered recommendations offered during the 2006 JARPA final review meeting (e.g. those related to the duration of the feeding period, digestion rate and examination at smaller spatial scales). We compared the feeding habits of the Antarctic minke whales during the JARPA period (1987/88–2004/05) and the JARPAII period (2005/06–2010/11). The Antarctic minke whales fed mostly on Antarctic krill (*Euphausia superba*) in offshore areas, and on ice krill *E. crystallorophias* in coastal (shallow) areas on the continental shelf of the Ross Sea and Prydz Bay. The whales fed mainly before 5AM suggesting that feeding activity decreases early in the day. The 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 daily prey consumptions of Antarctic minke whales per capita during the feeding season based on these two methods were 95.1–127.0 and 182.6–250.3kg for immature and mature males, 125.8–138.7 and 268.1–325.5kg for immature and mature females, respectively. This is equivalent to 2.65–4.02% of their body weight. The daily prey consumption per capita decreased between the JARPA period and the JARPAII period based on the results of the method of the diurnal change in stomach contents' mass, for all sexual classes. The seasonal prey consumptions for all Antarctic minke whales in the total research area was 3.51–3.98million tons, and this amounted to 7.6–8.6% of the krill biomass estimated by acoustic survey in the total research area. These results related to prey consumption are useful as input data for the development of ecosystem models.

**KEYWORDS:** FEEDING; ENERGETICS; FOOD/PREY; MODELLING; SCIENTIFIC PERMITS; ANTARCTIC; ANTARCTIC MINKE WHALE

## INTRODUCTION

The Antarctic minke whale (*Balaenoptera bonaerensis*), which grows up to 10m (Horwood, 1990), is the most abundant balaenopterid species in the Southern Ocean with abundance estimated at 515,000 animals south of 60°S in austral summer (95% CI:360,000–730,000). These estimates were based on sighting data collected between the 1992/93 and 2003/04 seasons (IWC, 2013). Like other balaenopterid species (except the Bryde's whale *B. edeni*) the Antarctic minke whale spends its breeding season at lower latitudes 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 (*Euphausia superba*) in offshore waters (Kawamura, 1980; Bushuev, 1986; Ichii and Kato, 1991), and on ice krill (*E. crystallorophias*) on the coastal shelf along such areas as the Ross Sea and Prydz Bay (Bushuev, 1986; Tamura and Konishi, 2009).

Previous studies estimated the daily prey consumption by 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' conditions 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. Therefore, for the estimation of prey consumption, it is important to assess the energy storage during the feeding season of Antarctic minke whales.

In the 2006 JARPA review, the meeting recommended additional analyses to consider factors such as: i) determination of the duration of the feeding period; ii) examination at smaller spatial scales; iii) using multivariate analysis to examine trends, incorporating covariates such as age, size and reproductive status of whales as well as the date and time of day. Furthermore in 2007 the IWC/SC summarized the three issues that would need to be addressed i) the length of the feeding season; ii) to what extent consumption rate is sensitive to digestion rate; and iii) the extent of feeding at night (IWC, 2008). The recommendation on multivariate analysis was addressed by Konishi *et al.* (2008), Konishi and Butterworth (2013), Konishi and Walloe (2014a, b) and Skaug (2012). In the present study we addressed the issues of feeding period, examination at smaller spatial scales and the effect of digestion rate.

In this paper, we summarize the results of monitoring the feeding ecology of whales, which is part of the first objective of JARPAII. The feeding habits and daily prey consumption by Antarctic minke whales is examined based on a large data set obtained during the research surveys of the JARPA (1987/88–2004/05) and JARPAII (2005/06–2010/11). It is expected that the output of this study will assist in understanding the role of whales in the ecosystem and the development of ecosystem models for management purposes (see Kitakado *et al.*, 2014).

## MATERIALS AND METHODS

### Research area, periods and number of samples

Data used in the present study was collected during the surveys of the JARPA and JARPAII in the International Whaling Commission (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), south of 60°S (JARPA) and 62°S (JARPAII) (Fig. 1). The northern boundary of the Ross Sea was fixed at 70°S in Area V and VI. The surveys were conducted in the austral summer seasons (December-March) of the 1987/88-2004/05 (JARPA) and the 2005/06-2010/11 (JARPAII) seasons. During the surveys a total of 10,042 Antarctic minke whales were sampled. Table 1 shows the number of samples divided by Area and sex. After sampling, whales were brought to the research base vessel where the animals were examined by a biologist onboard. All whales were sampled during daylight hours, between 06:00 and 19:00h (Ship time).

### Sighting and sampling methods

The survey track line was designed along each 10 degree longitudinal width interval in principle. The survey starting point was randomly selected from the arrangement of the survey track line and longitude standard lines in the survey. Sighting procedures were the same as in the previous JARPA surveys (Nishiwaki *et al.* 2006, 2014). The survey was operated under optimal research conditions (when the wind speed was below 25knots in the south strata and below 20knots in the north strata, and when visibility was more than 2n.miles). SSVs advanced along parallel track lines 7n.miles apart from each other at a standard speed of 11.5knots.

### Treatment 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 0.1kg. 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 prey in the forestomach was 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 the uniformity of prey within the stomachs of almost all whales, after checking the stomach contents, some fresh prey (200g) 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 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 10cm from the tip of the upper jaw to the deepest part of the fluke notch in a straight line. Body weight was measured using large weighing machine to the nearest 50kg. For some individuals, muscle, blubber and internal organs were weighed for calculating the 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 Ohsumi and Masaki (1975) and Kato (1986). Males with a single testis weight of 400g or more were defined as sexually mature. Females with at least one corpus luteum or albicans in their ovaries were defined as sexually mature.

### Analytical procedure of the daily prey consumption

The amount of krill consumed by Antarctic minke whales was estimated using two independent methods, which were from theoretical energy requirement calculations (method-1) and from diurnal changes of stomach contents (Total of forestomach (1<sup>st</sup>. stomach) and fundus (2nd. stomach)) (method-2).

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

The daily prey consumption ( $D_{kg}$ ) in each sexual maturity class was estimated from the standard metabolic rate ( $SMR_{kJ}$ ) and energy deposit according to the following equations:

$$\text{Male or Immature female} : D_{kg} = (SMR_{kJ} + ED_{kJ}) / E_{kJ} \quad (1)$$

$$\text{Mature female} : D_{kg} = (SMR_{kJ} + ED_{kJ} + R_{kJ}) / E_{kJ} \quad (2)$$

Where  $D_{kg}$  is daily prey consumption (kg day<sup>-1</sup>),  $SMR_{kJ}$  is the standard metabolic rate (kJ day<sup>-1</sup>),  $ED_{kJ}$  is Energy deposition (kJ day<sup>-1</sup>),  $R$  is Reproduction cost (kJ kg<sup>-1</sup>) and  $E_{kJ}$  is the caloric value of prey species (kJ kg<sup>-1</sup>). The details of these items are described as follows:

1)  $SMR_{kJ}$  (Standard metabolic rate)

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

$$SMR_{kJ}=1.45 \times BMR \times 4.184 \text{ (kJ day}^{-1}\text{)} \quad (3)$$

The basal metabolic rate ( $BMR$ ) was calculated following the Kleiber's equation (Kleiber, 1961):

$$BMR=70M^{0.75} \text{ (kcal day}^{-1}\text{)} \quad (4)$$

where  $M$  is the Antarctic minke whale body weight (kg). The figure 1.45 is the coefficient for energy spent on activities such as foraging, moving between food patches and migration. The figure 4.184 is the coefficient value from Kcal to KJ. The average body lengths of Antarctic minke whales were 6.5 and 8.4m for immature and mature males and 6.7 and 8.9 m for immature and mature females, respectively.

