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Decrease in stomach contents in the Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean

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Abstract

The Antarctic minke whale (*Balaenoptera bonaerensis*) is one of the major krill predators in Antarctic waters. A reported decline in energy storage over almost two decades indicates that food availability for the whales may also have declined recently. To test this hypothesis, catch data from 20 survey years in the Japanese Whale Research Program in the Antarctic (JARPA) and its second phase (JARPA II) (1990/91-2009/10), which covered the longitudinal sector between 35°E and 145°W south of 58°S, were used to investigate whether there was any annual trend in the stomach contents of Antarctic minke whales. A linear mixed-effects analysis showed a 31% (95% CI 12.6%-45.3%) decrease in the weight of stomach contents over the 20 years since 1990/1991. A similar pattern of decrease was found in both males and females, except in the case of females sampled at higher latitude in the Ross Sea. These results suggest a decrease in the availability of krill for Antarctic minke whales in the lower latitudinal range of the research area. The results are consistent with the decline in energy storage reported previously. The decrease in krill availability could be due to environmental changes or to an increase in the abundance of other krill-feeding predators. The latter appears somewhat more likely, given the recent rapid recovery of humpback whale. Furthermore, humpback whales are not found in the Ross Sea, where both Antarctic krill and ice krill (*E. crystallorophias*) are available, and where no change in prey availability for Antarctic minke whales is indicated.

KEYWORDS: Minke whale. Feeding ecology. *Balaenoptera*. Ross Sea. Antarctic krill

Introduction

The Antarctic minke whale (*Balaenoptera bonaerensis*) is a relatively small baleen whale species, but a major component of the Southern Ocean ecosystem with an estimated abundance of over 500,000 the period 1992/93- 2003/04 (IWC 2012). The minke whale was not hunted until very near the end of the commercial whaling period because of its small size, while other baleen whales, such as the blue (*Balaenoptera musculus*), fin (*B. physalus*) and humpback whales (*Megaptera novaeangliae*), were heavily depleted in the nineteenth and twentieth centuries. Laws (1977) therefore hypothesized that the high population of minke whales in the 1980s was a response to the krill surplus resulting from the reduction of the large baleen whales by commercial whaling. This hypothesis is based on the concept of species interactions between krill predators, and has since been evaluated by modeling based on population dynamics (Mori and Butterworth 2006). Nevertheless considerable controversy remains about whether or not the large-scale removal of whales caused changes in the species composition of other krill consumers, with some authors supporting “bottom-up” (Ballance et al. 2006; Nicol et al. 2007; Trivelpiece et al. 2011) and others “top-down” control theories (see Laws 1977; Reid and Croxall 2001; Ainley et al. 2007)). According to the former, krill population dynamics and krill availability for predators are controlled by production at lower trophic levels and oceanographic conditions. The latter involve control by predation. Long time series of ecological and biological data for baleen whales are needed to answer questions about ecosystem change in the Southern Ocean.

Energy storage in minke whales has been declining over a period of almost two decades (Konishi et al. 2008), and the age at sexual maturity, which declined from the 1950s to the late 1960s, then remained constant or increased slightly up to the 1990s (Zenitani and Kato 2006). These findings could be signs of negative pressures on the Antarctic minke whale after the earlier increase in population. They indicate that food availability may have declined in recent decades. In order to test this hypothesis, we used a 20-year time series of data on stomach contents obtained by the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA) and its second phase (JARPA II).

Materials and Methods

Research area and period

JARPA was conducted during the austral summer seasons (December to March) from 1987/1988 to 2004/2005, while JARPA II started in the 2005/2006 season and is still continuing. Data used in the present study were collected between the 1990/91 and 2009/10 seasons. These long-term programs include whale sampling to study biological parameters concurrently with sighting surveys and oceanographic surveys for management and monitoring purposes (Government of Japan 2005). The research area for the research programs is the longitudinal sector between 35°E and 145°W, south of 60°S (and a few catches between 58°S and 60°S in JARPA). This sector includes the Management Areas IIIE, IV, V and VIW of the International Whaling Commission (Donovan 1991; Fig. 1). The Ross Sea is the highest-latitude part of the study area, between 170°E and 160°W and south of 70°S. It lies largely above the continental shelf and is shallower than 1000m.

Samples

Antarctic minke whales were randomly sampled along predetermined tracklines. Sampling was carried out from one hour after sunrise to one hour before sunset, but limited to a maximum of 12 hours per day. The sampling positions for the Antarctic minke whales used in this study are shown in Figure 1. The number of samples used in the present study is shown in Table 1 for each sex. Samples were taken in the Ross Sea every second year, and Table 2 indicates the years when samples were taken in lower and higher latitudinal areas. The search lines and the positions where whales were found indicate where krill was available (Online Resource 1).

Examination of stomach contents

All whales were dissected on board the research base vessel *Nisshin-Maru*. Stomach contents were removed from each compartment and weighed to the nearest 0.1kg, and some subsamples were collected for species identification. Details of the treatments of stomach contents were given in Tamura and Konishi (2009). Minke whales have a four-chambered stomach (Hosokawa and Kamiya 1971; Olsen et al. 1994), and the forestomach serves mainly as a food storage chamber, like the rumen in bovids (Olsen et al. 1994). For statistical analysis, we used the weight of the sieved contents of the forestomach as the weight of the stomach contents (kg: SCW) which is the most consistent measure throughout JARPA - JARPA II period, with the exception of the first three seasons (1987/88 - 1989/90), when forestomach contents were not weighed. Since whales were caught during the day, the diurnal feeding pattern had to be included in the models. The weight of stomach contents showed a decline from morning to evening in a previous study (Tamura and Konishi 2009).

Statistical analysis

We first performed regression analyses using the weight of the stomach contents as the dependent variable, and with a selection of possible explanatory variables. In studies of feeding ecology, information on empty stomachs is meaningful. However, zero-inflated datasets are a problem commonly encountered in ecological and biological analyses when the number of zero observations is so large that the data do not readily fit any standard statistical distribution (Martin et al. 2005). In JARPA and JARPA II surveys, 36% of all stomachs sampled were found to be empty (Table 1). We therefore re-analyzed the data using a two-step procedure (Fletcher et al. 2005; Stefansson 1996). First we used a method appropriate for binary data (empty = 0, containing prey =1; BI-SCW) to examine the occurrence of empty stomachs. The distribution of the weight of stomach contents in non-empty stomachs was positively skewed, with a long tail to higher weights. The weights were therefore log-transformed (log-SCW: only non-empty stomachs included) to examine quantitative trends using generalized linear models for data with an error distribution not too far from a normal distribution.

For these generalized linear models possible explanatory variables were “year” (1990/91 =1, 1991/92=2, 1992/93=3…), “date” (December 1st= day 1), “local time” (hour), “latitude” (degree) and “longitude” (in degrees east), “sex” (male=1 female=2) and “body length” (m). To check for non-linear dependence of the explanatory variables, the square of “date” and “local time” and the cube of “body length” were included in some models. “Local time” was included as one of the possible explanatory variables because the minke whale is known to have a daily feeding cycle (Tamura and Konishi 2009). This variable was not available in the data for the 1990/91 survey season, so the average values for “local time” from all other seasons were used in this year. In addition to using continuous variables, some variables were split into categories and included in regression analyses. For some of the analyses, “latitude” and “longitude” were divided into eleven categories, “local time” into five categories and “year” into separate categories for each survey year, to see if there were non-continuous effects of any of these explanatory variables.

An important assumption in fixed effects models is that data are independent. Since JARPA and JARPA II sampling surveys were conducted in each survey seasons in only a part of the total sampling area, this assumption may be violated, and the data matrix may contain spatio-temporal correlations because the environmental factors driving the results are correlated. The use of random effect models is one common and convenient way to model such data structure (Faraway 2006), and we therefore included some random effects by some of the categorical variables in our models.

