

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

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ABSTRACT

The annual trend in energy storage in the Antarctic minke whale was examined using catch data from all 18 JARPA survey years. Stepwise multiple linear regression analyses clearly showed that blubber thickness at two positions and fat weight (blubber and visceral fat weight) of minke whales have been decreasing for nearly two decades. The decrease in blubber thickness is estimated at approximately 0.02 cm per year at a mid-lateral position, which corresponds to a decrease of 9% over the JARPA years. Furthermore, “date”, “extent of diatom adhesion”, “sex”, “body length”, “body weight”, “fetus length”, “latitude”, “age” and “longitude” were all identified as partially independent predictors of blubber thickness. At the anterior edge of the dorsal fin, the decrease is estimated at 0.12 cm per year or 36% over 18 years. The decrease in fat weight is estimated at 17 kg per year, which corresponds to 9.5% over 18 years. The direct interpretation of this substantial decline in energy storage in minke whales over time in terms of food availability is difficult, since no long-term krill abundance series is available. However, competition among krill feeders combined with the resulting krill population change must be considered as the most likely explanation of the decline, given the recent recovery of the stocks of large baleen whales.

INTRODUCTION

The Southern Ocean supports a simple food web with high productivity, and is an important feeding ground for many consumers. The Antarctic krill *Euphausia superba* is the most abundant and main prey for large baleen whales, seals and seabirds. The Antarctic minke whale *B. bonaerensis*, which is a small baleen whale, also depends largely on *E. superba* (Ohsumi 1979, Armstrong and Siegfried 1991, Ichii and Kato 1991, Ichii 1997). Krill availability in the Antarctic Ocean is generally considered to be the most important limiting factor for population sizes of many krill feeders. Krill biomass is very high 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 hypothesised that after more than 50 years of commercial whaling and overexploitation of the large baleen whales, the relative abundance of the whale species was 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, the minke whale population presumably started to grow. 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 this decline of the large baleen whale populations. Whales generally accumulate fat during the summer feeding period and migrate to low latitude areas for reproduction (Næss et al. 1998). The Antarctic minke whale migrates to the Antarctic, where it spends the austral summer feeding (Kato and Miyashita 1991, Kasamatsu et al. 1995). The fat reserves in blubber have commonly been used as an indication of body condition in whale studies (e.g. Lockyer et al. 1985, Lockyer and Waters 1986, Víkingsson 1995, Koopman 1998).

The main objective of the present study was to examine trends in body condition of the Antarctic minke whale during the JARPA 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 the Japanese Whaling Research Program under Special Permit in the Antarctic (JARPA) from 1987/88 to 2004/05. The energetics of baleen whales differ according to their reproductive status and sex (Lockyer 1986, 1987, Víkingsson 1995). To avoid any bias resulting from growth or lactation, we used only mature males and pregnant females, but not lactating females or immature animals, for the present analyses. The research area covers the International Whaling Commission (IWC) Management Area III (East), Area IV, Area V and Area VI (West), south of 60°S in austral summer seasons (Fig. 1). The two western areas and the two eastern areas were surveyed in alternate years. After capture by three sighting/sampling vessels, 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. In addition, blubber thickness in the first animal caught each day was also measured dorsally, at the anterior edge of the dorsal fin. In this animal, all the blubber including the ventral groove and visceral fat was also removed from body and weighed to the nearest kilogram. 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. The relevant stocks of Antarctic minke whale were defined as follows: Eastern Indian Ocean Stock (I-stock) Areas IIIE, IV and VW, Western South Pacific Stock (P-stock) Areas VE and VIW (Pastene 2006). 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 (Table 1). Fetus length was measured in the same way as adult body length.

