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ORIGINAL PAPER

Decline in energy storage in the Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean

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Abstract The annual trend in energy storage in the Antarctic minke whale was examined using catch data from all 18 survey years in the Japanese Whale Research Program (JARPA). Regression analyses clearly showed that blubber thickness, girth and fat weight have been decreasing for nearly 2 decades. The decrease per year is estimated at approximately 0.02 cm for mid-lateral blubber thickness and 17 kg for fat weight, corresponding to 9% for both measurements over the 18-year period. Furthermore, "date", "extent of diatom adhesion", "sex", "body length", "fetus length", "latitude", "age" and "longitude" were all identified as partially independent predictors of blubber thickness. The direct interpretation of this substantial decline in energy storage in terms of food availability is difficult, since no long-term krill abundance series is available. However, an increase in the abundance of krill feeders other than minke whales and a resulting decrease in the krill population must be considered as a likely explanation.

Keywords Antarctica · Minke whale · *Balaenoptera bonaerensis* · Long-term change · *Euphausia superba* · Prey availability

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Introduction

The Southern Ocean supports a food web with high productivity, and is an important feeding ground for many consumers (see Laws 1985; Hill et al. 2006). The Antarctic krill (*Euphausia superba*) is the most abundant and main prey for large baleen whales, seals and seabirds. The Antarctic minke whale (*Balaenoptera bonaerensis*), which is a small baleen whale, also depends largely on *E. superba* (Ohsumi 1979; Armstrong and Siegfried 1991; Ichii and Kato 1991).

Krill availability in the Antarctic Ocean is generally considered to be the most important limiting factor for population sizes of many krill feeders (Reid and Croxall 2001; Mori and Butterworth 2006). Krill biomass is very large and many animals depend on this species, so that a sudden decrease in certain krill consumers could cause drastic changes in the population sizes of other consumers in Antarctic ecosystem. It has been hypothesized that after more than 50 years of commercial whaling, which started at the beginning of the twentieth century and resulted in the overexploitation of the large baleen whales, the relative abundances of all whale species were totally changed from the situation in the pre-whaling period (Laws 1977; Brown and Lockyer 1984). In parallel with the decline in abundance of the large baleen whales, such as blue (*B. musculus*), fin (*B. physalus*) and humpback whales (*Megaptera novaeangliae*), the minke whale population presumably started to grow (Laws 1977; Mori and Butterworth 2006). This population change hypothesis was recently simulated in a krill predator dynamics model for the Antarctic ecosystem (Mori and Butterworth 2006). According to the "whale reduction" or "krill surplus" hypothesis (Laws 1977), this growth is considered to be a result of abundant food supplies available to the minke whale after the decline of the large baleen whale populations. About 30 years have passed since the large-scale hunting of krill-feeding large baleen whales was stopped, and recent sighting surveys by Southern Ocean Whale and Ecosystem Research (SOWER) and the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA) now suggest that the humpback and fin whales are starting to recover (Matsuoka et al. 2005). Branch (2007) and Branch et al. (2004) also report that the Antarctic blue whale (*B. musculus*) population has increased, although it is still small.

Whales generally accumulate fat during the summer feeding period at high latitudes and migrate to low latitude areas for reproduction (Næss et al. 1998). The Antarctic minke whale migrates from tropical latitudes around 10–30°S to the Antarctic (Kasamatsu et al. 1995), where it spends the austral summer feeding (Kato and Miyashita 1991; Kasamatsu et al. 1995). Whale blubber serves as energy storage in addition to its thermal function (Parry 1949; Lockyer et al. 1984), and it also gives the whale body a streamlined shape as described by Parry (1949). The fat reserves in blubber have commonly been used as an indication of body condition in whale studies (e.g. Lockyer et al. 1985a, b; Lockyer and Waters 1986; Víkingsson 1995; Koopman 1998; Ichii et al. 1998; Haug et al. 2002). Blubber thicknesses, blubber weight and whale girth have all been found to increase through the feeding season (Lockyer 1987; Víkingsson 1995; Næss et al. 1998). From the measurements presented in Lockyer et al. (1985b), it is reasonable to assume that blubber thickness is positively correlated with lipid content in the whale body.

The main objective of the present study was to examine trends in body condition of the Antarctic minke whale during a recent 18-year period.

Materials and methods

Sampling and measurements

Blubber thickness and all other variables used in the present investigation were measured in Antarctic minke whales taken by JARPA from 1987/1988 to 2004/2005. JARPA was started in 1987/88 under a special permit issued by the Government of Japan, based on Article VIII of the International Convention for the Regulation of Whaling. The survey period and sample sizes are shown in Table 1. The energetics of baleen whales differ according to their reproductive status and sex (Lockyer 1986; 1987; Aguilar and Borrell 1990; Víkingsson 1995). For instance, pregnant females have more lipid in the blubber than lactating females do (Aguilar and Borrell 1990). To avoid any bias resulting from growth or lactation, we used only mature males (n = 2,890) and pregnant females (n = 1,814), but not lactating females or immature animals, for the present analyses. Besides, mature males and pregnant females accounted for about 70% of all the JARPA samples (Table 1).