For first analyses with BI-SCW as the dependent variable, we used a linear mixed-effects logistic model with a logit link function. In the main analyses with log-SCW as the dependent variable, we used a linear mixed effects model, and the estimation was effected using restricted maximum likelihood methods (REML) (Baayen et al. 2008). The continuous variable "year" was included in all models to examine the linear yearly trend in stomach contents. To compare models and determine the most plausible model, the Akaike's Information Criterion (AIC) was used and the three models with smallest AIC were chosen as plausible models. We ran the various regression models including and excluding explanatory variables from the simple basic model (LMER1; Online Resource 2) and used AIC to show differences from the basic model. Since inferences regarding the fixed-effect parameters are more complicated in a linear mixed-effects model (Baayen et al. 2008), we also applied the Markov chain Monte Carlo (MCMC) technique with 10000 resamplings to estimate confidence intervals and *p*-value for year effects for each model. The main analyses were conducted for both sexes combined and the best models were selected. To investigate possible correlation between years, the jack-knife method was applied in one of the best models by excluding data from one year at a time. To confirm the jack-knife results, track line as a grouping factor for random effects was added into one of the best models. The analyses were also carried out without data from the first year (when 'local time' was not available). None of these analyses changed the conclusions. Analyses were then performed for males and females separately without the "sex" variable, using the three best models identified from the analyses for both sexes combined. Because the distribution of females covered such a wide range of latitudes, extending as far south as the Ross Sea (Figure 1), data from females were analyzed separately for lower and higher latitude areas, with 70°S as the dividing line. For these analyses, "latitude" was divided into twenty categories. Because there were few males in the higher latitude area (Table 2), data from lower latitudes for both sexes were analyzed to see the results without any effect of higher latitude. To confirm the robustness of the year effect in the analyses with respect to the statistical assumptions, the best models in Log-SCW were also run using ranked SCW and the original nontransformed SCW datasets.

All statistical analyses were conducted in R environment version 2.13 (R development core team 2011) using package “lme4” version 0.999375-41 (Faraway 2006; Bates 2007), “languageR” version 1.2 (Baayen 2011) for mixed effects models and “LMERConvenientFunctions” (Tremblay 2011) for graph illustration.

Results

In the first step, a total of eleven mixed effect logistic regressions using BI-SCW data (Table 3) were used to analyze whether there was any time trend from year to year in the proportion of empty stomachs for the two sexes combined. No statistically significant estimates of the coefficient for “year” (year effect) were found in any of the regression analyses. The regression coefficients ranged from -0.0061 to 0.0009 per year. These results show that there was no trend in the proportion of empty stomachs in Antarctic minke whales through the survey period. The effect of “local time” was statistically significant in all runs with an increase in empty stomachs of about 2% per hour from dawn to dusk.

Since no trend in the proportion of empty stomachs was evident, log transformed data from non-empty stomachs (log-SCW) were used for next analyses. For the main analyses for the two sexes combined, we used 24 mixed effects models including the explanatory variables (see Online Resource 2). In all regression models, the year effects were similar and ranged from -0.026 to -0.018 per year. They were significant at the 5% level in all models (Online Resource 3). The year effects indicate that the stomach contents of Antarctic minke whales have decreased substantially with time. The model LMER24, including crossed random effects of “date^2” grouped by categorical variables “year” and “latitude”, and “date^2” grouped by categorical variables “longitude” and “year”, gave the smallest AIC, followed by models LMER16 and LMER23. The coefficients of “local time”, “sex” and “body length” in LMER24 were -0.115 per hour, -0.128 less for females than males, and 0.311 per meter, respectively, indicating that minke whales with food in their stomach have fed more early in the day, and that males and larger individuals feed more (Table 4). The scatterplot of standardized residuals in

LMER24 shows that the distribution is acceptable for a parametric approach (Figure 2). Although it is still somewhat skewed even after the log transformation, the distribution is not too far from normal.

To explore possible biases, we have run some additional checks. In the jack-knife analysis, the mean effect of ‘year’ for 20 runs was -0.020 (95% C I: -0.027 to -0.012), showing that the effect of ‘year’ is stable between years, which suggests that there was little correlation between years. Random effects of ’date’, ’latitude’ and ’longitude’ grouped by track line were added into LMER24, giving similar negative ‘year’ effects at the 5% significant level (random effects of ‘date’ -0.020, SE: 0.0062, ‘latitude’ -0.026, SE: 0.0073, ‘longitude’ -0.031, SE: 0.0070). When the best three models were fitted to the data set for lower latitudes only, the results were similar to those for the whole area (Online Resource 3). The LMER 24 was also fitted to the data set without data from the first year as a sensitivity test for missing ‘local time’ in the first year, giving results similar to those from all years (coefficient of -0.0246, $p < 0.001$). This model was also fitted to the total data set, including both empty stomachs and stomachs with contents. The results were a ‘year’ effect of -0.338 (SE: 0.057, $p < 0.0001$). These additional analyses all support the results of the mixed-effects models.

As the next step, the three best models (LMER16, 23 and 24) identified in the earlier set of analyses were applied separately to the male-only and female-only dataset (Online Resource 3). The year effects in males were similar in the three models, ranging from -0.0278 to -0.0270 per year, and were significant at the 5% level. This is of the same order as in the analyses for the two sexes combined, showing a clear decrease of stomach contents over time in males. However, the ‘year’ effects in females were not significant in the three models (Online Resource 3). Because the distribution of females covers a wider range of latitudes, an area effect (lower and higher latitude areas, north and south of 70°S) against ‘year’ was included in the three best models for the female-only dataset. In two of the models, the area effects were significant at the 5% level (Online Resource 3), showing that the ‘year’ effects differ between the two latitude areas. Then the analyses were performed for two datasets separately, that is for females at lower and higher latitudes (Online Resource 3). In the analyses for females at lower latitudes, the year effects ranged from -0.0236 to -0.0215, which is significant at the 5% level. In the analyses for females at higher latitudes (including the Ross Sea), the coefficients of “year” show a small positive slope with large *p*-values, which means that no time trend in stomach contents was found for females in this area (Online Resource 3).

Additional regression analyses using ranked SCW and the original (nontransformed) SCW were conducted as robustness trials. The results are shown in Table 5. All year effects are negative with a significance probability of less than 5% except in one case. These results add support to the main regression results, which use log-SCW as the dependent variable.

Discussion

All the main regression analyses for both sexes show that the year effects on the weight of stomach contents are negative, indicating that food intake by Antarctic minke whales has decreased over the 20-year period. Based on the best model, the rate of decrease in stomach contents is exp(-0.0194) or 1.96% pa and the average SCW of non-empty stomachs is 25.62 kg. We used this as the average value for SCW in the 10th year (1999/2000). SCW in the first and last years can then be calculated as 25.62*exp(-0.0194)^(-9) and 25.62*exp(0.0194)^(10). In this way, the decrease in stomach content weight through the whole survey period was found to be approximately 9.41 kg (95%CI 3.44-15.42), or 31% (95%CI 12.6-45.3) of the mean weight in the first year (which is estimated at 30.5 kg). This large decrease is consistent with the results of earlier studies on energy storage (Konishi et al. 2008) and age at maturity (Zenitani and Kato 2006). A possible explanation for the results of all three investigations is that prey availability for minke whales has decreased in recent decades. As a supplement to the analyses in Konishi et al. (2008), blubber thicknesses from their study were reanalyzed using a linear mixed-effects model to examine year effects as in the present investigation. The results showed a negative year trend similar to the values obtained by Konishi et al. (2008) (Skaug 2011).