2)  $ED_{kJ}$  (Energy deposited during feeding season in Antarctic)

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 was 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 (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.

3)  $R_{kJ}$  (Reproduction cost)

The  $R_{kJ}$  for a female Antarctic minke whale was calculated by Lockyer (1981a) to be  $1.89 \times 10^6$ kJ, assuming that the length at birth is 273cm (Best, 1982). We assumed that almost all mature females were pregnant, and that all reproduction costs were during feeding season (120 days). The  $R_{kJ}$  for a female Antarctic minke whale was calculated to be  $15.8 \times 10^4$ kJ per day.

4)  $E_{kJ}$  (Energy value of *Euphausia superba*)

Antarctic minke whales feed mainly on *E. superba*. The energy value is 4,473kJkg<sup>-1</sup>. 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 the same value of assimilation efficiency for calculating the daily prey consumption. Therefore, the energy value of prey items of whales was estimated to be 3,757kJ kg<sup>-1</sup>.

5) Feeding period (residence days in the feeding ground)

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 peaked in January, followed by a steady decrease through February (Kasamatsu *et al.*, 1996). Lockyer (1981a, b) estimated the residence days of immature animals and mature males to be 90 days in the feeding ground, while mature females spent 120 days in the feeding ground. Antarctic minke whales were tagged for the first time in 2013 during the survey of the Southern Ocean Research Partnership (SORP). Their movement patterns are in the process of being analysed and include a variety of movement patterns. While some animals remained in close proximity to near-shore bays for over 120 days, other whales moved from the Antarctic Peninsula into both the Weddell Sea to the north and east and the Bellingshausen Sea to the south and west (Bell, 2013). Based on the results of these studies, we also assumed that they moved southward in November and northward in March. We also assumed that immature animals and mature males spend 90days, and mature females spend 120days, respectively, the same as Lockyer's (1981a, b) assumptions. The total prey consumption during the feeding period ( $SD_{kg}$ ) was applied as follows:

$$\text{Immature animals and mature males: } SD_{kg} = 90 D_{kg} \quad (5)$$

$$\text{Mature females: } SD_{kg} = 120 D_{kg} \quad (6)$$

*Method-2 Estimation of daily consumption of krill from diurnal change in stomach contents mass*

Miura (1969) proposed a method for estimating daily prey consumption from diurnal changes in stomach contents mass ( $V_i$ ) 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 ( $C_i$ ) is given by the following equations:

$$t_1: C_1=V_1 \quad (7-1)$$

$$t_2: C_2=V_2-SV_1 \quad (7-2)$$

$$t_3: C_3=V_3-SV_2-S^2V_1 \quad (7-3)$$

$$t_i: C_i = V_i - S V_{i-1} - S^2 V_{i-2} - \dots - S^{i-1} V_1 \quad (7-4)$$

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

$$\sum_{i=1}^k C_i = V_1 \frac{(1-2S+S^k)}{1-S} + V_2 \frac{(1-2S+S^{k-1})}{1-S} + \dots + V_{k-1}(1-S) + \dots + V_k \quad (7-5)$$

In this study, we calculated the mean stomach contents (forestomach and fundus stomach) mass as % of body mass ( $V_i$ ) at 1 hour intervals based on the stomach contents mass (kg) and body mass (kg). Nordøy *et al.* (1995) showed that krill were digested by bacterial fermentation, and that this digestion process was very rapid. Assuming that it takes 4 hours for prey to be digested in the stomach of Antarctic minke whales (Bushuev, 1986) and that  $d$  is exponential (Elliott and Persson, 1978), we estimated  $S$  to be 0.82, if the proportion of undigested prey in the stomach after 4 hours is 45% (Appendix 1). We estimated the daily prey consumption of krill from diurnal change in stomach contents' mass in research areas excluding the Ross Sea of JARPA and JARPAII periods. We eliminated the data with less than 10 samples in each hourly interval.

### Estimation of seasonal prey consumption in Areas III east, IV, V and VI west

The seasonal prey consumption for all Antarctic minke whales in the research area was estimated using information on abundance and residence days in the feeding ground. The information on abundance of Antarctic minke whales was described in Hakamada and Matsuoka (2014). The abundance of Antarctic minke whales without taking model error into account was applied in this study. The seasonal prey consumption of Antarctic minke whales in each area was applied using the results of Method-1 and Method-2 in the JARPAII period.

We estimated the seasonal prey consumption for all Antarctic minke whales in the research area from 2007/2008 to 2008/09 seasons. Furthermore, we also compared seasonal prey consumption of Antarctic minke whales with krill biomass in each sub area of the Antarctic from 2007/2008 to 2008/09 seasons. The krill biomass in Areas III east, IV, V and VI west was estimated by acoustic survey (Wada and Tamura, 2014).

## 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 (*Plerogramma antarcticum*, *Notolepis coatsi*, *Electona antarctica*, *Chinodraco* sp. and *Notothenis* sp.), were identified from the stomachs of the Antarctic minke whales (Table 2). The Antarctic krill was the dominant prey species, 66–100% of the weight composition of the whale stomachs examined in each area (Table 3, Figs. 2a, b), followed by ice krill, two euphausiids (*E. frigida*, *T. macrura*), one amphipod (*P. gaudichaudi*) and one fish species (*P. antarcticum*). The frequency of occurrence of ice krill in the Ross Sea decreased between the JARPA period and JARPAII period (Table 3).

### 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 proportion of fresh and lightly digested categories and the RSC gradually decreased from early morning to afternoon. After 19:00 h, the fresh categories and the weight of the mean stomach contents showed a slight increase in the survey area north of 70°S. In the Ross Sea, there was no trend for the proportion of fresh and lightly digested categories and the RSC.

### Stomach contents weight and RSC

The average and maximum weight and the ratio of stomach contents weight to body weight, expressed as a percentage (RSC) of fresh or lightly digested stomach contents (freshness category F and fff) by different reproductive classes are shown in Table 4. During the JARPA seasons, the average weight and RSC were 36.6±28.5kg (RSC:1.0%) and 43.6±31.8kg (RSC:1.1%) for immature males and females, respectively and 75.5±50.3kg (RSC:1.1%) and 77.1±55.0kg (RSC:1.0%) for mature males and females, respectively. The maximum weight and RSC were 130.8kg (RSC:3.1%) and 156.0kg (RSC:3.4%) for immature males and females, respectively and 343.8kg (RSC:4.2%) and 326.9kg (RSC:3.6%) for mature males and females, respectively. While, during the JARPAII seasons, the average weight and RSC were 33.2±28.3kg (RSC:0.8%) and 37.6±29.1kg (RSC:0.9%) for immature males and females, respectively and 63.5±47.1kg (RSC:0.9%) and 71.8±54.3kg (RSC:0.9%) for mature males and females, respectively. The maximum weight and RSC were 142.4kg (RSC:2.4%) and 136.9kg (RSC:3.0%) for immature males and females, respectively and 387.0kg (RSC:3.8%) and 301.6kg (RSC:4.0%) for mature males and females, respectively. The average weight and RSC decreased between the JARPA period and the JARPAII period for all sexual classes.