Table 1 JARPA survey periods and numbers of Antarctic minke whales captured

Year no.	Research periods	Survey areas	Number captured		
			Total catch	MM	PF
1	17.01.1988–26.03.1988	IV	273	118	57
2	12.01.1989–31.03.1989	V	241	57	95
3	06.12.1989–12.03.1990	IV	330	142	77
4	19.12.1990–22.03.1991	V	327	140	108
5	05.12.1992–25.03.1992	IV	288	135	70
6	03.12.1992–24.03.0993	V	330	156	118
7	03.12.1993–19.03.1994	IV	330	150	57
8	03.12.1994–21.03.1995	V	330	166	66
9	26.11.1995–22.03.1996	III(east) + IV	440	208	92
10	30.11.1996–13.03.1997	V + VI(west)	440	173	165
11	07.12.1997–14.03.1998	III(east) + IV	438	208	38
12	13.01.1999–31.03.1999	V + VI(west)	389	207	70
13	05.12.1999–10.03.2000	III(east) + IV	439	181	102
14	11.12.2000–20.03.2001	V + VI(west)	440	197	114
15	29.11.2001–08.03.2002	III(east) + IV	440	159	134
16	02.12.2002–08.03.2003	V + VI(west)	440	195	126
17	30.11.2003–03.03.2004	III(east) + IV	440	150	145
18	07.12.2004–08.03.2005	V + VI(west)	440	148	180

MM mature male, *PF* pregnant but not lactating female

The research area includes the International Whaling Commission (IWC) Management Area III (East), Area IV, Area V and Area VI (West), which together cover the area from 35°E to 145°W, south of 60°S in austral summer seasons (Fig. 1). The two western areas and the two eastern areas, split at 130°E, were surveyed in alternate years so that the entire broad survey area was covered in two years. One or two Antarctic minke whales were randomly sampled from each school observed within three nautical miles of the research track line. The minke whales were captured by three vessels using explosive harpoons and a large-caliber rifle as a secondary weapon in the event that death was not instantaneous (International Whaling Commission 2003). After capture, the animals were placed aboard a research base vessel where they were examined. The sighting positions of the captured animals were recorded by each sighting/sampling vessel. After outer observations were completed, body length (from snout tip to tail fluke notch in a straight line along the deck) and other morphological measurements were taken. Blubber thickness was measured to the nearest mm, by dissecting perpendicularly from skin to muscle without including connective tissue or black surface skin. The measurement positions are shown in Fig. 2. The measurements were usually made on the left side of the animal, but in several cases they were made on the right side, mainly because of damage to the left side caused by the harpoon. Blubber thickness at the lateral position was measured in all whales. The reasons for choosing this particular lateral point for blubber thickness measurements were that skin surface and muscle fascia are parallel in this area, and blubber thickness is close to constant in an area around the measurement site. Any tension in the blubber tissue was released by cutting through the blubber layer down to the muscle fascia around the measurement site, but at a certain distance from this site. In the first animal caught each day, all the blubber including the ventral groove and visceral fat was also removed from the body and weighed to the nearest kilogram. In addition, half girth at the level of the umbilicus was measured in all whales. Sex and maturity were recorded for each whale on the basis of routine observations of reproductive organs during dissection and tissue observations in the laboratory. The age of each whale was determined from the growth layers in the earplug using a stereoscopic microscope. A diatom film is sometimes observed on the surface of the whales and may cover the entire body. The extent of diatom adhesion on the skin is assumed to be a rough indicator of how long a whale has spent in cold waters (Hart 1935; Ohno and Fujino 1952; Nemoto 1980; Best 1982) (Table 2). Fetus length was measured in the same way as adult body length. Biological data including blubber thickness, sex, body length of adult animals, fetus and diatom films were collected routinely by biologists, including some of the authors, on board a research vessel. These data were stored in the database on JARPA held by the Institute of Cetacean Research. Data used in the present study were obtained from this database.

Statistical analysis

Previous studies in balaenopterid whale species have shown that lateral blubber thickness varies seasonally from the middle part of the body towards the tail, while blubber thickness in the anterior part of the whale body is more constant (Næss et al. 1998; Konishi 2006). Visceral fat acts as a secondary energy storage site in the body cavity (Næss et al. 1998). Blubber thickness in the mid-lateral region and "fat weight" (blubber weight + visceral fat) were therefore used as body condition indicators in this study (Fig. 2). A total of 4,704 Antarctic minke whales (mature males and pregnant but not lactating females) were examined on board the mother research vessel during the JARPA program (Tables 1, 2, 3). Blubber thickness measurements at the lateral position shown in Fig. 2 were available from 4,689 of these. The discrepancy is largely explained by the fact that in some whales, the blubber at the measurement points on both sides of the body was damaged. Half girth measurements were available for 4,681 animals. Fat weight was available from only 740 whales.

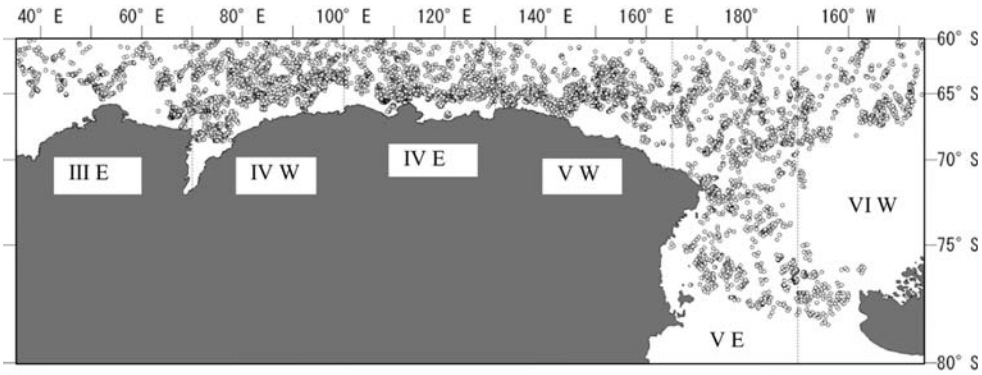


Fig. 1 Map of main JARPA survey area (Areas III-East, IV, V, and VI-West, which together cover the area from 35°E to 145°W). *Open circles* indicate the observation positions for the Antarctic minke whales captured by JARPA and analysed in this study