Statistical analysis

Previous studies in baleenopteran whale species have shown that both lateral and dorsal blubber thickness varies seasonally from the middle part of the body towards the tail (Næss et al. 1998, Konishi 2006), and that visceral fat acts as secondary energy storage in the body cavity (Næss et al. 1998). Blubber thickness in the mid-lateral and dorsal region and “fat weight” (Blubber weight + visceral fat) were therefore used as body condition indicators in this study (Fig. 2). A total of 4704 Antarctic minke whales (mature males and pregnant but not lactating females) were examined on board the mother research vessel during the JARPA programme (Table 2). Blubber thickness measurements at the lateral position shown in Fig 2 were available from 4689 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. Blubber thickness at the dorsal position and fat weight were available from only 734 and 740 whales respectively.

Regression analysis was therefore first carried out on blubber thickness at the lateral position in 4689 whales. All other variables except age, body weight, fetus length and percentage fat weight were available for all 4704 whales. Fetus lengths were of course only available for the females, and mean fetus lengths were used for fourteen pairs of twins. Age was only available for 4268 whales with missing whales randomly distributed over the 18 years. Body weights were not measured during the first survey year (1987/88), 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 possibly exclude some of them, we conducted stepwise multiple linear regression analyses.

At each step of the regression analysis, the next variable was included in the equation if the corresponding p-value was below 5 %. In the first set of runs, blubber thickness at the lateral position (in cm) 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, respectively: “date” (December 1st=day 1), “diatom adhesion” (0 to 4, Table 1), “latitude (degree)”, “stock” (1: I-stock, 2: P-stock), “body length” (in m) and “fetus length” (in cm) for females. “Year” was also included as an independent variable to investigate a possible annual trend (87/88=1 88/89=2 89/91=3...). In a second set of runs, “longitude” (in degrees east) was substituted for “stock” for mature males and pregnant females separately. In a third set of runs, the regression analyses were carried out for all 4689 whales, including “sex” (1: male, 2:

female) and body weight (tons) as possible explanatory variables, with a software option (*SPSS Rel. 13.01 software package*) that uses average values for the missing values. We also performed separate regression analyses for “stock” and “longitude”.

In addition, we conducted other stepwise multiple linear regression analyses using either “dorsal blubber thickness” or “fat weight” 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. These analyses were carried out for 734 and 740 whales respectively using average values for the few missing values. We allowed the following independent variables: “date”, “diatom adhesion”, “latitude”, “stock”, “body length”, “sex”, “fetus length”, “age”, “body length”, and “year”. In two of the runs, “longitude” (in degrees east) was substituted for “stock”. 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 2). 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. Blubber thickness at the dorsal point ranged from 2.3 to 13.5 cm in mature males, and 2.9 to 15.0 cm in pregnant females.

In the first four runs for each sex, without body weight (Table 3), “date” in mature males and “fetus length” in pregnant females were the best predictors of blubber thickness at the lateral point. However, “age” was not included in any of the runs. “Year” was included as a predictor of blubber thickness at the 5 % level in all runs. In the next two runs, where “body weight” and “sex” were pooled (Table 4), all independent variables were included as predictors. “Date” was the best predictor of blubber thickness followed by “body weight”, “diatom”, “body length”, “latitude”, “year”, sex “fetus length”, “stock” and “age”. The runs using “longitude” instead of “stock” gave similar results, although the order of inclusion of some of the predictor variables in the stepwise procedure differs between the two runs. In all these analyses, the coefficients for “year” ranged from -0.0182 to -0.0208 cm per year, showing that the blubber thickness of the Antarctic minke whale at the lateral point has decreased significantly over the years (Table 3 and 4). The results further indicated 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 0.24 cm thinner in males than in females.

The runs using “dorsal blubber thickness” and “fat weight” as dependent variables also gave similar results (Table 5), showing “year” to be a significant independent variable. The decrease in blubber thickness at the dorsal position and in fat weight was found to be approximately 0.12 cm/year and 17 kg/year respectively. There was no indication that any of the explanatory variables had non-linear effects on blubber thickness.

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 time 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 reproductive area and the timing of conception timing in the minke whale are related.