## Per capita daily and seasonal prey consumption by sex and maturity

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

#### Body weight of whales

We calculated the average body length and weight during the JARPA and the JARPAII. The average body lengths were  $6.5 \pm 0.9$  (Average  $\pm$  S.D) and  $8.4 \pm 0.4$  m for immature and mature males, and  $6.7 \pm 1.0$  and  $8.9 \pm 0.4$  m for immature and mature females, respectively. The mean body weight was  $3,500 \pm 1,400$  and  $6,900 \pm 1,000$  kg for immature and mature males, and  $3,800 \pm 1,600$  and  $8,100 \pm 1,200$  kg for immature and mature females, respectively.  $SMR_{kJ}$  of immature and mature males were  $193 \times 10^3$  and  $322 \times 10^3$  kJ, respectively.  $SMR_{kJ}$  of immature and mature females were  $206 \times 10^3$  and  $363 \times 10^3$  kJ, respectively (Table 5).

#### Energy deposited during feeding season

Fig. 5 shows the relationship between blubber weight (t) and body length (m), classified by sex and maturity class. Immature and mature males had an increase in blubber energy contents per day of 79,866 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 5). 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 29,353 kJ and 50,245 kJ, respectively.

Immature and mature females had an increase in muscle energy contents per day of 20,088 kJ and 31,175 kJ, respectively (Table 5). The weight of the fat deposition of other parts (*e.g.* internal organs) was estimated to deduct the weight of blubber deposition and the weight of muscle deposition from the total body weight (Figs. 5, 6 and 7). Immature and mature males had an increase in the fat energy contents of other parts per day of 54,693 kJ and 151,704 kJ, respectively. Immature and mature females had an increase in muscle energy contents per day of 150,950 kJ and 368,105 kJ, respectively (Table 5).

There was an increase in the energy density of blubber of males from 14,435 to 20,711 kJ kg<sup>-1</sup> (wet weight) and of females from 16,443 to 28,075 kJ kg<sup>-1</sup> (wet weight) between December and March. There was also an increase in the energy density of muscle in males from 5,858 to 6,234 kJ kg<sup>-1</sup> (wet weight) and in females from 5,941 to 6,192 kJ kg<sup>-1</sup> (wet weight) between December and March (Table 6). These results were obtained on the basis of the JARPA and JARPAII data sets combined (amount of data of the JARPAII alone was small for this analyses).

#### Daily and seasonal prey consumption

The calculated daily energy requirements during feeding season were  $425 \times 10^3$  and  $817 \times 10^3$  kJ for immature and mature males, and  $620 \times 10^3$  and  $1,456 \times 10^3$  kJ for immature and mature females, respectively (Table 7).

When the mean prey energy value of 4,473 kJ kg<sup>-1</sup> and the assimilation efficiency of 84 % were considered, the daily prey consumption during the feeding season was 95.1 and 182.6 kg for immature and mature males, and 138.7 and 325.5 kg for immature and mature females, respectively. These values were equivalent to 2.70 and 2.65% of body weight for immature and mature males, and 3.65 and 4.02% of body weight for immature and mature females, respectively (Table 7). The total prey consumption of Antarctic minke whale per capita during the feeding season was 8.6 and 21.9 tons for immature and mature males, and 12.5 and 39.1 tons for immature and mature females, respectively (Table 7).

### *Method-2 Estimation of daily consumption of krill from diurnal change in stomach contents mass*

During the JARPA period, estimated rates of daily prey consumption were 3.63% of the body mass of Antarctic minke whales. The daily prey consumption during the feeding season was 127.0 and 250.3 kg for immature and mature males, and 137.9 and 293.9 kg for immature and mature females, respectively. The total prey consumption of Antarctic minke whale per capita during the feeding season was 11.4 and 22.5 tons for immature and mature males, and 12.4 and 35.3 tons for immature and mature females, respectively (Table 8).

During the JARPAII period, estimated rates of daily prey consumption were 3.31% of the body mass of Antarctic minke whales. The daily prey consumption during the feeding season was 115.9 and 228.4 kg for immature and mature males, and 135.8 and 268.1 kg for immature and mature females, respectively. The total prey consumption of Antarctic minke whale per capita during the feeding season was 10.4 and 20.6 tons for immature and mature males, and 11.3 and 32.2 tons for immature and mature females, respectively (Table 8).

## Seasonal prey consumption for all Antarctic minke whales in the research area

In Areas III east and IV in the 2007/2008 season, the abundance was estimated to be 9,406 and 14,739, respectively. In Area V and VI west in the 2008/2009 season, the abundance was estimated to be 108,097 and 26,364, respectively (Table 9). In Area III east and IV in the 2007/2008 season, the krill biomass was estimated to be 6.6 million tons and 12.5 million tons, respectively. In Area V and VI west in the 2008/2009 season, the biomass was estimated to be 24.0 million tons and 3.4 million tons, respectively (Table 9).

In Areas III east and IV in the 2007/2008 season, seasonal prey consumption of krill for all Antarctic minke whales in the research area was estimated to be 0.17-0.19 and 0.33-0.37 million tons, respectively. On the other hand, in Areas V and VI west in the 2008/2009 season, seasonal prey consumption of krill by Antarctic minke whales was estimated to be between 2.51-2.88 and 0.50-0.54 million tons, respectively (Table 9).

The seasonal prey consumption for all Antarctic minke whales in the total research area was 3.51-3.98 million tons, amounting to 7.6-8.6% of the krill biomass estimated by acoustic survey in the total research area (Table 9).

## DISCUSSION

### Diversity of prey species

The main prey species of Antarctic minke whales during austral summer were two krill species (Antarctic krill and ice krill). Consumption of these species depended on the distributional difference of the krill species. The Antarctic minke whales fed mostly on Antarctic krill in the offshore area, and ice krill in the coastal (shallow) area on the continental shelf along such areas as the Ross Sea and Prydz Bay. Ice krill is a 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). It is strongly suggested that Antarctic minke whales feed on local predominant prey species. The frequency of occurrence of ice krill in the stomachs of Antarctic minke whales sampled in the Ross Sea changed between the JARPA period and the JARPAII period. Regional differences of the prey species of minke whales might reflect changes in the distribution of these prey species in the research area.

### The diurnal feeding rhythm

Our results suggest 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 do not feed at night (Folkow and Blix, 1993; Haug *et al.*, 1997; Tamura, 1998). Our results showed that Antarctic minke whales fed on prey easily and may reduce their feeding earlier in the day due to sufficient food intake. If they feed on prey fully at one feeding time, they can satisfy their daily energy-requirement.

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 the future.

### Daily prey consumption of Antarctic minke whales

Following a recommendation from the IWC SC the estimations of prey consumption in this study was carried out at smaller spatial scales e.g. by management Areas in contrast with the previous study where the estimations were made for the whole research area.

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 estimates may be overestimates because those values would require a maximum of two feeding times per day for the daily energy requirement. However, the results of this study indicated a range of maximum weight for the stomach contents from 2.6 to 4.0% 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 (RSC) ranged from 2.7 to 4.0% of their body weight. These values were similar to the estimates by Lockyer (1981b), Bushuev (1986) and Mori and Butterworth (2004).

Using the modelling approach, Mori and Butterworth (2004) indicate that the daily prey consumption rate of Antarctic minke whales ranged from 3.0 to 5.0% of their body weight. The estimates from our energy requirement calculations almost corresponded with the results of maximum weight of the stomach contents in the field data. Therefore, these results can be used with confidence as the estimation of daily prey consumption by Antarctic minke whales. In the 2006 JARPA review, we estimated daily prey consumption ranged from 2.67 to 4.95% of the body weight, while we estimated daily prey consumption ranged from 2.65 to 4.02% of the body weight in this study. We obtained the actual data in this study by applying the actual digestion rate (see Appendix 1) for method 2 in the daily prey consumption estimation. Tamura and Konishi (2006) assumed the digestion rate based on previous published reports. They assumed that the proportion of undigested prey in the stomach after 4 hours was between 20% and 30%. The previous IWC SC recommendation on digestion rate was addressed in this study (see Appendix 1). The proportion of undigested krill in the stomach after 4 hours was 45%. This value was similar to those in Sekiguchi (1994). We applied this digestion rate for method 2 in this study.