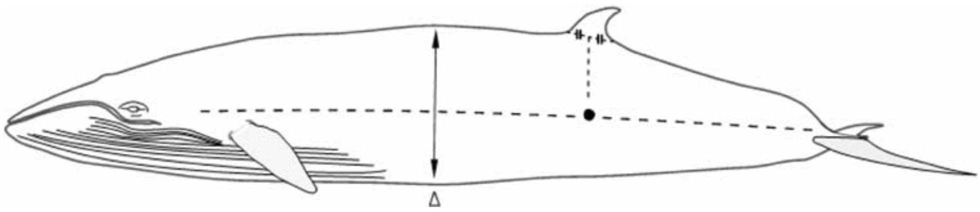


Fig. 2 Positions of blubber thickness and half girth measurements. *Closed circle* lateral point, *open triangle* position of the umbilicus, *arrow* half girth at the level of the umbilicus

Table 2 Diatom adhesion level. Scale is used as a predictor variable for the analyses

Scale	Level
0	None
1	Limited
2	Moderate
3	Most of body
4	Entire body

Regression analysis was therefore first carried out on blubber thickness at the lateral position in 4,689 whales. All other variables except age, body weight, fetus length and total fat weight were available for all 4,704 whales. Fetus lengths were of course only available for the females, and mean fetus lengths were used for fourteen pairs of twins. Age was available for 4,268 whales, with missing whales randomly distributed over the 18 years. Body weights were not measured during the first survey year (1987/1988), because no weighing machine had been installed on the mother research vessel. Regression analyses were therefore carried out first independently for males and females and without body weight as a possible independent variable.

The time spent in the feeding area, and geographical and biological variables that could possibly be related to blubber thickness, should be considered in body condition analyses. To take these factors into account and to possibly exclude some of them, we conducted stepwise multiple linear regression analyses, using average values for the missing values.

At each step of the regression analysis, the next variable was included in the equation if the corresponding P value was below 5%. In an adaptation to a recently developed criteria-based subset selection procedures, we also calculated the Bayesian information criterion (BIC) (Schwarz 1978), formulated as

$$\mathrm{BIC} = -2 \ln L + K \log n$$

where L is likelihood and K is the number of parameters. At each step of the regression analysis, the BIC value was calculated. According to this method, the model with the lowest BIC value should be preferred.

In the first set of runs, blubber thickness at the lateral position (in centimeter) was the dependent variable as a body condition indicator, because of the large sample size for this variable. We allowed the following independent variables for separate regression analyses for mature males and pregnant females: “date” (December 1st = day 1), “diatom adhesion” (0–4, Table 2), “latitude (degree)”, “longitude” (in degrees east), “body length” (in meter) and, for females,

Table 3 Data used in the analyses

	Variables	n	Mean	SD	Minimum	Maximum
Mature males	Body length (m)	2,890	8.36	0.41	6.32	9.63
	Body weight (t)	2,766	6.85	1.06	3.05	11.05
	Age	2,595	19.75	10.73	3	63
	Diatom adhesion level	2,886	1.70	1.24	0	4
	Blubber thickness (lateral) (cm)	2,883	3.56	0.922	1.1	7.2
	Half girth (cm)	2,872	214.00	14.35	162	269
	Fat weight (t)	464	2.79	0.49	1.36	4.56
Pregnant females (not lactating)	Body length (m)	1,814	8.89	0.40	7.57	10.22
	Body weight (t)	1,753	8.11	1.19	4.9	12.50
	Age	1,673	21.94	10.20	5	59
	Fetus length (cm)	1,772	73.11	46.66	1.3	301
	Diatom adhesion level	1,810	1.38	1.15	0	4
	Blubber thickness (lateral) (cm)	1,806	4.02	0.978	1.5	7.7
	Half girth (cm)	1,809	224.00	16.17	175	291
	Fat weight (t)	276	3.52	0.60	2.30	5.51

"fetus length" (in centimeter). "Year" was also included as an independent variable to investigate a possible annual trend (87/88 = 1 88/89 = 2 89/91 = 3…). This regression was also carried out without "fetus length" as a possible independent variable for females to see the effect of this change on the other regression coefficients.

In a second set of runs, the regression analyses were carried out for all 4,689 whales, including "sex" (1: male, 2: female) as a possible explanatory variable, using mean values for the missing values. "Fetus length" is of course only available for females, and assigning mean "fetus length" to all males is likely to reduce the regression coefficient for this variable in the analysis where males and females are combined. To illustrate this effect and to show that the main conclusions from the regression analysis are unaltered, the regression was carried out with and without "fetus length" as a potential explanatory variable. "Body weight" is also considered to be an important variable in studies of energetics of animals, but it is strongly correlated with other variables. To examine how "body weight" affects the results, the regression was carried out both with and without "body weight" as a potential explanatory variable.

In addition, we conducted other stepwise multiple linear regression analyses using either "fat weight" or "half girth" as dependent variables to confirm, using the corresponding sub-samples of the whales, whether other body condition indicators showed a similar decline in these variables over the 18 JARPA years. These analyses were carried out for 740 and 4,681 whales respectively, using average values for the few missing values. We allowed the following independent variables: "date", "diatom adhesion", "latitude", "longitude" (in degrees east), "body length", "sex", "age", and "year". For runs with "fat weight" as the dependent variable, we calculated "lean body weight" (= "body weight" − "fat weight") for each animal and used this new variable as a possible predictor variable instead of "body weight".