The results of the statistical analyses clearly show that blubber thickness and fat weight in Antarctic minke whales have decreased during the 18 years of the JARPA research period. Analyses of residuals show that there has been a linear decline in blubber thickness at both the lateral and the dorsal position and in percentage fat weight over the 18-year period. The total magnitude of the decline over these 18 years is 9% for blubber thickness in the lateral position, 9.5% for percentage fat weight and as much as 36% for dorsal blubber thickness. 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. The results primarily indicate an increasing shortage of food for the Antarctic minke whales

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, Ichii 1997), so the amount of krill available for the minke whales must have declined in its feeding areas.

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). However, no such environmental trend has been observed 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 the 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) programme and JARPA have demonstrated the recent recovery of humpback (*Megaptera novaeangliae*) and fin whales (*B. physalus*) (Matsuoka *et al.* 2006). Branch *et al.* (2004) also reported 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 also now occur (Matsuoka *et al.* 2006, see Nishiwaki *et al.* 2006). Thus, the ongoing recovery of humpbacks may have reduced food supplies and niche space for the minke whale.

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.

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REFERENCES

- Armstrong, A.J. and Siegfried W.R. 1991. Consumption of Antarctic krill by Minke whales. *Ant. Sci.*; 3: 13-18.
- Atkinson, A., Siegel, V., Pakhomov, E. and Rothery, P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432: 100-103.
- Branch *et al.* 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. *Mar. Mammal Sci.* 20:726-754.
- Brown, S.G., Lockyer, C.H. 1984. Whales. In: R. M. Laws (eds). Antarctic Ecology Volume Two. Academic Press, Cambridge.; 717-781.
- Butterworth, D.S., Punt, A.E., Geromont, H.F., Kato, H. and Fujise, Y. 1999. Inferences on the dynamics of Southern Hemisphere minke whales from ADAPT analyses of catch-at-age information. *J. Cetacean Res. Manage.* 1(1): 11-32.
- Ichii, T., Kato, H. 1991. Food and daily food consumption of southern minke whales in the Antarctic. *Polar Biology* 11: 479-487.
- Ichii, T., Shinohara, N., Fujise, Y., Nishiwaki, S. and Matsuoka, K. 1998. Interannual changes in body fat condition index of minke whales in the Antarctic. *Mar. Biol. Prog. Ser.* 175: 1-12.
- Kasamatsu, F., Nishiwaki, S. and Ishikawa, H. 1995. Breeding areas and southbound migrations of southern minke whales *Balaenoptera acutorostrata*. *Mar. Ecol. Prog. Ser.* 119: 1-10.
- Kasamatsu, F., Matsuoka, K. and Hakamada, T. 2000. Interspecific relationships in density among the whale community in the Antarctic. *Polar Biology* 23: 466-473.
- Kato, H. and Miyashita, T. 1991. Migration Strategy of Southern Minke Whales in relation to Reproductive Cycle Estimated from Foetal Length. *Rep. Int. Whal. Commn.* 41: 363-369.