In the logistic regression analyses using binary SCW, no time trend in the proportion of empty stomachs was observed. This indicates that the weight of the stomach contents is independent of the reason for empty forestomachs in minke whales. The occurrence of empty stomachs is probably related to the feeding behavior of minke whales. The Antarctic minke whale has a daily feeding cycle, feeding most actively in the morning, but with individual variation between whales (see Tamura and Konishi 2009), and this could explain the absence of food in the forestomachs at certain times of day. Furthermore, aggregation of Antarctic krill is not uniform in the study area (see Sara et al. 2002; Taki et al. 2008), and minke whales may therefore not feed while moving between krill aggregations. The time series appears to be consistent with this feeding pattern.

A reviewer has suggested that a harpooned whale might vomit part of its stomach contents if the kill is not instantaneous, and that this might bias the results of our analyses. Vomiting has never been observed in harpooned minke whales, even when there have been systematic observations since the first year of JARPA II to attempt to detect this. Nevertheless, to examine this possibility further, information on whether the kill was instantaneous or not (using the death criteria as agreed by the IWC) was added as a new binomial variable, and the best fitted model LMER 24 was run both with and without this variable. This information was not available for the first six years of JAPRA, so the two models were run for the last 15 years of JARPA and JARPA II only. During these years about 40% of the whales were killed instantaneously. Both models gave virtually the same rate of decline in stomach contents with year, which for both models was statistically highly significant. AIC increased when the instantaneous death variable was added to the models, and the coefficient for this new variable was very small and far from significant. These results are not consistent with the possibility of vomiting leading to a bias in our estimate of the rate of decline in stomach contents.

Year effects were negative in males and in females at lower latitudes, while no year effect was observed in females at higher latitudes, including the Ross Sea. This indicates that prey availability has decreased north of 70 °S, but not in the Ross Sea. This can be explained by the fact that different krill species are available in the southern Ross Sea and other areas, and by the overlap in distribution between minke whales and humpback whales. Minke whales have a sex-segregated distribution pattern, and pregnant females occur at high density in the Ross Sea (Kato et al. 1991; Ichii et al. 1998), especially above the continental shelf in areas shallower than 1000 m. In this area, ice krill *E. crystallorophias* is common and is the most important prey of the Antarctic minke whales (see Ichii et al. 1998; Tamura and Konishi 2009), while the Antarctic krill (Sala et al. 2002; Taki et al. 2008) is only occasionally found in this area. Ice krill probably functions as a stable prey species for minke whales, and its abundance shows no correlation with that of the Antarctic krill, which suggests that evidence of a decrease in krill availability would not be expected in this area. In contrast, the results here suggest that a decline in krill availability for minke whales has occurred in the main distribution area of Antarctic krill, north of the continental shelf. Humpback whales occur in the offshore area, with almost no observations south of 70°S in the study area (see Matsuoka et al. 2005; Matsuoka et al. in press), suggesting that interactions with the Antarctic minke whale are only likely north of 70°S. Fin whales also occur in the study area, but tend only to be present in small numbers in offshore waters (see Matsuoka et al. 2005). These possible interactions are described in more detail below.

A 31% reduction in food intake as measured by stomach content weight of the Antarctic minke whale over two decades needs to be taken into account in quantitative studies of the Antarctic ecosystem such as the modeling studies by Mori and Butterworth (2006) because the species is such an important consumer. Total consumption by minke whales in the feeding season was estimated at approximately 1.1 million tonnes in 2001/02 in IWC management area IV and 4.1 million tonnes in 2002/03 in area V, corresponding to the western part of this study area (Tamura and Konishi 2009), and annual consumption by mature animals was estimated at 35.5 million tonnes south of 60°S in the 1970s and 1980s (Armstrong and Siegfried 1991).

Possible changes in the abundance of minke whales, krill and other krill predators are important in any discussion of the reasons for the decrease in stomach contents in minke whales (Plagányi and Butterworth 2012). Intra-species interactions can reduce food availability per capita if minke whale abundance in the feeding areas is close to carrying capacity. However, the abundance of Antarctic minke whales in ice-free areas most likely decreased from the 1970s to the early 2000s (Branch and Butterworth 2001; IWC 2012) and age at sexual maturity stopped declining in the 1970s (Zenitani and Kato 2006), so that it is unlikely that the decline in krill availability was caused by intra-species interactions such as an increase in minke whale abundance in the study area. Two alternative hypotheses can be suggested to explain the decline in krill availability for minke whales, especially at the lower latitudes of the study area. The first is that krill availability for the Antarctic minke whales has changed in response to oceanographic and environmental changes. The oceanographic environment is an important factor for krill abundance and distribution (Sala et al. 2002). The most obvious changes around the Antarctic Peninsula are due to global warming (Meredith 2005): rising temperature and increasing current strength is resulting in a decrease in sea ice extent and duration, which causes low blooming success and a low density of krill (Loeb et al. 1997; Atkinson et al. 2004; Siegel 2005; Siegel and Loeb 1995; Trathan et al. 2003; Hunt and Hosie 2006; Nicol 2006). Scientific echo sounders were carried on board to collect data on krill abundance during JARPAII (Government of Japan 2005), but no results on trends in krill abundance are available from the study area at present. Changes in temperature, sea ice thickness and the extent and persistence of polynyas have been observed in the study area (see Ainley et al. 2010; Comiso et al. 2011), and these environmental changes could be affecting krill reproduction in the study area. Further information is needed to make projections of krill population trends.

A second hypothesis to explain the decrease in krill availability is interactions between krill predators. West of the Antarctic Peninsula, the recovery of baleen whale and fur seal populations is one of the reasons suggested for the decline in krill availability to penguins (Trivelpiece et al. 2011). Different studies indicate that the recovery of the populations of humpback, fin and blue whales started more than twenty years ago (Bannister 1994; Matsuoka et al. 2005; Branch 2006; Branch; 2007; Noad et al. 2011). In particular, the annual rate of increase in humpback whale abundance in Area IV has been over 12% during the JARPA survey period (1989/1990-2004/2005), and abundance was estimated at approximately 37000 whales in this area after 2000 (Matsuoka et al. in press). This is higher than the estimated minke whale biomass in Area IV (see Matsuoka et al. 2005; Matsuoka et al. in press). In the study area, the humpback whale feeds on the Antarctic krill (Mizue and Murata 1951; Kawamura 1978; Stone and Hamner 1988). The two whale species may have different spatial feeding patterns to avoid "direct" competition or maintain spatial niche separation (see Kasamatsu et al. 2000; Friedlaender et al. 2009; Santora et al. 2010). However, minke and humpback whale distributions overlap between 60 and 65°S (see Murase et al. 2002), suggesting that they share the same krill resources. Furthermore, humpback whale biomass was less than half of minke whale biomass in the early 1990s, but rose to more than twice total minke whale biomass by the early 2000s in Area IV (see Matsuoka et al. 2005). Thus, the rapid recovery of the humpback whale is likely to have reduced krill availability for the minke whale, although a decline in the krill population in response to environmental change may have accelerated the decline and thus its availability for the minke whale.

We have demonstrated consistent long-term changes in the nutritional status of the Antarctic minke whale in the JARPA research area. However, we need to be cautious in interpreting the scale and other details of the decline, because whales presumably change their feeding behavior in response to changes in food availability. For instance, whales are expected to compensate for lower food density by travelling further in search of food and more lunge feeding, but the latter has high energetic costs, especially in large whales (Acevedo-Gutiérrez et al. 2002; Goldbogen et al. 2006; Goldbogen et al. 2008). For a deeper understanding of minke whale feeding, we need to know whether and how minke whales have changed their distribution to adapt to the change in food availability. According to an ecosystem model developed on the assumption that krill predators compete, species other than baleen whales, such as crabeater seals (*Lobodon carcinophagus*), may play an important role (Mori and Butterworth 2006). Thus there is also a need to investigate how the other important krill predators interact with each other and with minke whales in order to gain a deeper understanding of the Antarctic minke whale's environment. If future studies provide this information, it may help to confirm or reject the krill surplus hypothesis put forward by Laws (1977). If the decrease in food availability for minke whales continues, the population will decline, partly as a result of the rise in age at sexual maturity. Thus, continuous monitoring of food availability as indicated by stomach contents and of energy storage in the form of blubber thickness can contribute important information for the management and conservation under the mandates of both the IWC and CCAMLR of the krill fishery and of the predators that depend on krill for food in the Southern Ocean. Such monitoring may also give information about the extent to which changes in abundance of krill are driven by top-down (consumption) compared to bottom-up (environmental) effects.