Results

Although we used only mature males and pregnant but not lactating females, there was a wide range of values for the variables used (Table 3). Blubber thickness at the lateral point ranged from 1.1 to 7.2 cm in mature males, and from 1.5 to 7.7 cm in pregnant females. Half girth at umbilical position ranged from 162 to 269 cm in mature males, and 175–291 cm in pregnant females. Fat weight ranged from 1.36 to 4.56 t in mature males, and 2.30–5.51 t in pregnant females.

The results from the regression analyses are presented in Tables 4, 5, 6 and 7. The format of the tables is as follows: the first line in each table represents the constant in the regression equation. Each of the next lines represents one explanatory variable. The variables are listed from the top of the table in the order in which they were entered into the equation during the stepwise procedure. Variables that were not included in the regression equation at the 5% level are listed below the table. The numbers in the column captioned "*R* square" show the value of *R* square after the corresponding variable has been entered into the equation (in addition to all variables above it). The values in the column captioned "*F* value" show the value of *F* for inclusion of this variable before its inclusion. The values in the other columns show values of the corresponding parameters for the final model.

In the first three runs the two sexes were analysed separately, and females both with and without "fetus length" were used as a possible explanatory variable (Table 4). "Date" in mature males and "fetus length" in pregnant females were the best predictors of blubber thickness at the lateral point. "Date" was an important predictor variable in the other two runs as well. "Year" was included as a predictor of blubber thickness at the 5% level in all three runs and gave a similar regression coefficient. In the next set of runs, where the two sexes were pooled and "sex" was included as a possible predictor variable (Table 5), all independent variables were included as predictors at the 5% level In the first run, "date" was the best predictor of blubber thickness, followed by "diatom", "sex", "longitude", "year", "age", "latitude" and "body length". The results of the other runs show very similar results, although "age" was not included as a predictor variable in the second run at the 5% level (Table 5b). In all these analyses (Tables 4, 5), the point estimates of the coefficients for "year" ranged from −0.0180 to −0.0280 cm per year, showing that the blubber thickness of the Antarctic minke whale at the lateral point has decreased substantially over the years (Tables 4, 5, Fig. 3a). The results further indicate that blubber thickness increased with time spent feeding, and from west to east and north to south. Blubber thickness also increased with diatom adhesion level and fetus length. The blubber layer was found to be approximately 0.33 cm thinner in males than in females. The order of inclusion of independent variables in the regression equations did not differ between the procedure using a *P* value based criterion and that using BIC except for a small and unimportant difference in Table 5a. In all regression runs, the minimum BIC model included "date", "diatom" and "year" as predictor variables.

The runs using "fat weight" and "half girth" as dependent variables also gave similar results (Tables 6, 7), showing "year" to be a significant independent variable. "Fat weight" was found to decrease by approximately 17 kg/year and "half girth" by approximately 0.46 cm/year (Fig. 3b, c), corresponding to 0.92 cm/year for the

Table 4 Results of three multiple stepwise regression analyses with "lateral blubber thickness" as the dependent variable. Females were analysed both with and without "fetus length" as a possible explanatory variable. The BIC value in bold is the minimum value

Independent variables	Coefficient		*P* Value	95% Confidence interval of B				BIC	
	B	*SE*		Lower bound	Upper bound	*R* Square	*F* value	Value	Variables included
(a) Mature males: *N* = 2,883									
Constant	0.1822	0.4461	0.683	−0.6925	1.0569	–	–	1817.343	Constant
Date (Dec. 1 = 1)	0.0157	0.0005	0.000	0.0147	0.0167	0.310	1297.054	754.047	Date
Diatom	0.2053	0.0107	0.000	0.1844	0.2262	0.392	928.354	399.333	Diatom
Longitude (°E)	0.0029	0.0003	0.000	0.0022	0.0035	0.412	673.592	308.751	Longitude
Year (87/88 = 1)	−0.0180	0.0028	0.000	−0.0234	−0.0125	0.420	520.271	281.04	Year
Latitude (°)	0.0189	0.0054	0.001	0.0082	0.0296	0.422	419.670	**278.567**	Latitude
Body length (m)	0.0859	0.0326	0.008	0.0221	0.1498	0.423	351.0609	279.567	Body length
–	–	–	–	–	–	–	–	286.797	Age
(b) Pregnant females with "fetus length" as a possible explanatory variable: *N* = 1,806									
Constant	1.1846	0.5299	0.026	0.1453	2.2240	–	–	1115.653	Constant
Fetus length (cm)	0.0095	0.0006	0.000	0.0084	0.0106	0.335	910.562	385.597	Fetus length
Date (Dec. 1 = 1)	0.0044	0.0009	0.000	0.0028	0.0061	0.351	487.957	349.789	Date
Year (87/88 = 1)	−0.0208	0.0035	0.000	−0.0276	−0.0140	0.361	339.224	330.005	Year
Diatom	0.0765	0.0212	0.000	0.0348	0.1182	0.365	259.064	325.278	Diatom
Latitude (°)	0.0140	0.0042	0.001	0.0059	0.0222	0.368	209.934	**323.895**	Latitude
Body length (m)	0.1145	0.0467	0.014	0.0228	0.2062	0.370	176.430	325.385	Body length
–	–	–	–	–	–	–	–	330.902	Age
–	–	–	–	–	–	–	–	337.449	Longitude
(c) Pregnant females: *N* = 1,806									
Constant	1.7640	0.2850	0.000	1.2060	2.3220	–	–	794.461	Constant
Diatom	0.2950	0.0180	0.000	0.2600	0.3300	0.178	390.339	448.408	Date
Date (Dec. 1 = 1)	0.0080	0.0010	0.000	0.0060	0.0100	0.238	281.263	319.316	Diatom
Year (1987/1988 = 1)	−0.0280	0.0040	0.000	−0.0360	−0.0210	0.258	208.328	279.517	Longitude
Latitude (°)	0.0220	0.0040	0.000	0.0130	0.0300	0.268	164.683	261.824	Year
Age	0.0070	0.0020	0.001	0.0030	0.0110	0.273	134.919	**257.429**	Latitude
–	–	–	–	–	–	–	–	262.528	Body length
–	–	–	–	–	–	–	–	269.959	Age