- Kawamura, A. 1980. A review of food of Balaenopterid whales. *Sci. Rep. Whales Res. Inst.* 32: 155-197.
- Koopman, H.N. 1998. Topographical Distribution of the Blubber of Harbor Porpoises (*Phocoena phocoena*). *J. of Mammal.* 79: 260-270.
- Konishi, K. 2006. Characteristics of the blubber and body condition indicator for the Antarctic minke whales (*Balaenoptera bonaerensis*) *Mammal Study* 31:14-22.
- Laws, R.M. 1977. Seals and whales of the southern ocean. *Philos. Trans. R. Soc. Lond. B.* 279: 81-96.
- Lockyer, C.H., McConnell, L.C., and Waters, T.D. 1985. Body condition in terms of anatomical and biochemical assessment of body fat in North Atlantic fin and sei whales. *Can. J. Zool.* 63: 2328-2338.
- Lockyer, C. 1986. Body fat condition in Northeast Atlantic fin whales, *Balaenoptera physalus*, and its relationship with Reproduction and food resource. *Can. J. Fish. Aquat. Sci.* 43: 142-147.
- Lockyer, C. and Waters, T. 1986. Weight and anatomical measurements of northeastern Atlantic fin (*Balaenoptera physalus*, Linnaeus) and sei (*B. borealis*, Lesson) whales. *Mar. Mammal Sci.* 2: 169-185.
- Lockyer, C. 1987. The relationship between body fat, food resource and reproductive energy costs in north Atlantic fin whales (*Balaenoptera physalus*). *Symp. Zool. Soc. Lond.* 57: 343-361.
- Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W. and Trivelpiece, S. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387: 897-900.
- Matsuoka, K., Hakamada, T., Kiwada, H., Murase, H. and Nishiwaki, S. 2006. Distribution and abundance estimates for humpback, fin and blue whales in the Antarctic Areas III, IV, V and VIW (35°E-145°W), south of 60°S. Report of the Intersessional Workshop to Review Data and Results from Special Permit Research on Minke Whales in the Antarctic, Tokyo 4-8 December. SC/D06/J7.
- Mori, M. and Butterworth, D.S. 2006. A first step towards modelling the krill-predator dynamics of the Antarctic ecosystem. *CCAMLR Science* 13: 217-277.
- Mori, M., Butterworth, D.S. and Kitakado, T. 2006. Application of ADAPT-VPA to Antarctic minke whales in the JARPA research area. Report of the Intersessional Workshop to Review Data and Results from Special Permit Research on Minke Whales in the Antarctic, Tokyo 4-8 December. SC/D06/J14.
- Næss, A., Haug, T. and Nilssen, M. 1998. Seasonal variation in body condition and muscular lipid contents in Northeast Atlantic minke whale *Balaenoptera acutorostrata*. *Sarsia* 83: 211-218.
- Nemoto, T. 1962. Food of baleen whales collected in recent Japanese Antarctic whaling expeditions. *Sci. Rep. Whales Res. Inst.* 16: 89-103.
- Nishiwaki, S., Ishikawa, H. and Fujise, Y. 2006. Review of general methodology and survey procedure under the JARPA. Report of the Intersessional Workshop to Review Data and Results from Special Permit Research on Minke Whales in the Antarctic, Tokyo 4-8 December. SC/D06/J2.
- Ohsumi, S. 1979. Feeding habits of the minke whale in the Antarctic. *Rep. Int. Whal. Commn.* 29: 473-476.
- Ohsumi, S., Fujise Y., Ishikawa H., Hatanaka T., Zenitani R., Matsuoka K. 1997. The fattyness of the Antarctic Minke Whale and Its Yearly Change. Paper SC/M97/18 presented to the JARPA review meeting, May 1997 (unpublished). 21p.
- Pastene, L.A. 2006. What do we know about the stock structure of the Antarctic minke whale? A summary of studies and hypotheses. Report of the Intersessional Workshop to Review Data and Results from Special Permit Research on Minke Whales in the Antarctic, Tokyo 4-8 December. SC/D06/J12.
- Reid, K. and Croxall, J. P. 2001. Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. *Proc. R. Soc. Lond. B* 268: 377-384.
- Víkingsson, G.A. 1995. Body condition of fin whales during summer off Iceland. In: A. S. Blix, L. Walløe and Ø. Ulltang. (eds). Whales, seals, fish and man. Elsevier, Amsterdam: 361-369.
- Watanabe, T., Yabuki, T., Suga, T., Hanawa, K., Matsuoka, K. and Kiwada, H. 2006. Results of oceanographic analyses conducted under JARPA and possible evidence of environmental changes. Report of the Intersessional Workshop to Review Data and Results from Special Permit Research on Minke Whales in the Antarctic, Tokyo 4-8 December. SC/D06/J30.
- Weimerskirch, H., Inchausti, P., Guinet, C. and Barbraud, C. 2003. Trends in bird and seal population as indicators of a system shift in the Southern Ocean. *Ant. Sci.* 15(2): 249-256.