The average weight of stomach contents and RSC decreased between the JARPA period and the JARPAII period for all sexual classes. Furthermore, the daily prey consumption based on method 2 decreased from 3.63% to 3.31% between the JARPA period and the JARPAII period. Regression analyses clearly showed that blubber thickness, girth, fat weight and stomach contents weight have been decreasing for nearly 2 decades (Konishi and Walloe, 2014a, b). Our results

indicate an increasing shortage of food for the Antarctic minke whales per capita during the JARPA and the JARPAII period.

As the next step an assessment of geographical, seasonal and yearly changes 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.

### **Uncertainties in the prey consumption estimates**

Some uncertainties in the prey consumption estimates were discussed in some IWC/SC meetings (e.g. Tamura *et al.*, 2009) and by Leaper and Lavigne (2007). The important parameters used for estimating prey consumption in this study are the energy contents of prey, muscle and blubber of whales themselves. However, in this study, these values were calculated on the basis of very few samples. To account for differences within the season a sufficient number of samples should be examined in the future.

Regarding the duration of the feeding period, we assumed 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. This issue had some progress recently. Antarctic minke whales were tagged for the first time in 2013 by the Southern Ocean Research Partnership (SORP) surveys. Their movement patterns are in the process of being analyzed but include a variety of movement patterns. While some animals remained in close proximity to near-shore bays for over 120 days, other whales moved from the Antarctic Peninsula into both the Weddell Sea to the north and east and the Bellingshausen Sea to the south and west (Bell, 2013). It might be possible in the future to provide more information on residence time using satellite tagging.

### **Prey consumption as an input parameter for ecosystem modelling**

At present there is little information about the consumption by other krill predators such as seabirds and pinnipeds in our study region for comparison with our results. Furthermore, krill biomass above 150m depth was used in this study (Wada and Tamura, 2014). It is a limitation for the echo sounder system. The value of krill biomass seems to be an underestimate. If Antarctic minke whales can feed on prey deeper than 150m of depth, these values for the rates are overestimates. The foraging diving depth of Antarctic minke whales has not been reported so we need information on the foraging diving depth of Antarctic minke whales in the future.

Many parameters for application in the multi-species ecosystem modeling should be improved in the future (Kitakado *et al.*, 2014). Improving estimates of the daily and seasonal consumption by Antarctic minke whales is also important. Our results are useful to apply as the input data for the daily consumption by Antarctic minke whales for ecosystem-based management.

As the next step, the assessment of geographical, monthly and yearly changes of the energy requirements of minke whales is needed. This is needed for the comparison of krill resources and other krill predators' distribution and consumption.

## **ACKNOWLEDGMENTS**

The stomach contents examined in this study were collected by many researchers and crews. We would like to thank the captains, crews and researchers who were involved in the JARPA and JARPAII research cruises for their efforts. We appreciate very much the helpful analysis of the digestion experiment on krill by Chihiro Kobayashi. This work was a part of her master's thesis. Our sincere thanks also go out to Hiroshi Hatanaka and Luis A. Pastene of the Institute of Cetacean Research (ICR) for their valuable suggestions and useful comments on this paper.

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Table 1

Sample size of Antarctic minke whales 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	638	517	1,856	1,645	1,863	2,110	595	310	4,952	4,582

Table 2

Prey species found in the stomachs of Antarctic minke whales sampled in this study.

Species	
<b>Major prey</b>	
Amphipods	<i>Parathemisto gaudichaudi</i>
Krill	<i>Euphausia superba</i>
	<i>E. crystallophias</i>
	<i>E. frigida</i>
	<i>Thysanoessa macrura</i>
Fish	<i>Pleuragramma antarcticum</i>
<b>Minor prey</b>	
Fish	<i>Notolepis coatsi</i>
	<i>Electona antarctica</i>
	<i>Chionodraco</i> sp.
	<i>Notothenis</i> sp.

Table 3

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

Species		Area III-E	Area IV	Area V < 70S	Area VI-W < 70S	Area V and VI-W ≥ 70S (Ross Sea)
<b>JARPA (1987/88-2004/05)</b>		N=314	N=926	N=633	N=232	N=324
Krill	<i>Euphausia superba</i>	99.4	94.5	95.0	93.5	66.9
	<i>E. crystallophias</i>	0.2	2.6	0.9	0.0	29.5
	<i>E. frigida</i>	0.5	0.0	0.2	0.0	0.0
	<i>Thysanoessa macrura</i>	0.0	2.7	3.8	6.5	2.3
Amphipods	<i>Parathemisto gaudichaudi</i>	0.0	0.2	0.2	0.0	0.0
Fish	<i>Pleuragramma antarcticum</i>	0.0	0.0	0.0	0.0	1.3
<b>JARPA II (2005/06-2010/11)</b>		N=45	N=72	N=85	N=44	N=86
Krill	<i>Euphausia superba</i>	100.0	89.0	92.6	93.2	96.7
	<i>E. crystallophias</i>	0.0	6.9	3.8	0.0	3.1
	<i>E. frigida</i>	0.0	0.0	0.0	0.0	0.0
	<i>Thysanoessa macrura</i>	0.0	4.0	3.7	6.8	0.1
Amphipods	<i>Parathemisto gaudichaudi</i>	0.0	0.0	0.0	0.0	0.0
Fish	<i>Pleuragramma antarcticum</i>	0.0	0.0	0.0	0.0	0.0

Table 4

The average and maximum weight of fresh or lightly digested stomach contents (freshness category F and fff) and RSC (the ratio of stomach contents weight to body weight, expressed as a percentage) of Antarctic minke whales sampled by the JARPA and JARPAII surveys.

Sex	Maturity	Number	Weight (Categories F and fff)		
			Average (kg)	S.D.	Maximum (kg)
<b>JARPA (1987/88-2004/05)</b>					
Male	Immature	250	36.6	28.5	130.8
			(RSC: 0.98%)		(RSC: 3.14%)
Male	Mature	1,161	75.5	50.3	343.8
			(RSC: 1.07%)		(RSC: 4.21%)
Female	Immature	325	43.6	31.8	156.0
			(RSC: 1.08%)		(RSC: 3.40%)
Female	Mature	780	77.1	55.0	326.9
			(RSC: 0.95%)		(RSC: 3.60%)
<b>JARPA II (2005/06-2010/11)</b>					
Male	Immature	131	33.2	28.3	142.4
			(RSC: 0.82%)		(RSC: 2.39%)
Male	Mature	566	63.5	47.1	387.0
			(RSC: 0.92%)		(RSC: 3.76%)
Female	Immature	182	37.6	29.1	136.9
			(RSC: 0.86%)		(RSC: 3.04%)
Female	Mature	513	71.8	54.3	301.6
			(RSC: 0.90%)		(RSC: 4.02%)

Table 5

Required energy contents (KJ d<sup>-1</sup>) of Antarctic minke whales

Sex	Maturity	Body length (m)	Body weight (kg)	SMR (KJ/day)	Blubber deposition (KJ/day)	Muscle deposition (KJ/day)	Fat deposition (KJ/day)	Reproduction cost (KJ/day)
Male	Immature	6.5	3,500	193,245	79,866	29,353	54,693	
	Mature	8.4	6,900	321,510	162,664	50,245	151,704	
Female	Immature	6.7	3,800	205,540	144,620	20,088	150,950	
	Mature	8.9	8,100	362,595	303,619	31,175	368,105	157,500