a) "Age" was not included at the 5% level. b) "Age" and "longitude" were not included at the 5% level. c) "Body length" and "longitude" were not included at the 5% level

total girth and 17 cm (4%) for the 18-year JARPA period. The results were similar when the two sexes were analysed separately.

Discussion

The results of the stepwise regression analyses demonstrate that many factors affect the body condition of the Antarctic minke whale. Not unexpectedly, there is a significant increase in blubber thickness and fat weight during the feeding season ("date"). This result clearly confirms that the fattening is caused by intensive feeding in the Antarctic Ocean after long-distance migration from the reproductive areas. Similar seasonal fattening has been documented in fin whales (Lockyer 1987; Víkingsson 1995) and in common minke whales (Næss et al. 1998) in the North Atlantic. Fattening and diatom adhesion are also positively correlated, confirming that the extent of this adhesion can be used as a measure of how long a whale has spent in cold water. The results also show that blubber thickness and total fat weight increase from west to east and with increasing length of the fetus. Fetus length was one of the most important predictors of blubber thickness in the pregnant females in the JARPA data set, suggesting that departure from the reproductive area and the timing of conception in the minke whale are related.

Table 5 Results of four multiple stepwise regression analyses with the sexes combined and "lateral blubber thickness" as the dependent variable and "sex" and different combinations of "body weight" and "fetus length" as additional potential predictor variables

Independent variables	Coefficient		P value	95% Confidence interval of B		Results of each model		BIC	
	B	SE		Lower bound	Upper bound	R square	F value	Value	Variables included
(a) Regression with "sex" as the only new predictor variable compared to Tables 4a and c. $N = 4{,}689$									
Constant	0.4619	0.3270	0.158	−0.1791	1.1029	–	–	2569.834	Constant
Date (Dec. 1 = 1)	0.0138	0.0004	0.000	0.0129	0.0147	0.247	1535.272	1249.987	Date
Diatom	0.2305	0.0094	0.000	0.2119	0.2490	0.314	1070.329	822.912	Diatom
Sex (male = 1, female = 2)	0.3325	0.0306	0.000	0.2724	0.3925	0.356	862.763	533.067	Sex
Longitude (°E)	0.0022	0.0003	0.000	0.0016	0.0028	0.368	680.439	455.921	Longitude
Year (1987/1988 = 1)	−0.0213	0.0023	0.000	−0.0257	−0.0169	0.378	569.173	386.122	Year
Age	0.0031	0.0012	0.011	0.0007	0.0055	0.380	478.104	379.666	Age
Latitude (°)	0.0122	0.0037	0.001	0.0050	0.0195	0.381	411.898	**378.616**	*1
Body length (m)	0.0799	0.0306	0.009	0.0200	0.1399	0.382	361.714	380.384	Age
(b) Regression with "sex" and "fetus length" $N = 4{,}689$									
Constant	0.3839	0.3115	0.218	−0.2269	0.9946	–	–	2812.916	Constant
Date (Dec. 1 = 1)	0.0131	0.0004	0.000	0.0122	0.0139	0.247	1535.272	1493.060	Date
Diatom	0.1814	0.0099	0.000	0.1619	0.2008	0.314	1070.329	1065.994	Body weight
Sex (male = 1, female = 2)	0.3346	0.0297	0.000	0.2763	0.3928	0.356	862.763	776.149	Diatom
Fetus length (cm)	0.0056	0.0004	0.000	0.0048	0.0065	0.383	728.189	575.671	Body length
Longitude (°E)	0.0021	0.0003	0.000	0.0015	0.0027	0.392	604.386	520.846	Longitude
Year (1987/1988 = 1)	−0.0194	0.0022	0.000	−0.0237	−0.0151	0.401	523.466	457.152	Sex
Body length (m)	0.0965	0.0276	0.000	0.0423	0.1507	0.403	451.209	**454.635**	Year
Latitude (°)	0.0076	0.0037	0.037	0.0005	0.0148	0.403	395.639	458.704	Latitude
–	–	–	–	–	–	–	–	464.914	Age
(c) Regression with "sex" and "body weight" $N = 4{,}689$									
Constant	4.1572	0.3239	0.000	3.5223	4.7922	–	–	3520.420	Constant
Date (Dec. 1 = 1)	0.0103	0.0004	0.000	0.0094	0.0111	0.247	1535.272	2200.564	Date
Body weight (t)	0.4492	0.0150	0.000	0.4198	0.4785	0.329	1151.310	1647.762	Body weigth
Diatom	0.1778	0.0088	0.000	0.1605	0.1951	0.395	1018.124	1172.910	Diatom
Body length (m)	−0.7109	0.0385	0.000	−0.7864	−0.6355	0.424	863.289	909.600	Body length
Longitude (°E)	0.0031	0.0003	0.000	0.0026	0.0036	0.453	777.054	670.358	Longitude
Sex (male = 1, female = 2)	0.2216	0.0283	0.000	0.1661	0.2771	0.467	684.774	576.566	Sex
Year (87/88 = 1	−0.0196	0.0021	0.000	−0.0236	−0.0155	0.477	611.061	491.277	Year
Latitude (°)	0.0159	0.0034	0.000	0.0093	0.0226	0.480	539.611	475.131	Latitude
Age	−0.0047	0.0012	0.000	−0.0069	−0.0024	0.482	483.070	**464.914**	Age