Table 1 Diatom adhesion level. Scale is used as dummy variable for analyses.

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

Table 2 Data used in the analyses.

	Variables	<i>n</i>	mean	SD	min	max
Mature males	Body length (m)	2890	8.36	0.41	6.32	9.63
	Body weight (t)	2766	6.85	1.06	3.05	11.05
	Age	2595	19.75	10.73	3	63
	Diatom adhesion level	2886	1.70	1.24	0	4
	Blubber thickness (lateral) (cm)	2883	3.56	0.922	1.1	7.2
	Blubber thickness (dorsal) (cm)	459	4.79	1.342	2.3	13.5
	Fat weight (t)	464	2.79	0.49	1.36	4.56
Pregnant (not lactating)	Body length (m)	1814	8.89	0.40	7.57	10.22
	Body weight (t)	1753	8.11	1.19	4.9	12.50
	Age	1673	21.94	10.20	5	59
	Fetus length (cm)	1772	73.11	46.66	1.3	301
	Diatom adhesion level	1810	1.38	1.15	0	4
	Blubber thickness (lateral) (cm)	1806	4.02	0.978	1.5	7.7
	Blubber thickness (dorsal) (cm)	275	5.29	1.544	2.9	15.0
Fat weight (t)	276	3.52	0.60	2.30	5.51	

Table 3 Results of four multiple stepwise regression analyses with "lateral blubber thickness" as the dependent variable, but without "body weight" as a potential predictor variable.

a: mature males N=2,883

Independent variables	Coefficient		P value	95% confidence interval of B		Results of each model	
	B	SE		Lower bound	Upper bound	R square	F value
Constant	0.3661	0.4607	0.427	-0.5373	1.2694	-	-
Date (Dec. 1st=1)	0.0164	0.0005	0.000	0.0154	0.0174	0.310	1297.054
Diatom	0.2064	0.0107	0.000	0.1853	0.2275	0.392	928.354
Stock	0.2259	0.0349	0.000	0.1575	0.2944	0.405	652.555
Year (87/88=1)	-0.0182	0.0028	0.000	-0.0237	-0.0127	0.412	505.161
Latitude (deg)	0.0170	0.0060	0.004	0.0053	0.0287	0.414	406.461
Body length (m)	0.0836	0.0329	0.011	0.0192	0.1480	0.415	340.441

"Age" was not included at the 5 % level

b: mature females N=1,806

Independent variables	Coefficient		P value	95% confidence interval of B		Results of each model	
	B	SE		Lower bound	Upper bound	R square	F value
Constant	0.7191	0.5772	0.213	-0.4130	1.8512	-	-
Fetus length (cm)	0.0095	0.0006	0.000	0.0084	0.0106	0.335	910.562
Date (Dec. 1st=1)	0.0039	0.0009	0.000	0.0022	0.0057	0.351	487.957
Year (87/88=1)	-0.0208	0.0035	0.000	-0.0276	-0.0140	0.361	339.224
Diatom	0.0721	0.0213	0.001	0.0303	0.1140	0.365	259.064
Latitude (deg)	0.0254	0.0070	0.000	0.0117	0.0392	0.368	209.934
Body length	0.1037	0.0470	0.027	0.0115	0.1959	0.370	176.430
Stock (I=1,P=2)	-0.1329	0.0656	0.043	-0.2615	-0.0042	0.372	152.073

"Age" was not included

c: mature males "longitude" was substituted for "stock" N=2,883

Independent variables	Coefficient		P value	95% confidence interval of B		Results of each model	
	B	SE		Lower bound	Upper bound	R square	F value
Constant	0.1822	0.4461	0.683	-0.6925	1.0569	-	-
Date (Dec. 1st=1)	0.0157	0.0005	0.000	0.0147	0.0167	0.310	1297.054
Diatom	0.2053	0.0107	0.000	0.1844	0.2262	0.392	928.354
Longitude (deg E)	0.0029	0.0003	0.000	0.0022	0.0035	0.412	673.592
Year (87/88=1)	-0.0180	0.0028	0.000	-0.0234	-0.0125	0.420	520.271
Latitude (deg)	0.0189	0.0054	0.001	0.0082	0.0296	0.422	419.670
Body length (m)	0.0859	0.0326	0.008	0.0221	0.1498	0.423	351.609