Table 6

Energy value of blubber and muscle (KJ kg<sup>-1</sup>) of Antarctic minke whales

Sex	Blubber (KJ/kg)		Muscle (KJ/kg)	
	December	March	December	March
Male	14,435	20,711	5,858	6,234
Female	16,443	28,075	5,941	6,192

Table 7

The daily and seasonal prey consumption for all Antarctic minke whales in the research area using Method-1

Sex	Maturity	Body length (m)	Body weight (kg)	Daily prey consumption			Seasonal consumption (tons)
				(KJ/day)	(kg/day)	(% of B.W.)	
Male	Immature	6.5	3,500	425,188	95.1	2.72	8.6
	Mature	8.4	6,900	816,813	182.6	2.65	16.4
Female	Immature	6.7	3,800	620,473	138.7	3.65	12.5
	Mature	8.9	8,100	1,455,945	325.5	4.02	39.1

Table 8

The daily and seasonal prey consumption for all Antarctic minke whales in the research area using Method-2

Sex	Maturity	Body weight (kg)	JARPA period		Seasonal consumption (tons)	JARPA II period		Seasonal consumption (tons)
			(kg)	(%)		(kg)	(%)	
Male	Immature	3,500	127.0	3.63	11.4	115.9	3.31	10.4
	Mature	6,900	250.3	3.63	22.5	228.4	3.31	20.6
Female	Immature	3,800	137.9	3.63	12.4	125.8	3.31	11.3
	Mature	8,100	293.9	3.63	35.3	268.1	3.31	32.2

Table 9

Seasonal prey consumption and comparison with krill biomass in Areas IV and V (Hakamada and Matsuoka, 2014; Wada and Tamura, 2014).

#### Method-1

Stratum	Year	Abundance (inds.)	Prey consumption (A: million tons)	Krill biomass (B: million tons)	Ratio A/B (%)
III East	2007/08	9,406	0.19	6.6	2.8
IV	2007/08	14,739	0.37	12.5	3.0
V	2008/09	108,097	2.88	24.0	12.0
VI West	2008/09	26,364	0.54	3.4	15.8
Total		158,606	3.98	46.5	8.6

#### Method-2

##### JARPA II period

Stratum	Year	Abundance (inds.)	Prey consumption (A: million tons)	Krill biomass (B: million tons)	Ratio A/B (%)
III East	2007/08	9,406	0.17	6.6	2.6
IV	2007/08	14,739	0.33	12.5	2.6
V	2008/09	108,097	2.51	24.0	10.5
VI West	2008/09	26,364	0.50	3.4	14.6
Total		158,606	3.51	46.5	7.6

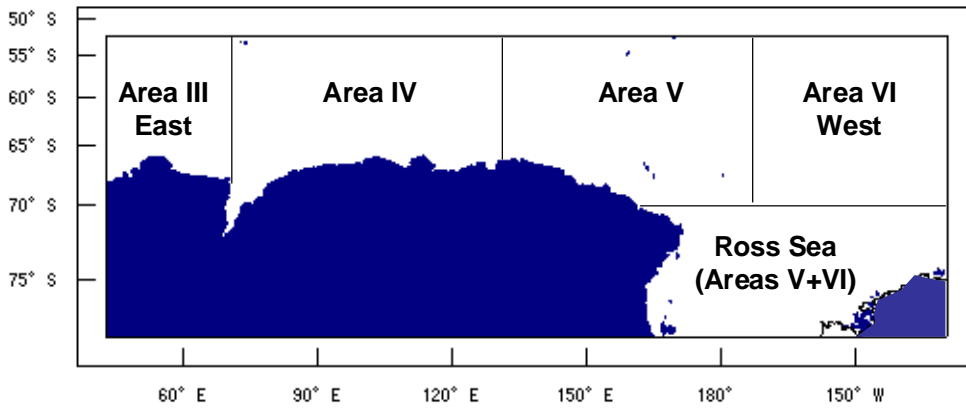


Fig.1. Research area in the Antarctic

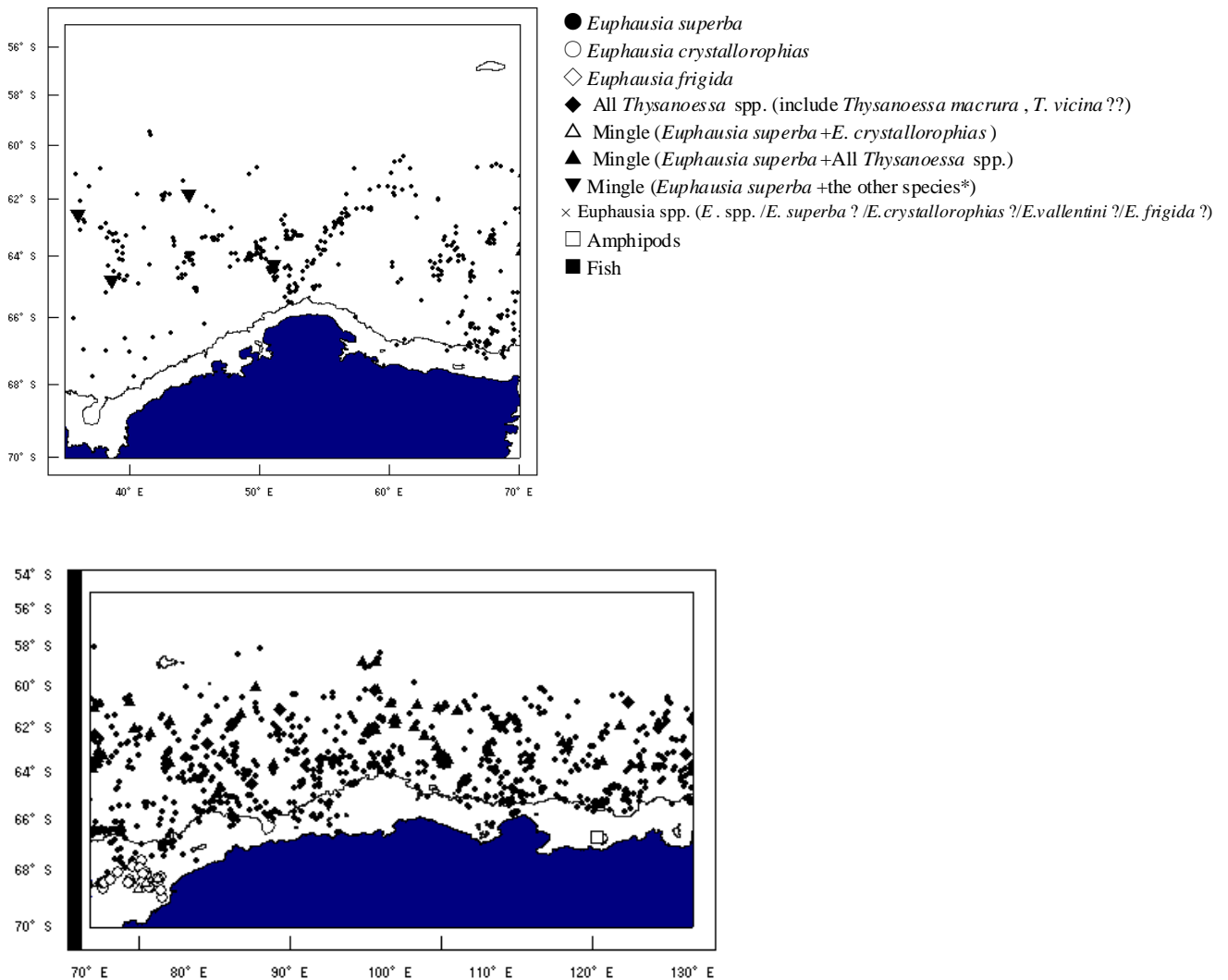
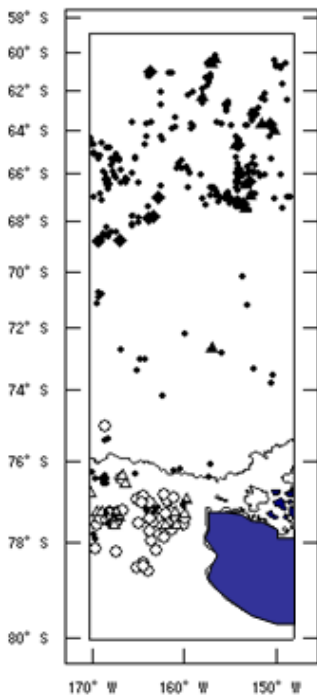
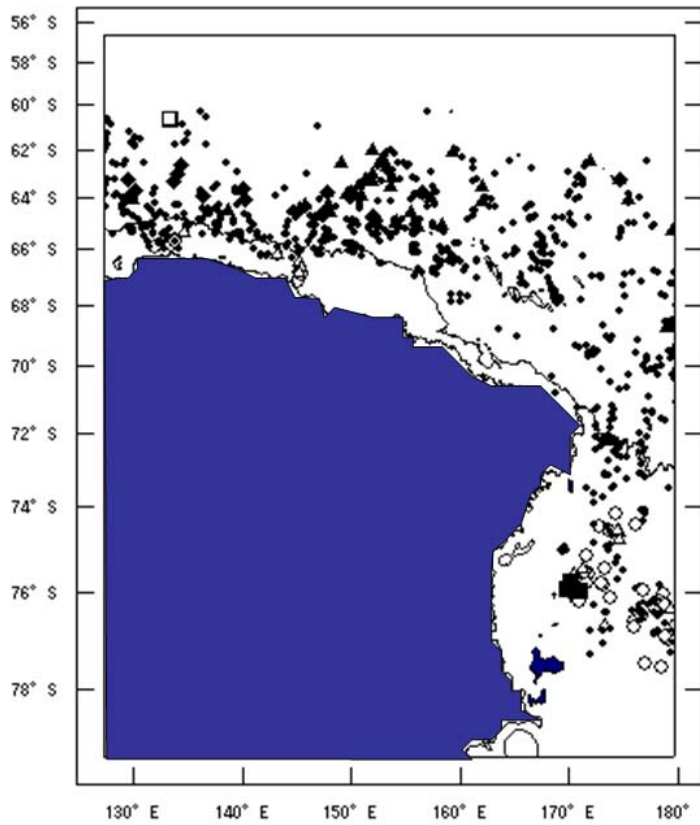