Table 5 continued

Independent variables	Coefficient		*P* value	95% Confidence interval of B		Results of each model		BIC	
	B	*SE*		Lower bound	Upper bound	*R* square	*F* value	Value	Variables included
(d) Regression with “sex”, “fetus length” and “body weight” $N = 4{,}689$									
Constant	3.9736	0.3224	0.000	3.3416	4.6057	–	–	3666.078	Constant
Date (Dec. 1 = 1)	0.0100	0.0004	0.000	0.0092	0.0109	0.247	1535.272	2346.222	Date
Body weight (t)	0.4242	0.0152	0.000	0.3944	0.4540	0.329	1151.310	1793.419	Body weight
Diatom	0.1526	0.0093	0.000	0.1344	0.1708	0.395	1018.124	1318.567	Diatom
Body length (m)	−0.6674	0.0386	0.000	−0.7430	−0.5918	0.424	863.289	1055.258	Body length
Longitude (°E)	0.0030	0.0003	0.000	0.0025	0.0035	0.453	777.054	816.015	Longitude
Sex (male = 1, female = 2)	0.2332	0.0281	0.000	0.1780	0.2883	0.467	684.774	722.224	Sex
Year (1987/1988 = 1)	−0.0187	0.0021	0.000	−0.0228	−0.0147	0.477	611.061	636.934	Year
Fetus length (cm)	0.0033	0.0004	0.000	0.0025	0.0041	0.485	551.553	579.538	Fetus length
Age	−0.0050	0.0011	0.000	−0.0073	0.0028	0.487	494.195	567.367	Age
Latitude (°)	0.0130	0.0034	0.000	0.0064	0.0196	0.489	447.547	**557.896**	Latitude

a), c) and d) All independent variables were included as predictors at the 5% level. b) “Age” was not included at the 5% level. a) This was the only run that showed some differences between the *P* value based stepwise procedure and BIC values. The BIC value in bold is the minimum value

*1 Latitude and Longitude were added and Age removed at this step by BIC

Table 6 Results of a multiple stepwise regression analysis with “fat weight” as the dependent variable

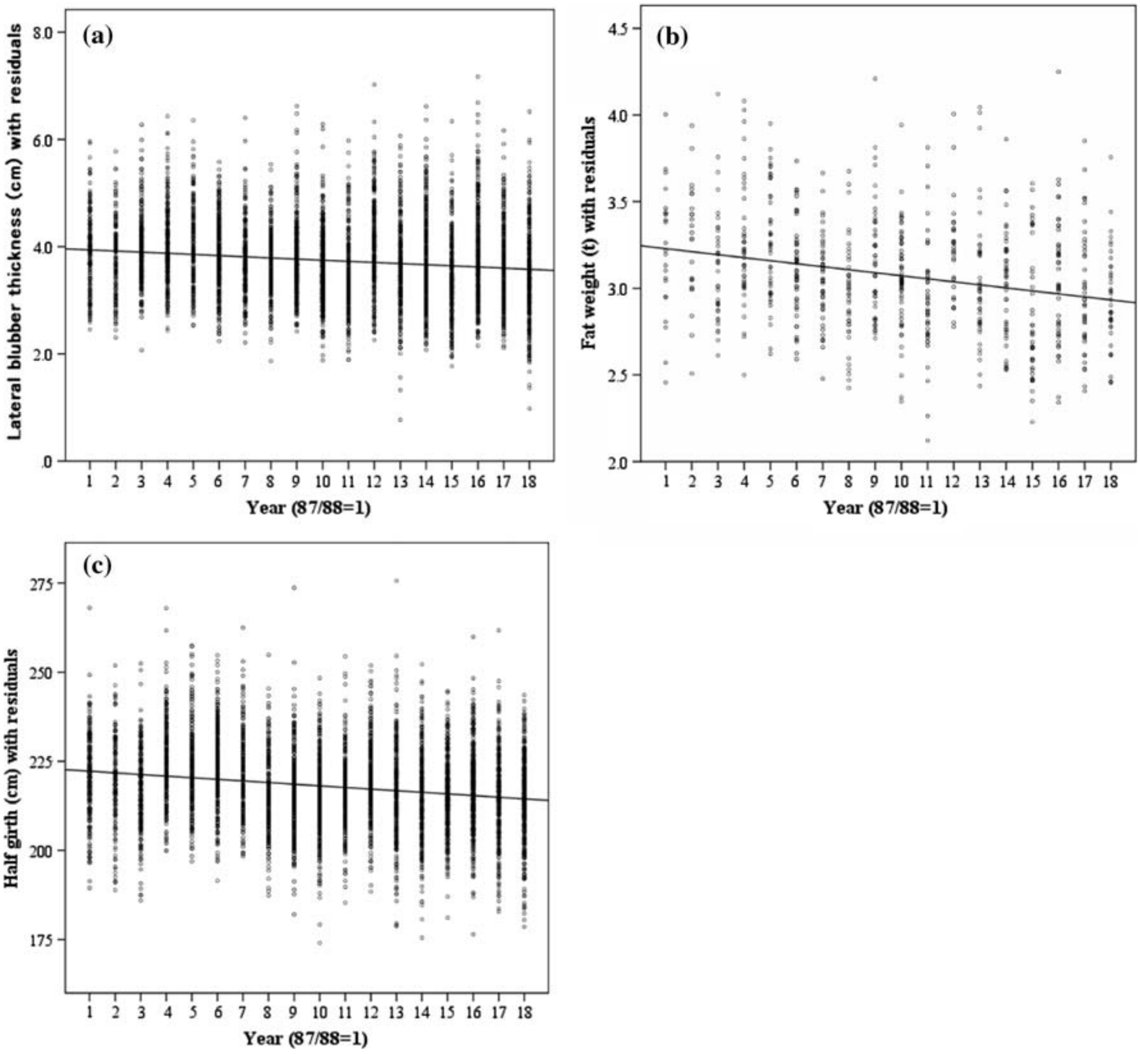
Independent variables	Coefficient		*P* value	95% Confidence interval of *B*		Result of each model		BIC	
	B	*SE*		Lower bound	Upper bound	*R* square	*F* value	Value	Variables included
Constant	−3.7685	0.3781	0.000	−4.5107	−3.0263	–	–	1273.160	Constant
Body length (m)	0.5191	0.0438	0.000	0.4332	0.6051	0.558	932.335	675.994	Body length
Date (Dec. 1 = 1)	0.0043	0.0005	0.000	0.0033	0.0052	0.646	671.609	521.267	Date
Sex (1 = male, 2 = female)	0.2807	0.0338	0.000	0.2144	0.3470	0.667	490.793	483.635	Sex
Lean body weight (t)	0.2196	0.0253	0.000	0.1700	0.2692	0.697	422.569	438.933	Lean body weight
Diatom adhesion	0.0700	0.0105	0.000	0.0494	0.0907	0.712	362.579	406.661	Diatom adhesion
Year (1987/1988 = 1)	−0.0174	0.0025	0.000	−0.0223	−0.0124	0.725	322.305	377.875	Year
Age	0.0062	0.0013	0.000	0.0036	0.0087	0.734	288.206	358.712	Age
Latitude (°)	0.0111	0.0038	0.004	0.0036	0.0186	0.737	255.819	**357.809**	Latitude
–	–	–	–	–	–	–	–	363.217	Longitude