"Age" was not included

d: pregnant females "longitude" was substituted for "stock" N=1,806

Independent variables	Coefficient		P value	95% confidence interval of B		Results of each model	
	B	SE		Lower bound	Upper bound	R square	F value
Constant	1.1846	0.5299	0.026	0.1453	2.2240	-	-
Fetus length (cm)	0.0095	0.0006	0.000	0.0084	0.0106	0.335	910.562
Date (Dec. 1st=1)	0.0044	0.0009	0.000	0.0028	0.0061	0.351	487.957
Year (87/88=1)	-0.0208	0.0035	0.000	-0.0276	-0.0140	0.361	339.224
Diatom	0.0765	0.0212	0.000	0.0348	0.1182	0.365	259.064
Latitude (deg)	0.0140	0.0042	0.001	0.0059	0.0222	0.368	209.934
Body length (m)	0.1145	0.0467	0.014	0.0228	0.2062	0.370	176.430

"Age" and "longitude" were not included

Table 4: Results of two multiple stepwise regression analyses with “body weight” and “sex” as a potential predictor variables.

a: “Stock” was used as an independent variable N=4,689

Independent variables	Coefficient		P value	95% confidence interval of B		Results of each model	
	B	SE		Lower bound	Upper bound	R square	F value
Constant	4.1586	0.3373	0.000	3.4973	4.8199	-	-
Date (Dec. 1st=1)	0.0107	0.0004	0.000	0.0098	0.0115	0.247	1535.272
Body weight (t)	0.4168	0.0153	0.000	0.3868	0.4467	0.329	1151.310
Diatom	0.1553	0.0094	0.000	0.1370	0.1737	0.395	1018.124
Body length (m)	-0.6641	0.0388	0.000	-0.7402	-0.5879	0.424	863.289
Latitude	0.0108	0.0040	0.007	0.0030	0.0185	0.449	763.012
Year (87/88=1)	-0.0190	0.0021	0.000	-0.0231	-0.0150	0.459	661.544
Fetus length (cm)	0.0034	0.0004	0.000	0.0026	0.0042	0.466	583.591
Sex (male=1, female=2)	0.2433	0.0285	0.000	0.1875	0.2991	0.474	527.246
Stock (I=1,P=2)	0.2330	0.0300	0.000	0.1742	0.2917	0.480	480.581
Age	-0.0043	0.0011	0.000	-0.0065	-0.0020	0.482	435.113

All independent variables were included as predictors

b: The variable “longitude” (in degrees east) was substituted for “stock” N=4,689

Independent variables	Coefficient		P value	95% confidence interval of B		Results of each model	
	B	SE		Lower bound	Upper bound	R square	F value
Constant	3.9736	0.3224	0.000	3.3416	4.6057	-	-
Date (Dec. 1st=1)	0.0100	0.0004	0.000	0.0092	0.0109	0.247	1535.272
Body weight (t)	0.4242	0.0152	0.000	0.3944	0.4540	0.329	1151.310
Diatom	0.1526	0.0093	0.000	0.1344	0.1708	0.395	1018.124
Body length (m)	-0.6674	0.0386	0.000	-0.7430	-0.5918	0.424	863.289
Longitude (deg E)	0.0030	0.0003	0.000	0.0025	0.0035	0.453	777.054
Sex (male=1, female=2)	0.2332	0.0281	0.000	0.1780	0.2883	0.467	684.774
Year (87/88=1)	-0.0187	0.0021	0.000	-0.0228	-0.0147	0.477	611.061
Fetus length (cm)	0.0033	0.0004	0.000	0.0025	0.0041	0.485	551.553
Age	-0.0050	0.0011	0.000	-0.0073	-0.0028	0.487	494.195
Latitude (deg)	0.0130	0.0034	0.000	0.0064	0.0196	0.489	447.547

All independent variables were included as predictors.