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Tables

Table 1

Data on body length and stomach contents used in the analyses.

Table 2

Average stomach content weight (kg) for non-empty stomachs and the number of samples from two latitudinal areas.

Table 3

Results of generalized logistic regression analyses with binary stomach content weight (BI-SCW) as the dependent variable. Data for both sexes were combined.

Table 4

The model evaluation with random and fixed effects for model LMER24.

Table 5

Results of linear mixed-effects models with ranked (Ranked SCW) and normal (SCW) stomach content weight.

Online Resource 1

Efforts of sighting and sampling vessels and position of the Antarctic minke whales with stomach contents caught in JARPA and JARPAII periods (1990/91-2009/10). Grey lines represent search lines and black circles represent sampling positions where whales were sampled.

Online Resource 2

List of linear mixed-effects models used in the main analyses with log-transformed stomach content weight (log SCW) as the dependent variable. The covariates in models were selected by an inclusion and exclusion process depending on whether the AIC value was smaller than in a previous model (Online Resource 3).

Online Resource 3

Results of linear mixed-effects models with log-transformed stomach content weight (log SCW) as the dependent variable. Results are shown for both sexes combined and for males and females separately. The female dataset was divided into two, for lower (<70°S) and higher (>70°S) latitude areas. The Markov chain Monte Carlo (MCMC) method was applied for each model to evaluate and estimate *p*-values. Delta-AIC = 0 for the minimum AIC in each group of results.

Figures

Figure 1

Map of the study area in the Pacific sector of the Southern Ocean for the 1990/91 to 2009/10 survey seasons. Dots show positions where Antarctic minke whales were sampled during JARPA and JARPA II (blue: male, red: female). The Ross Sea extends into the Antarctic from the Pacific Ocean and its northern limit is at approximately 70°S near Cape Adare. The dotted line shows the 1000m depth contour, which roughly indicates the border between the south continental shelf and offshore waters. The figure at the lower left is a large-scale map showing IWC Management Areas (Donovan 1991), and the black border shows the boundary of the study area.

Figure 2

Scatterplot of standardized residuals versus fitted values for the linear mixed-effects model LMER24.

Table 1 Data on body length and stomach contents used in the analyses.

		Body length (m)		Stomach content weight (kg)		
All whales		mean	SD	mean	SD	*N*
	male	7.96	0.96	17.23	29.55	4407
	female	8.20	1.20	15.68	30.17	4061
Whales without empty stomach						
	male	8.06	0.87	26.08	33.03	2912
	female	8.27	1.13	25.10	34.94	2537

Stomach contents = sieved stomach contents from forestomach

	Lower Latitude				Higher Latitude (>70° S)			
	Male		Female		Male		Female	
Survey Year	Average	N	Average	N	Average	N	Average	N
90/91	26.28	103	31.87	62	21.18	3	15.42	38
91/92	30.64	106	30.51	81				
92/93	37.43	90	33.15	70	21.16	14	17.08	32
93/94	36.62	148	29.35	82				
94/95	21.09	106	24.35	30	22.77	14	27.83	59
95/96	33.67	147	21.93	69				
96/97	26.29	95	30.14	76	40.53	13	36.18	58
97/98	31.62	176	28.27	83				
98/99	29.11	156	24.83	74		–		–
99/00	27.78	147	27.34	131				
00/01	21.32	146	23.1	59	19.8	19	18.81	57
01/02	27.49	137	17.38	151				
02/03	26.05	126	25.94	70	27.23	13	45.57	63
03/04	25.87	129	24.69	140				
04/05	18.07	88	18.64	61	30.06	19	21.03	80
05/06	21.48	274	23.17	219				
06/07	29.52	51	20.43	26	19.82	12	26.99	148
07/08	15.00	166	19.66	169				
08/09	16.32	207	19.55	96	31.22	50	27.58	91
09/10	29.74	157	24.69	162				

Table 3 Results of generalized logistic regression analyses with binary stomach content weight (BI-SCW) as the dependent variable. Data for both sexes were combined.

Models	AIC	Coefficient of Year: Year effect	SE	z-value	*P* value
BI-SCW1 = (Date|Latitude(c))+Year+Local Time+Sex+Body Length	10643	−0.0061	0.0043	−1.421	0.155
BI-SCW2 = (Date|Latitude(c))+Year+Local Time+Sex+Longitude(c)+Body Length	10631	−0.0059	0.0045	−1.305	0.192
BI-SCW3 = (Date|Latitude(c))+Year+Local Time+Sex+Latitude(c)+Body Length	10608	−0.0038	0.0044	−0.870	0.384
BI-SCW4 = (Date|Latitude(c))+Year+Local Time^2+Sex+Body Length+Latitude(c)	10619	−0.0034	0.0044	−0.775	0.438
BI-SCW5 = (Date|Latitude(c))+Year+Local Time+Sex+Body Length^3+Latitude(c)	10629	−0.0041	0.0044	−0.943	0.345
BI-SCW6 = (Date^2|Latitude(c))+Year+Local Time+Sex+Body Length+Latitude(c)	10608	−0.0038	0.0044	−0.870	0.384
BI-SCW7 = (Latitude|Date(c))+Year+Local Time+Sex+Body Length+Date^2+Latitude(c)	10608	−0.0036	0.0044	−0.822	0.411
BI-SCW8 = (Latitude|Date(c))+Year+Local Time+Sex+Body Length+Latitude(c)	10603	−0.0042	0.0044	−0.956	0.339
BI-SCW9 = (Date^2|Longitude(c):Year(c))+(Date^2−1|Year(c))+Year+Local Time+Sex+Body Length+Latitude(c)	10515	0.0009	0.0062	0.138	0.891
BI-SCW16 = (Date^2|Latitude(c):Longitude(c))+(Date^2−1|Longitude(c)11:Year(c))+Year+Local Time+Sex+Body Length+Latitude(c)	10524	−0.0038	0.0072	−0.530	0.596
BI-SCW17 = (Date^2|Latitude(c):Year(c))+(Date^2−1|Longitude(c):Year(c))+Year+Local Time+Sex+Body Length+Latitude(c)	10491	−0.0038	0.0073	−0.518	0.605

(A:B) means A grouped by B.
Variable name plus (c) means categorical variable
Left side of vertical bar '|' is fixed effect and right side grouping factor to which the random effect applies.
In mixed effects models (GLM3 and GLM4), the symbol ':' indicates a crossed random effect, which means grouping factors are crossed.

Table 4 The model evaluation with random and fixed effects for model 24.