“Longitude” was not included at the 5% level. The BIC value in bold is the minimum value. $N = 688$

Table 7 Results of a multiple stepwise regression analysis with "half girth at the level of umbilicus" as the dependent variable

Independent variables	Coefficient		*P* value	95% Confidence interval of *B*		Result of each model		BIC	
	B	SE		Lower bound	Upper bound	*R* square	*F* value	Value	Variables included
Constant	95.5769	5.0849	0.000	85.6081	105.5457	–	–	2985.049	Constant
Body length (m)	15.0267	0.4756	0.000	14.0942	15.9591	0.287	1882.144	1416.357	Body length
Date (Dec. 1 = 1)	0.1497	0.0070	0.000	0.1360	0.1634	0.359	1310.931	929.737	Date
Diatom	2.6522	0.1470	0.000	2.3639	2.9404	0.393	1009.756	685.451	Diatom
Year (87/88 = 1)	−0.4557	0.0350	0.000	−0.5244	−0.3870	0.416	831.306	517.926	Year
Longitude (deg E)	−0.0273	0.0045	0.000	−0.0362	−0.0184	0.424	688.556	457.303	Longitude
Age	0.1700	0.0190	0.000	0.1327	0.2073	0.433	594.079	394.602	Age
Sex (1 = male, 2 = female)	2.2827	0.4765	0.000	1.3485	3.2170	0.434	511.757	393.084	Sex
Latitude (°)	−0.2680	0.0575	0.000	−0.3808	−0.1552	0.437	452.486	**380.172**	Latitude

All independent variables were included as predictors. The BIC value in bold is the minimum value. $N = 4{,}681$



Figs. 3 Temporal trends in body condition indicators for the Antarctic minke whale in its feeding season, from the results of stepwise multiple regressions. Regression lines were drawn using the population mean for all the other predictor variables than "year". *Open circles* represent residuals from the regression line. The three figures are based on the following tables: **a** Table 5a, **b** Table 6, **c** Table 7

The results of the statistical analyses clearly show that blubber thickness, fat weight and girth in Antarctic minke whales have decreased during the 18-year JARPA research period. Analyses of residuals show that there has been a linear decline in blubber thickness at the lateral position, fat weight and girth over this period. The total magnitude of the decline over these 18 years is 9% for blubber thickness in the lateral position, 9% for fat weight and 4% for girth measurements. The inclusion or exclusion of other independent variables in the regression equations resulted in only small changes in these results, showing that the finding of a substantial decline in fat storage is a robust result. This is the first time a long-term decline in energy storage in minke whales has been demonstrated, although Ohsumi et al. (1997) found some non-significant indications of a decline in blubber thickness in the lateral position starting in the early 1980s. Our result shows a decrease of 0.02 cm/year in blubber thickness at the lateral position over a period of 18 years. This is roughly equivalent to 36 intensive summer feeding days, indicating that the overall decrease in energy storage in Antarctic minke whale must be large.