Table 5 Results of four multiple stepwise regression analyses with “dorsal blubber thickness” and “fat weight” as the dependent variable

a: “Dorsal blubber thickness” as the dependent variable was used with “stock” as a potential predictor variable. N = 734

Independent variables	Coefficient		P value	95% confidence interval of B		Results of each model	
	B	SE		Lower bound	Upper bound	R square	F value
Constant	2.5086	0.3158	0.000	1.8886	3.1285	-	-
Year (87/88=1)	-0.1226	0.0088	0.000	-0.1399	-0.1054	0.166	145.376
Date (Dec. 1st=1)	0.0097	0.0015	0.000	0.0067	0.0128	0.267	133.178
Body weight (t)	0.2321	0.0399	0.000	0.1537	0.3105	0.311	109.921
Fetus length (cm)	0.0064	0.0017	0.000	0.0030	0.0098	0.340	93.792
Stock (l=1,P=2)	0.3149	0.0967	0.001	0.1251	0.5048	0.353	79.570
Diatom	0.1410	0.0386	0.000	0.0652	0.2168	0.363	69.061
Sex (1=male, 2=female)	0.2335	0.1020	0.022	0.0333	0.4337	0.368	60.290

"Body length", "latitude", and "age" were not included

b: “Fat weight” used as the dependent variable. N=740

Independent variables	Coefficient		P value	95% confidence interval of B		Results of each model	
	B	SE		Lower bound	Upper bound	R square	F value
Constant	-3.3304	0.2942	0.000	-3.9081	-2.7528	-	-
Body length (m)	0.5201	0.0433	0.000	0.4351	0.6052	0.558	932.335
Date (Dec. 1st=1)	0.0045	0.0004	0.000	0.0036	0.0053	0.646	671.609
Sex (1=male, 2=female)	0.3025	0.0310	0.000	0.2417	0.3634	0.667	490.793
Lean body weight (t)	0.2282	0.0256	0.000	0.1779	0.2785	0.697	422.569
Fetus length (cm)	0.0020	0.0005	0.000	0.0010	0.0030	0.715	367.888
Year (87/88=1)	-0.0169	0.0025	0.000	-0.0219	-0.0119	0.727	324.588
Diatom	0.0543	0.0111	0.000	0.0324	0.0762	0.734	288.021
Age	0.0053	0.0013	0.000	0.0027	0.0078	0.740	260.370
Stock (l=1,P=2)	0.0757	0.0281	0.007	0.0205	0.1309	0.743	234.225

"Latitude" was not included.

c: “Dorsal blubber thickness” was used as the dependent variable, and “longitude” was substituted for “stock” as a possible predictor variable. N=734

Independent variables	Coefficient		P value	95% confidence interval of B		Results of each model	
	B	SE		Lower bound	Upper bound	R square	F value
Constant	3.0126	0.2771	0.000	2.4686	3.5565	-	-
Year (87/88=1)	-0.1196	0.0088	0.000	-0.1369	-0.1024	0.166	145.376
Date (Dec. 1st=1)	0.0099	0.0016	0.000	0.0068	0.0129	0.267	133.178
Body weight (t)	0.1946	0.0385	0.000	0.1190	0.2701	0.311	109.921
Fetus length (cm)	0.0070	0.0017	0.000	0.0036	0.0104	0.340	93.792
Diatom	0.1500	0.0388	0.000	0.0739	0.2261	0.350	78.529
Sex (1=male, 2=female)	0.3023	0.1004	0.003	0.1052	0.4994	0.358	67.677

"Body length", "latitude", "age" and "longitude" were not included.

d: “Fat weight” was used as the dependent variable. “Longitude” was substituted for “stock” as a potential predictor variable. N=740