Random effects:

Groups	Name	Variance	SD
Latitude(c):Year(c)	$Date^2$	5.95E−09	7.71E−05
Longitude(c):Year(c)	$Date^2$	4.29E−09	6.55E−05
Residual		2.6855	1.6388

Fixed effects

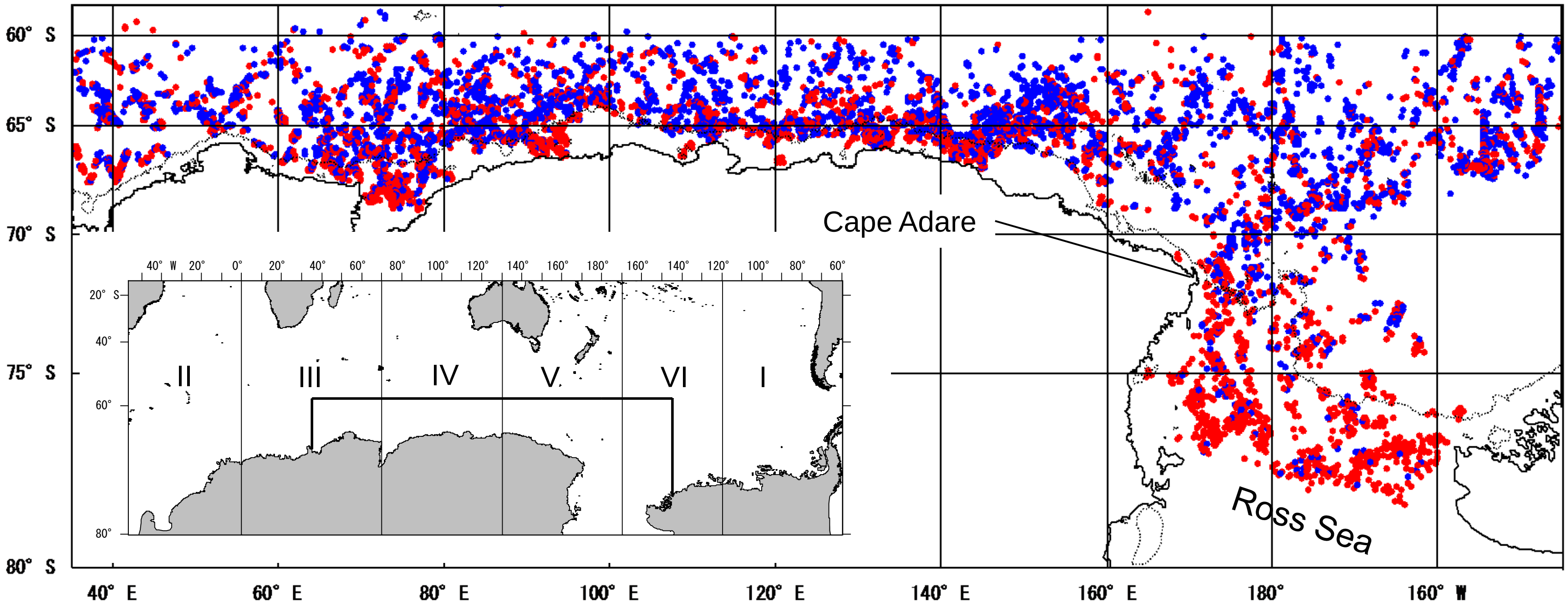
	Estimate	SE	t−value	pMCMC
(Intercept)	0.2969	0.4594	0.6460	0.5182
Year (1990/91 = 1)	−0.0194	0.0063	−3.0840	0.0021
Local time (h)	−0.1154	0.0064	−17.9730	0.0000
Sex (male=1, female=2)	−0.1279	0.0487	−2.6270	0.0086
Body length (m)	0.3112	0.0236	13.1970	0.0000

Variable name plus (c) means categorical variable.

Table 5 Results of linear mixed-effects models with ranked (Ranked SCW) and normal (SCW) stomach content weight.

	Model No.	Delta-AIC	Coefficient			MCMC			
			B	SE	t-value	MCMCmean	HPD95lower	HPD95upper	p by MCMC
Ranked-SCW	model16	23	−16.95	5.692	−2.978	−16.55	−28.085	−5.251	0.0062
	model23	21	−17.52	5.155	−3.398	−17.39	−27.390	−6.597	0.0006
	model24	0	−17.39	5.578	−3.118	−17.28	−27.990	−6.242	0.0016
SCW	model16	36	−0.227	0.124	−1.828	−0.222	−0.465	0.039	0.090
	model23	16	−0.280	0.110	−2.541	−0.267	−0.481	−0.041	0.020
	model24	0	−0.267	0.122	−2.193	−0.267	−0.508	−0.029	0.029

The Markov chain Monte Carlo (MCMC) technique was applied to each model to evaluate the year effect in the model.
Highest posterior density (HPD) interval is calculated for posterior value.



Cape Adare
Ross Sea
60° S
65° S
70° S
75° S
80° S
40° E
60° E
80° E
100° E
120° E
140° E
160° E
180°
160° W
II
III
IV
V
VI
I

Figure 1

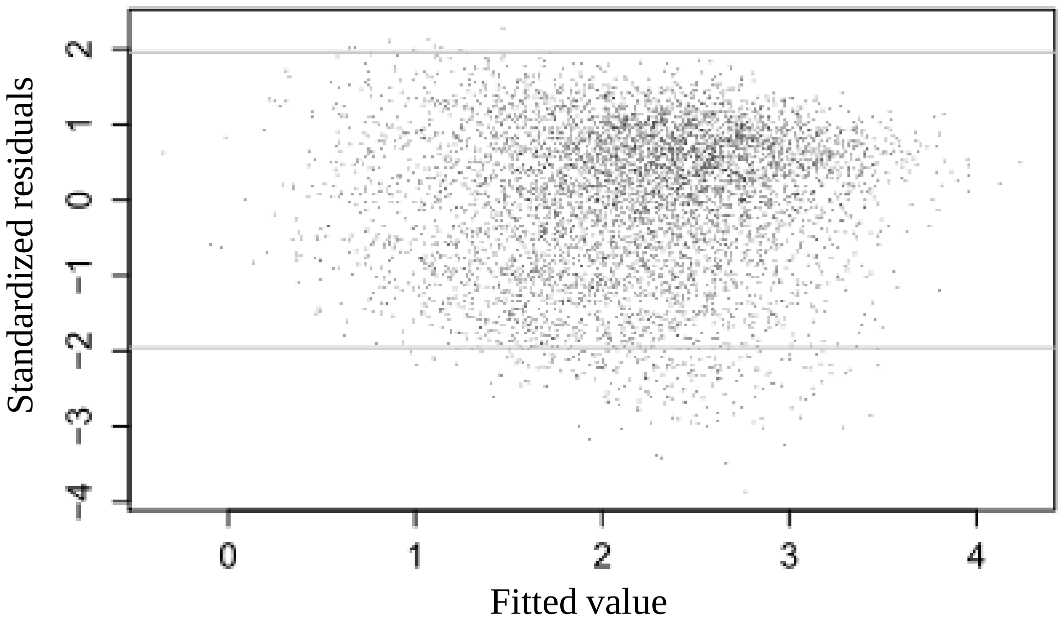


Figure 2

Decrease in stomach contents in the Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean. Polar Biology.

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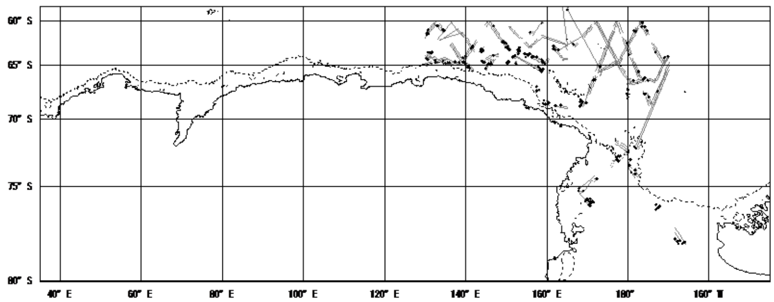
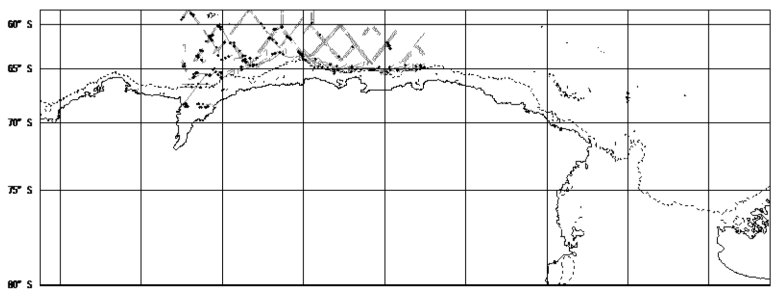
Online Resource 1

Efforts of sighting and sampling vessels and position of the Antarctic minke whales with stomach contents caught in JARPA and JARPAII periods (1990/91-2009/10).