Fig.2(A). Sampling position of Antarctic minke whales and their dominant prey species in Areas III-East and IV. Line shows water depth contour of 1,000m.



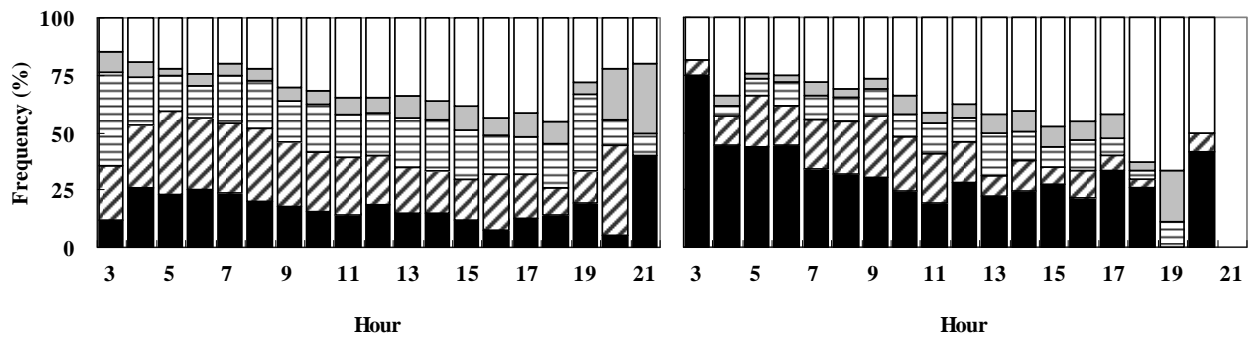
- *Euphausia superba*
- *Euphausia crystallorophias*
- ◇ *Euphausia frigida*
- ◆ All *Thysanoessa* spp. (include *Thysanoessa macrura*, *T. vicina*??)
- △ Mingle (*Euphausia superba* + *E. crystallorophias*)
- ▲ Mingle (*Euphausia superba* + All *Thysanoessa* spp.)
- ▼ Mingle (*Euphausia superba* + the other species\*)
- × *Euphausia* spp. (*E.* spp. / *E. superba* ? / *E. crystallorophias* ? / *E. vallentini* ? / *E. frigida* ?)
- Amphipods
- Fish

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 1,000m.

**North of 70°S**

JARPA periods (1987/88-2004/05) N=4,901

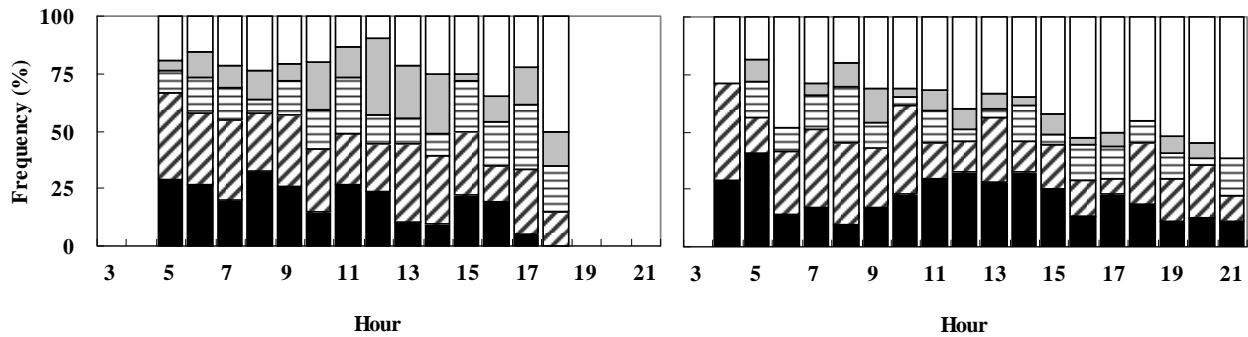
JARPAII periods (2005/06-2010/11) N=2,380



**Ross Sea area (South of 70°S)**

JARPA periods (1987/88-2004/05) N=647

JARPAII periods (2005/06-2010/11) N=612



(F ■ : fresh, fff ▨ : lightly digested, ff ▩ : moderately digested, f ▪ : heavily digested, 0 □ : empty)