Independent variables	Coefficient		P value	95% confidence interval of B		Results of each model	
	B	SE		Lower bound	Upper bound	R square	F value
Constant	-3.7713	0.3744	0.000	-4.5063	-3.0363	-	-
Body length (m)	0.5234	0.0434	0.000	0.4383	0.6085	0.558	932.335
Date (Dec. 1st=1)	0.0040	0.0005	0.000	0.0031	0.0050	0.646	671.609
Sex (1=male, 2=female)	0.2834	0.0335	0.000	0.2177	0.3491	0.667	490.793
Lean body weight (t)	0.2190	0.0250	0.000	0.1699	0.2681	0.697	422.569
Fetus length (cm)	0.0020	0.0005	0.000	0.0010	0.0029	0.715	367.888
Year (87/88=1)	-0.0167	0.0025	0.000	-0.0217	-0.0118	0.727	324.588
Diatom	0.0543	0.0112	0.000	0.0324	0.0762	0.734	288.021
Age	0.0055	0.0013	0.000	0.0030	0.0081	0.740	260.370
Latitude (deg)	0.0091	0.0038	0.017	0.0017	0.0166	0.742	233.582

“Longitude” was not included.

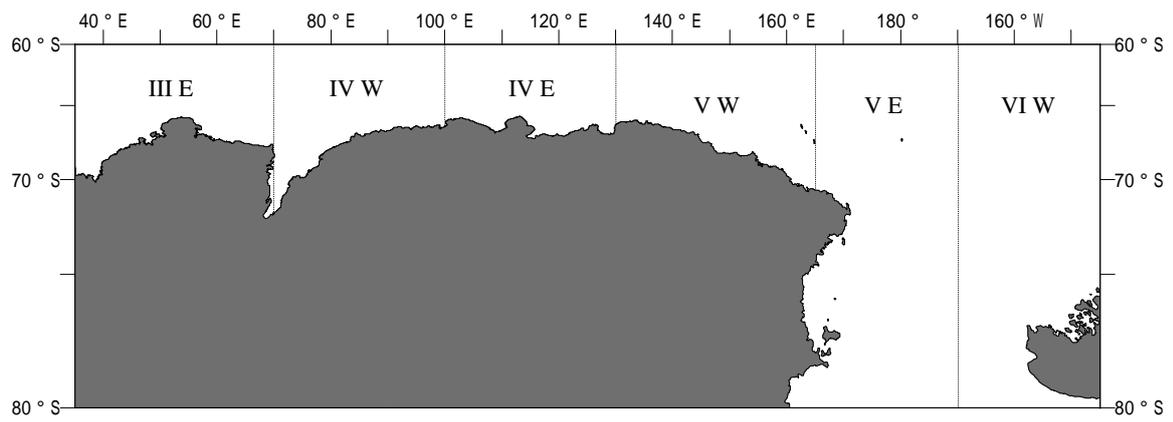


Fig. 1. Map of JARPA survey area (Areas III-East, IV, V, and VI-West).

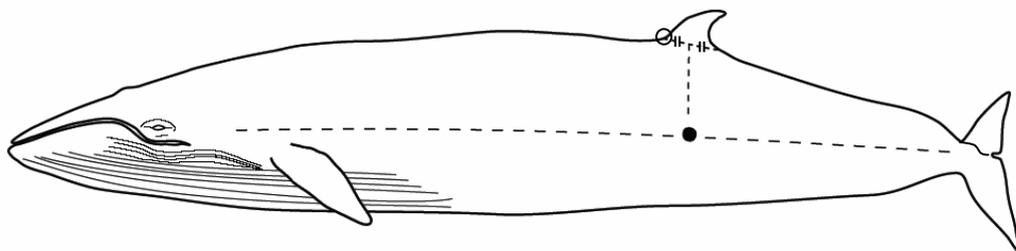


Fig. 2. Positions of blubber thickness measurement.
 Closed circle: lateral point, open circle: dorsal point at the anterior edge of the dorsal fin.