1990/91



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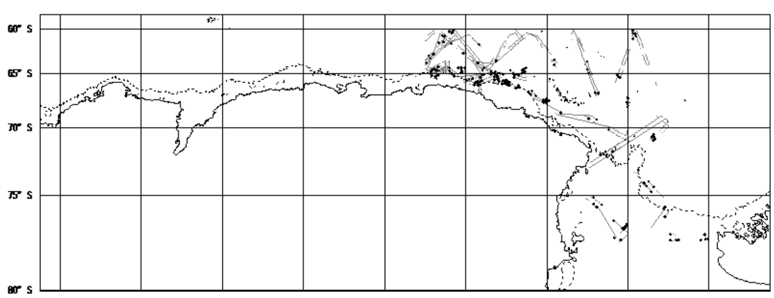

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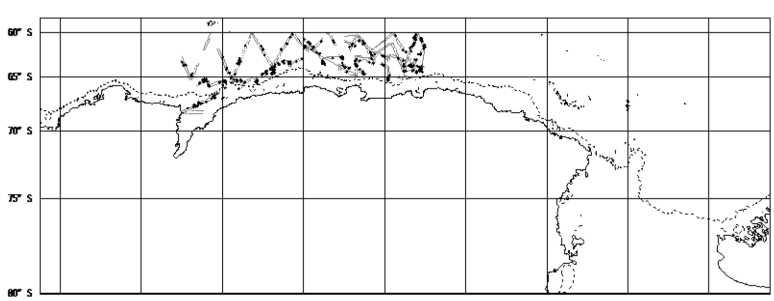
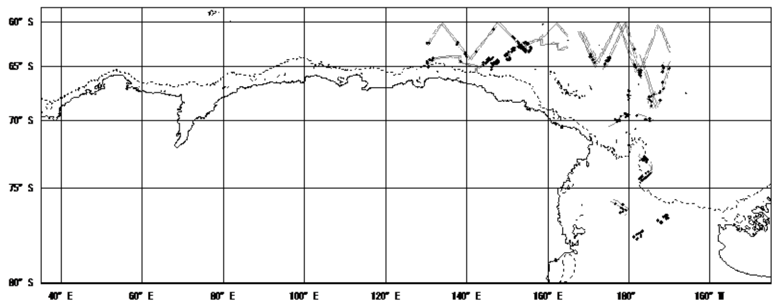
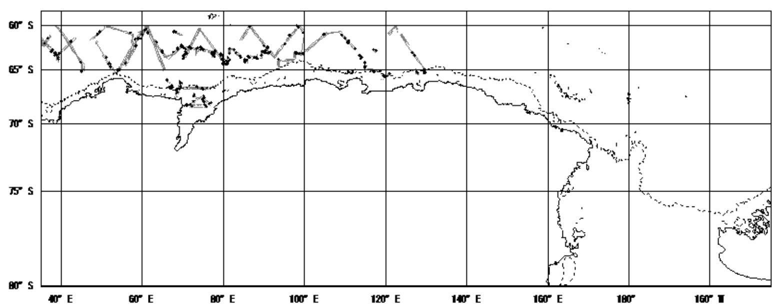


1993/94



1994/95



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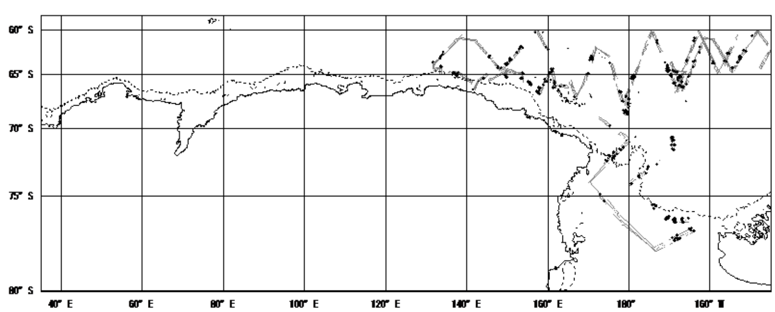

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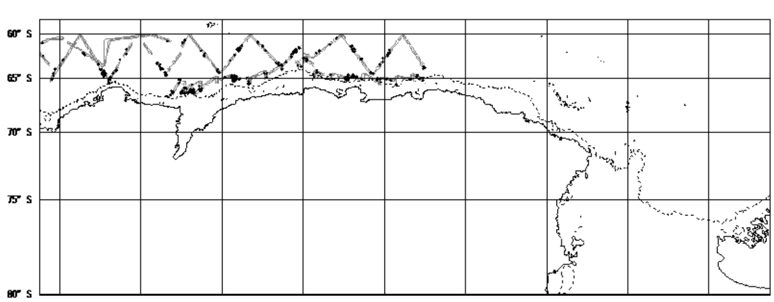

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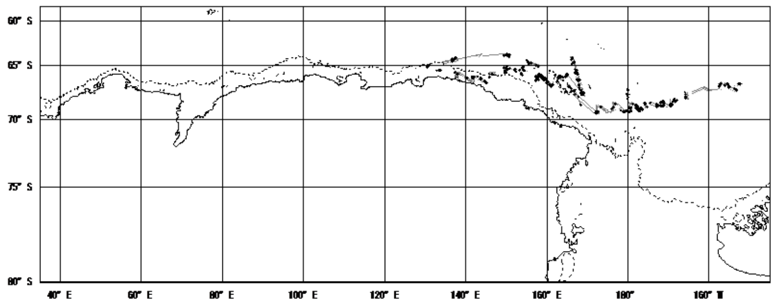

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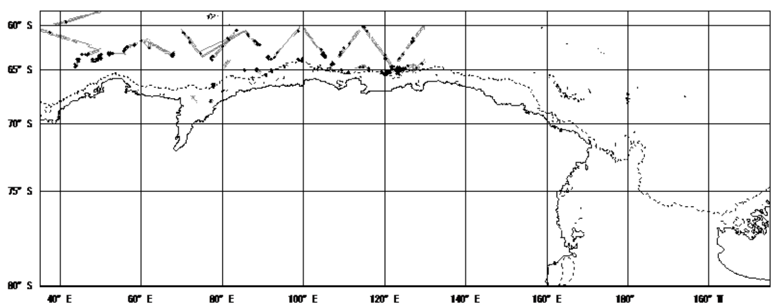

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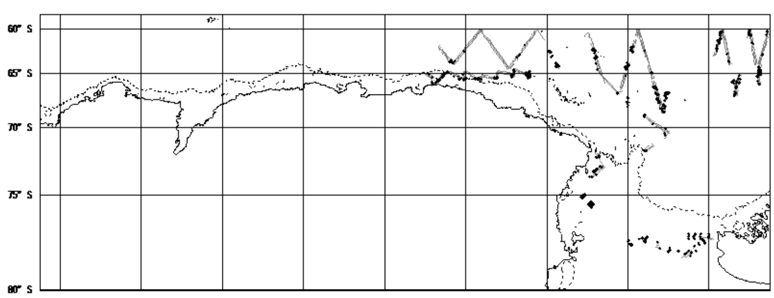