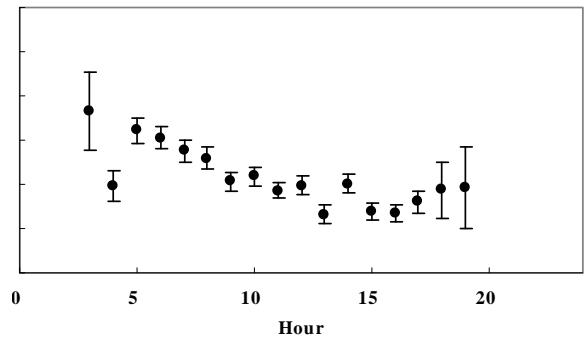
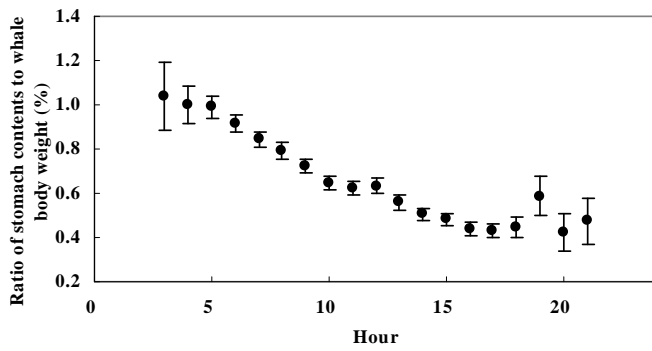
Fig 3. Composition of prey freshness categories throughout the day in Antarctic minke whales in North of 70°S and in the Ross Sea area (South of 70°S) in the JARPA and JARPAII period.



### North of 70°S

JARPA periods (1987/88-2004/05) N=4,693

JARPAII periods (2005/06-2010/11) N=1,071



### Ross Sea area (South of 70°S)

JARPA periods (1987/88-2004/05) N=628

JARPAII periods (2005/06-2010/11) N=363

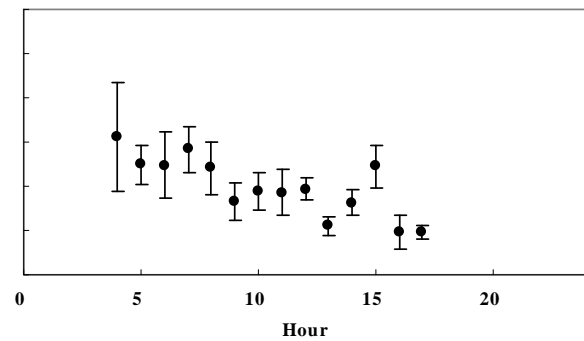
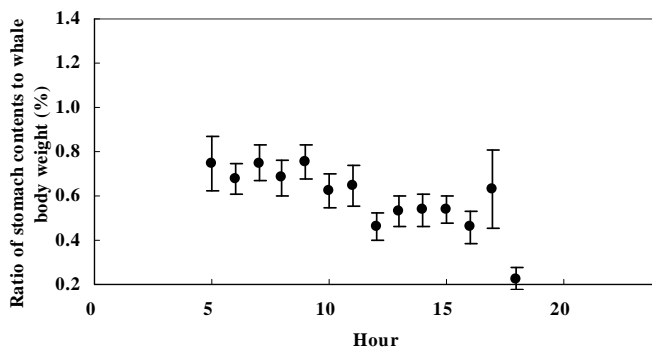
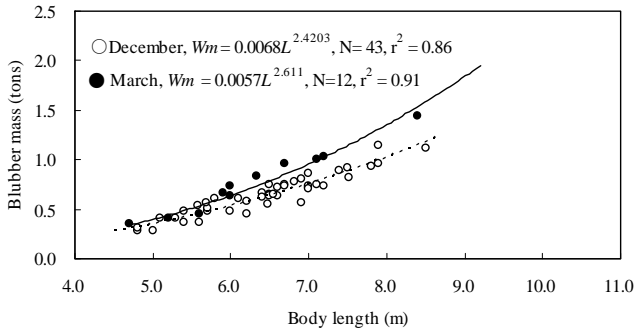
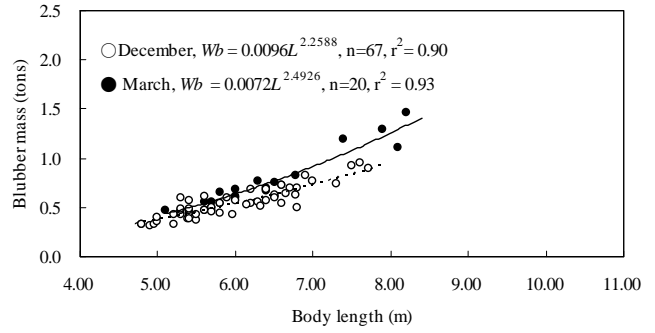


Fig.4. Change in the ratio of stomach contents to whale body weight (RSC) throughout the day in North of 70°S and in the Ross Sea area (South of 70°S) in the JARPA and JARPAII period. Error bars are  $\pm 1$  S.E.

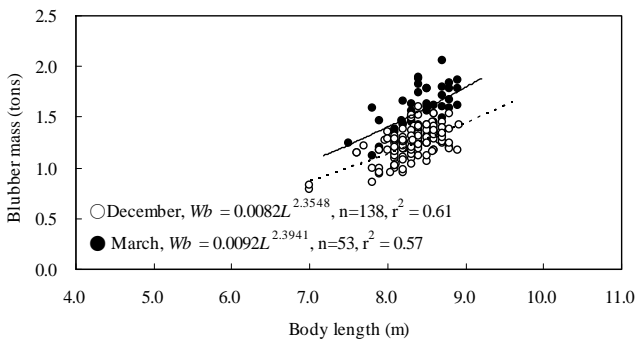
Immature male



Immature female



Mature male



Mature female

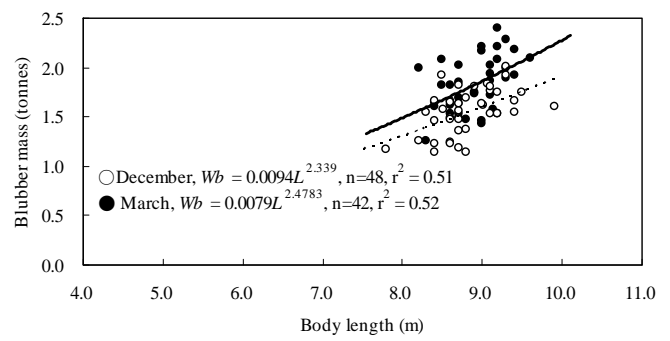
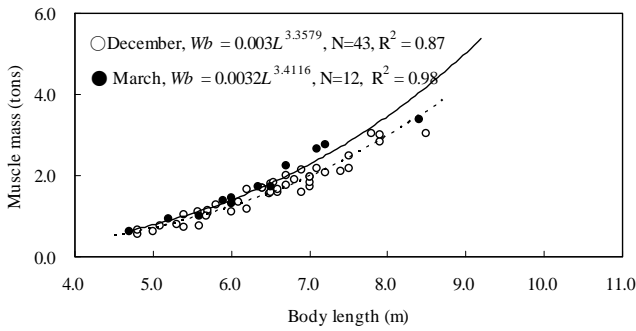
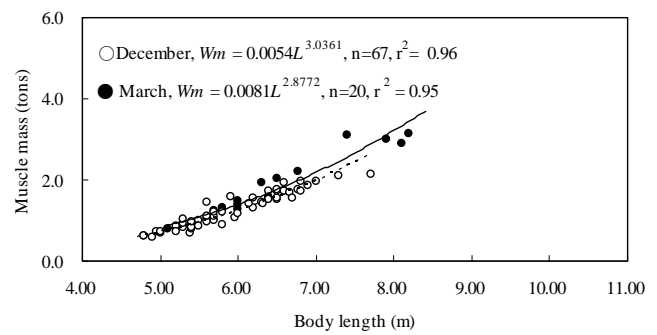


Fig. 5. The blubber weight ( $W_b$ , t) as a function of body length ( $L$ , m) for Antarctic minke whales sampled in December and March.