The results primarily indicate an increasing shortage of food for the Antarctic minke whale over the last two decades and perhaps even longer. The Antarctic minke whale depends largely on the Antarctic krill (Ohsumi 1979; Armstrong and Siegfried 1991; Ichii and Kato 1991), so the amount of krill available for the minke whales must have declined in its feeding areas. Kawamura (1978) mentioned that there was some surplus of krill after populations of the large baleen whales had been depleted by hunting and up to the 1970s. And Clapham and Brownell (1996) noted that there is no evidence that baleen whales are resource-limited. However, our results clearly show that baleen whales are resource-limited animals, indicating that the minke whale population may be affected by krill availability.

Environmental change could perhaps have been an important causal factor, since this is known to affect krill abundance. The abundance of krill around the Antarctic Peninsula is known to have declined since the 1970s, because high temperatures have resulted in a decrease in the extent of the sea ice (Loeb et al. 1997; Atkinson et al. 2004). But no such environmental trend has been observed in austral summer in the JARPA survey area (Watanabe et al. 2006). Of course, other environmental factors could have been responsible. Unfortunately, information about long-term trends in krill abundance is not available from this area.

Interspecies competition for krill is another possible explanation for the decline in body condition of the Antarctic minke whale. There is overlap between the habitats of different whale species (Kasamatsu et al. 2000), suggesting the possibility of interference between the different species in Antarctic waters. Sighting surveys carried out by the Southern Ocean Whale and Ecosystem Research (SOWER) program and JARPA have demonstrated the recent recovery of humpback (*M. novaeangliae*) and fin whales (*B. physalus*) (Matsuoka et al. 2005). Branch (2007) and Branch et al. (2004) also report that the Antarctic blue whale (*B. musculus*) population has increased, although it is still small. These large whales also feed on the Antarctic krill and thus share the same food niche as the minke whale (Nemoto 1962; Kawamura 1980). Interestingly, humpback whales have recently shifted their distribution further south to areas where minke whales now also occur (Matsuoka et al. 2005; see Nishiwaki et al. 2006). Friedlaender et al. (2006) showed niche separation between humpback and Antarctic minke whales on the western side of the Antarctic Peninsula. Ballance et al. (2006) also mentioned that in the Southern Ocean, the bottom-up effect is more likely to occur than the top-down effect, because of physical and biological factors such as ice extent that cause year-to-year variations in krill abundance. However, krill abundance varies in a roughly 5-year cycle (see Ballance et al. 2006), which is considerably shorter than the period covered by this study. Moreover, a recent population trend model, which includes krill, four baleen whale species and two seal species in the Antarctic ecosystem, gives evidence that these predator species interact (Mori and Butterworth 2006). Another example of competition for food was reported between Antarctic fur seals *Arctocephalus gazella* and Macaroni penguins *Eudyptes chrysolophus,* although in this case it was regional (Ballance et al. 2006). These results suggest that competition for food may affect Antarctic minke whales, in addition to other factors.

Competition with krill predators other than baleen whales may be important. Reilly et al. (2004) estimated that consumption by whales corresponds to 4–6% of the estimated krill biomass in the South Atlantic sector around the Antarctic Peninsula. Although our study area was in another part of the Antarctic Ocean, interactions between baleen whales and other krill consumers must be considered. Much information is available on other krill predators, such as penguins and seals, in Antarctic waters. However, unlike baleen whales, these animals live, feed and breed in or near Antarctic waters throughout the year, and are mainly affected by climate and the extent of the sea ice in the winter season. For example, the Adélie penguin (*Pygoscelis adeliae*) population is primarily affected by the extent of the sea ice in winter (Wilson et al. 2001). Populations of phocid seals such as crabeater seals, Weddell seals (*Leptonychotes weddellii*) and leopard seals (*Hydrurga leptonyx*) also show periodic fluctuations every 5 years, which are related to the El Niño-Southern Oscillation (ENSO) (Testa et al. 1991). Thus, we do not have enough data to understand the interactions between whales and other krill consumers, and need further studies so that all possible explanations for the decline in body condition of the Antarctic minke whale can be considered.

Global warming and climate change could cause changes in the Southern Ocean ecosystem. Population changes that are considered to be caused by warming have already been reported in penguins (Fraser et al. 1992), pinnipeds (Reid and Croxall 2001, Weimerskirch et al. 2003) and invertebrates (Loeb et al. 1997) around the Antarctic Peninsula, where rapid regional warming was been observed (Vaughan et al. 2001). Although there are no obvious signs of warming in the present study area, this process may have serious effects on krill-feeding animals in the near future.

Understanding how krill demography is affected by changes in physical environmental factors and by predator consumption, and how, in turn, this influences predator reproduction and survival, is an essential basis for predicting future change in the Antarctic marine ecosystem (Reid and Croxall 2001). However, investigating and understanding the dynamics of the widely distributed krill population is quite difficult, so that monitoring energy storage by a krill consumer, such as the minke whale, can be most useful. Recent studies of upper trophic-level predators, such as seabirds, penguins and pinnipeds, indicate Antarctic ecosystem changes (Reid and Croxall 2001; Weimerskirch et al. 2003). Understanding the status of the Antarctic minke whale is one of the keys to predicting changes in the populations of krill consumers, and also of crucial importance in detecting food web interactions and changes in the krill population itself. Standardized krill abundance surveys are needed throughout the area where Antarctic minke whales and large krill-eating large baleen whales occur. The JARPA survey has been carrying out krill abundance surveys for several years, and the results are useful in interpreting the interactions identified in the analyses.

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