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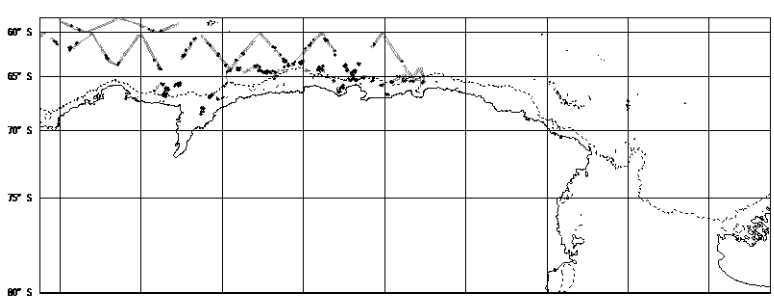

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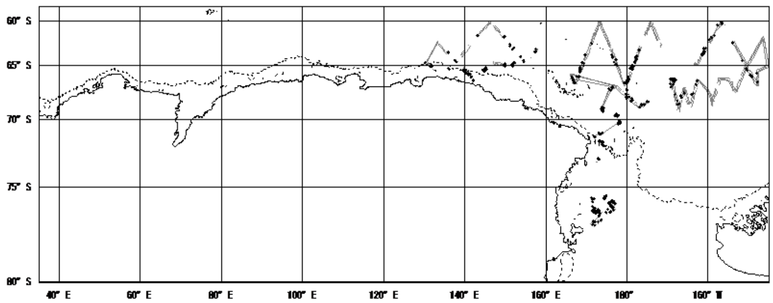

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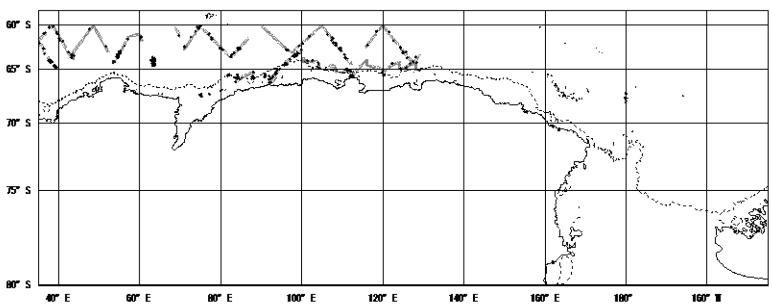

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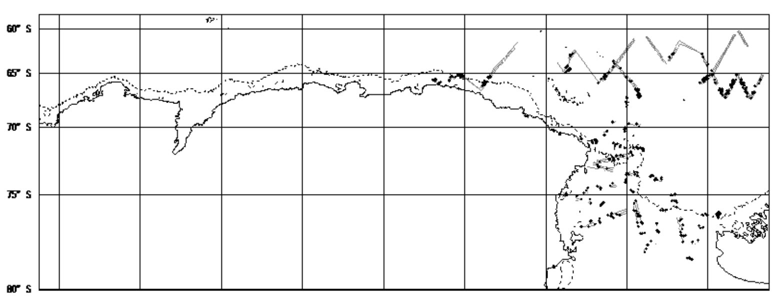

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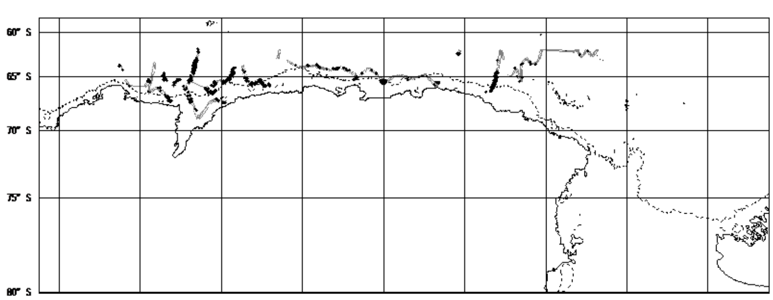

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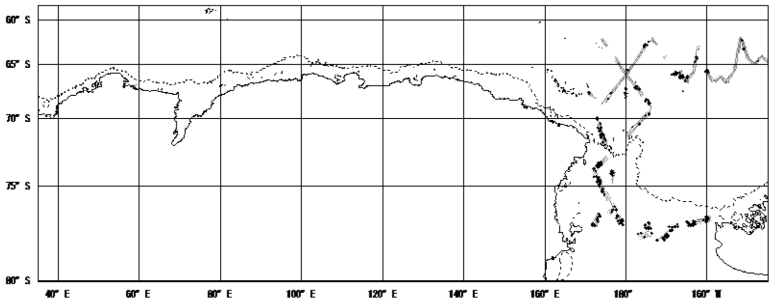

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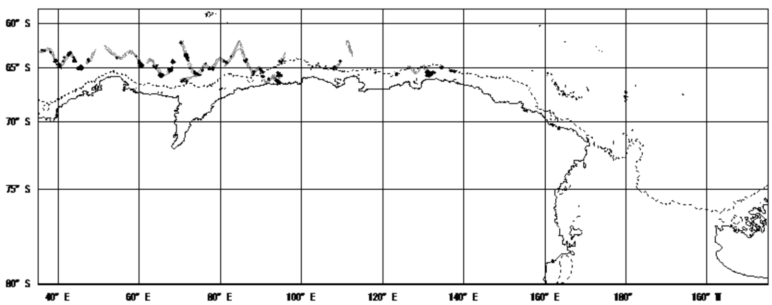

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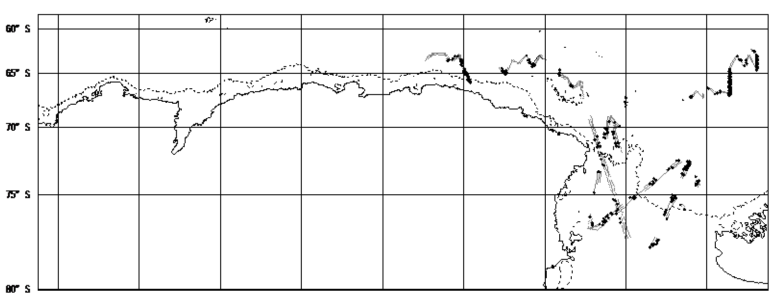

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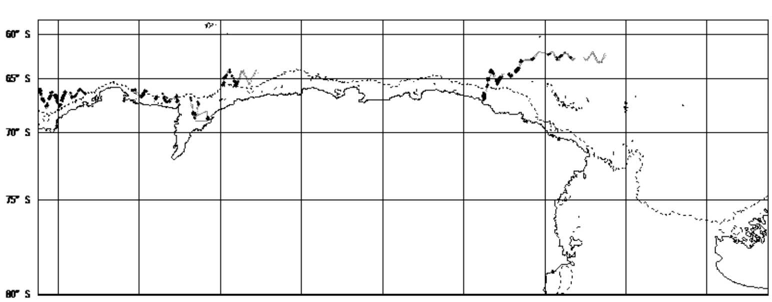

2009/10

Decrease in stomach contents in the Antarctic minke whale (Balaenoptera bonaerensis) in the Southern Ocean. Polar Biology.
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Online Resource2 List of linear mixed-effects models performed in main analyses with log-transformed stomach content weight (log SCW) as dependent variable.