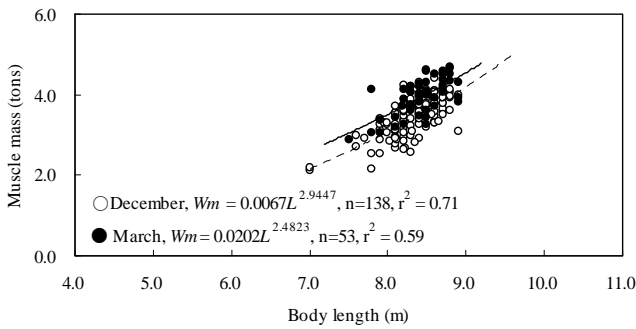
Immature male



Immature female



Mature male



Mature female

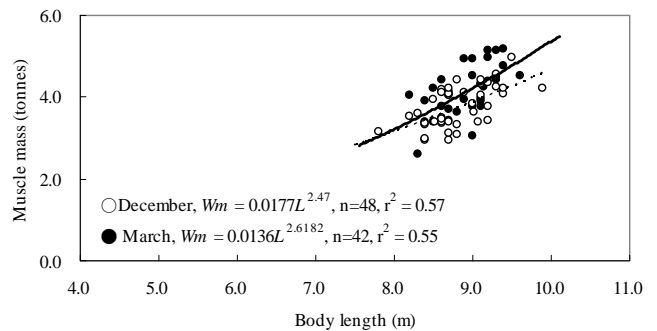
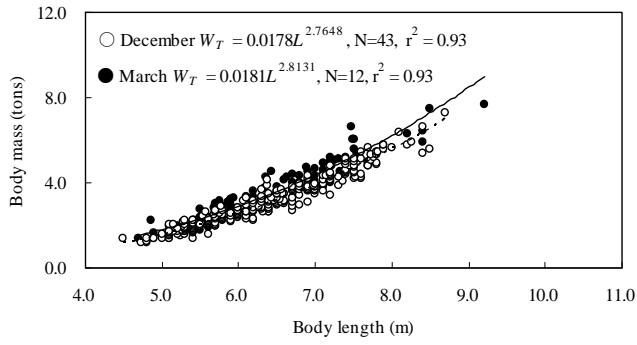
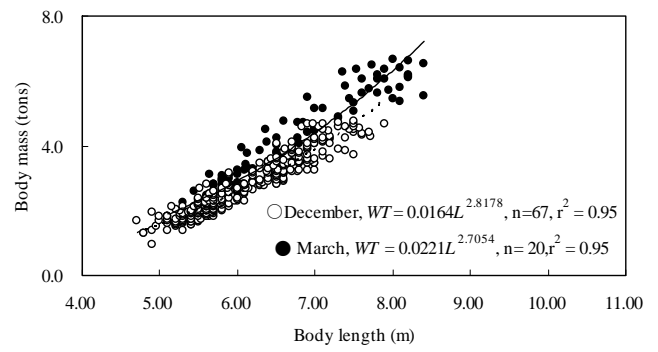


Fig. 6. The muscle weight ( $W_m$ , t) as a function of body length ( $L$ , m) for Antarctic minke whales sampled in December and March.

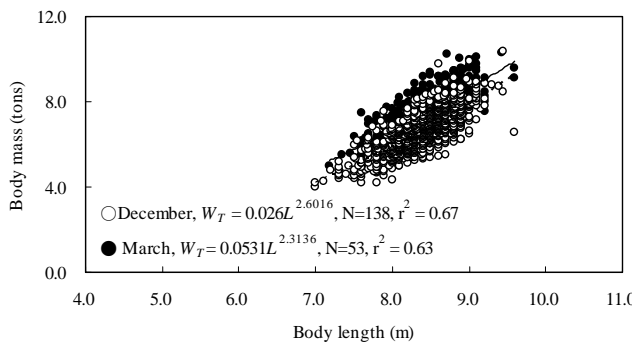
Immature male



Immature female



Mature male



Mature female

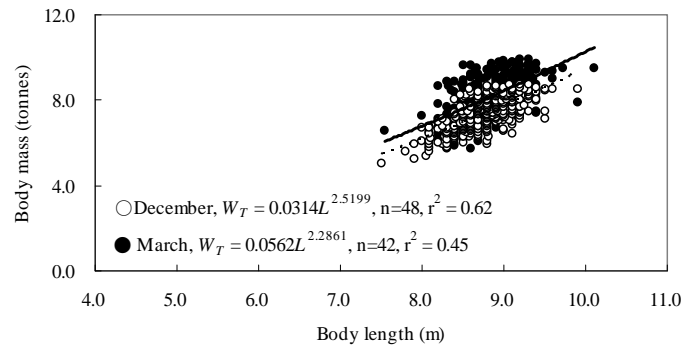


Fig. 7. Total body weight ( $W_T$ , t) as a function of body length ( $L$ , m) for Antarctic minke whales sampled in December and March.

### Appendix 1. The digestion experiment of krill using an artificial solution

This experiment addressed the recommendation on digestion rate by the IWC SC in 2007. The purpose of this experiment was to estimate the appropriate digestion rate of Antarctic minke whales.

For this experiment, the set-up and procedure followed that of Jackson *et al* (1987). The digestive solution was made up of 10% HCL, 10% Na<sub>2</sub>CO<sub>3</sub> and the digestive enzyme from fundus of Antarctic minke whales same as 1.0% pepsin. The temperature of the solution in the container was maintained at 37 °C. The digestive solution was adjusted to ph 2.3 (Sekiguchi, 1994). The pH value was maintained by the occasional addition of 10% HCL.

The digestive solution (500ml) filled the beakers. The beakers were set in the water bath which were agitated (in a rocking motion) 30-40times per minute and maintained the solution at 37 °C. Krill (50g) was put in a small bag of glass fiber with a mesh size of 0.5 x 0.5mm and placed in the solution.

Every hour, the bag was lifted from the solution. All excess solution wiped off by paper towel, and then weighed to the nearest 0.1g. The physical appearance of the sample was recorded at the same time.

The result is shown in figure 1. The proportion of undigested krill in the stomach after 4 hours is 45 %. This value was similar to those in Sekiguchi (1994). We applied this value for estimating daily prey consumption of Antarctic minke whales based on method 2 in this study.

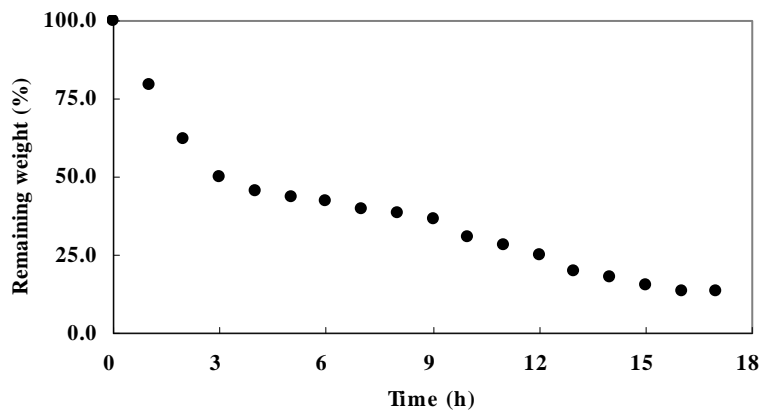


Fig. 1 The rate of digestion of *Euphausia superba* in an artificial solution, expressed as a percentage of their original weight remaining at hourly intervals.