Model No.	Models
LMER1	Log-SCW = (Date|Latitude(c))+Year+Local time+Sex+Body length
LMER2	Log-SCW = (Date|Latitude(c))+Year+Local time+Sex+Body length+Longitude(c)
LMER3	Log-SCW = (Date|Latitude(c))+Year+Local time+Sex+Body length+Latitude(c)
LMER4	Log-SCW = (Date|Latitude(c))+Year+Local time^2+Sex+Body length+Latitude(c)
LMER5	Log-SCW = (Date|Latitude(c))+Year+Local time+Sex+Body length^3+Latitude(c)
LMER6	Log-SCW = (Date^2|Latitude(c))+Year+Local time+Sex+Body length+Latitude(c)
LMER7	Log-SCW = (Latitude|Date(c))+Year+Local time+Sex+Body length+Latitude(c)+Date^2
LMER8	Log-SCW = (Latitude|Date(c))+Year+Local time+Sex+Body length+Latitude(c)
LMER9	Log-SCW = (Date^2|Longitude(c))+Year+Local time+Sex+Latitude(c)+Body length
LMER10	Log-SCW = (Date^2|Year(c))+Year+Local time+Sex+Longitude(c)+Latitude(c)+Body length
LMER11	Log-SCW = (Date^2|Latitude(c):Longitude(c))+Year+Local time+Sex+Body length
LMER12	Log-SCW = (Date^2|Latitude(c):Year(c))+Year+Local time+Sex+Body length
LMER13	Log-SCW = (Date^2|Longitude(c):Year(c))+Year+Local time+Sex+Body length
LMER14	Log-SCW = (Date^2|Latitude(c):Longitude(c))+(Date|Year(c))+Year+Local time+Sex+Body length
LMER15	Log-SCW = (Date^2|Latitude(c):Year(c))+(Date|Year(c))+Year+Local time+Sex+Body length
LMER16	Log-SCW = (Date^2|Longitude(c):Year(c))+(Date|Year(c))+Year+Local time+Sex+Body length
LMER17	Log-SCW = (Date^2|Latitude(c):Longitude(c))+(Latitude|Latitude(c))+Year+Local time+Sex+Body length
LMER18	Log-SCW = (Date^2|Latitude(c):Year(c))+(Latitude|Latitude(c))+Year+Local time+Sex+Body length
LMER19	Log-SCW = (Date^2|Longitude(c):Year(c))+(Latitude|Latitude(c))+Year+Local time+Sex+Body length
LMER20	Log-SCW = (Date^2|Latitude(c):Longitude(c))+(Latitude|Longitude(c))+Year+Local time+Sex+Body length
LMER21	Log-SCW = (Date^2|Latitude(c):Year(c))+(Latitude|Longitude(c))+Year+Local time+Sex+Body length
LMER22	Log-SCW = (Date^2|Longitude(c):Year(c))+(Latitude|Longitude(c))+Year+Local time+Sex+Body length
LMER23	Log-SCW = (Date^2|Latitude(c):Longitude(c))+(Date|Longitude(c):Year(c))+Year+Local time+Sex+Body length
LMER24	Log-SCW = (Date^2|Latitude(c):Year(c))+(Date^2|Longitude(c):Year(c))+Year+Local time+Sex+Body length

Variable name plus (c) means categorical variable.
Left side of vertical bar ‘|’ is random effect and right side grouping factor which the random effect applies.
The symbol ‘:’ indicates a crossed random effect, which means grouping factors are crossed.

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Online Resource3 Results of linear mixed-effects models with log-transformed stomach content weight (log SCW) as the dependent variable.

Sex combined			Delta-AIC	Coefficient			Markov chain Monte Carlo (MCMC) technique		
		Model No.		Year effect	SE	*t*.value	HPD95lower	HPD95upper	*P* by MCMC
		LMER1	155	−0.0264	0.00419	−6.296	−0.0346	−0.0182	0.0001
		LMER2	172	−0.0243	0.00443	−5.484	−0.0329	−0.0156	0.0001
		LMER3	147	−0.0246	0.00433	−5.679	−0.0330	−0.0161	0.0001
		LMER4	176	−0.0242	0.00434	−5.564	−0.0325	−0.0156	0.0001
		LMER5	168	−0.0250	0.00434	−5.762	−0.0337	−0.0168	0.0001
		LMER6	144	−0.0245	0.00434	−5.657	−0.0328	−0.0162	0.0001
		LMER7	172	−0.0248	0.00430	−5.758	−0.0330	−0.0163	0.0001
		LMER8	152	−0.0253	0.00429	−5.891	−0.0332	−0.0166	0.0001
		LMER9	132	−0.0253	0.00437	−5.382	−0.0332	−0.0166	0.0001
		LMER10	60	−0.0201	0.00634	−3.169	−0.0322	−0.0072	0.0022
		LMER11	105	−0.0217	0.00442	−4.916	−0.0301	−0.0127	0.0001
		LMER12	54	−0.0207	0.00586	−3.533	−0.0319	−0.0095	0.0002
		LMER13	21	−0.0204	0.00592	−3.451	−0.0315	−0.0082	0.0008
		LMER14	38	−0.0175	0.00635	−2.761	−0.0292	−0.004	0.0102
		LMER15	43	−0.0208	0.00647	−3.212	−0.0332	−0.0077	0.0012
		LMER16	**14**	**−0.0189**	**0.00647**	**−2.926**	**−0.0312**	**−0.0047**	**0.0078**
		LMER17	107	−0.0216	0.00443	−4.884	−0.0305	−0.0128	0.0001
		LMER18	56	−0.0207	0.00586	−3.526	−0.0319	−0.0087	0.0001
		LMER19	23	−0.0204	0.00592	−3.451	−0.0323	−0.0087	0.0014
		LMER20	106	−0.0206	0.00453	−4.545	−0.0296	−0.0118	0.0002
		LMER21	45	−0.0185	0.00608	−3.041	−0.0304	−0.0066	0.0022
		LMER22	21	−0.0196	0.00605	−3.233	−0.0311	−0.0073	0.0014
		LMER23	**17**	**−0.0198**	**0.00589**	**−3.355**	**−0.0317**	**−0.0084**	**0.0006**
		LMER24	**0**	**−0.0194**	**0.00628**	**−3.084**	**−0.0315**	**−0.0071**	**0.0022**
	Lower latitude								
		LMER16	0	−0.0203	0.00673	−3.012	−0.0335	−0.0069	0.0042
		LMER23	9	−0.0231	0.00589	−3.915	−0.0338	−0.0093	0.0012
		LMER24	5	−0.0221	0.00629	−3.506	−0.0345	−0.0097	0.0004
Male									
		LMER16	0	−0.0270	0.00793	−3.400	−0.0423	−0.0107	0.0012
		LMER23	6	−0.0274	0.00671	−4.079	−0.0409	−0.0135	0.0001
		LMER24	12	−0.0278	0.00708	−3.924	−0.0421	−0.0136	0.0001
Female									
		LMER16	0	−0.0136	0.00923	−1.471	−0.0316	0.0046	0.1528
		LMER23	11	−0.0132	0.00799	−1.657	−0.0298	0.0019	0.0826
		LMER24	13	−0.0147	0.00860	−1.708	−0.0310	0.0025	0.0870
	Higher latitude	LMER16	28	0.0288	0.02234	1.287	−0.0260	0.1289	0.1590
		LMER23	24	0.0382	0.02345	1.630	−0.0097	0.0922	0.0874
		LMER24	0	0.0392	0.02424	1.616	−0.0096	0.0961	0.1094
	Lower latitude	LMER16	0	−0.0215	0.00957	−2.244	−0.0407	−0.0025	0.0298
		LMER23	2	−0.0233	0.00880	−2.644	−0.0410	−0.0059	0.0116
		LMER24	2	−0.0236	0.00887	−2.664	−0.0415	−0.0056	0.0104

Bold type shows the three models with the lowest AIC values for both sexes combined. These models were run for separate male and female datasets.

The Markov chain Monte Carlo (MCMC) technique was applied to each model to evaluate the year effect in the model.

The female dataset was divided into two different latitudinal groups because of the wide latitudinal distribution of female whales (higher (Ross Sea) and lower latitudes, split at 70° S).

Highest posterior density (HPD) interval is calculated for posterior value.