Substantial decline in energy storage and stomach fullness in Antarctic minke whales (*Balaenoptera bonaerensis*) during the 1990s

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ABSTRACT

A substantial decline in energy storage in the Antarctic minke whale during the 18-year Japanese JARPA research programme (austral summers 1987/88–2004/05) was reported in 2008 (Konishi *et al.,* 2008). The statistical method used in the study was simple multiple linear regression. The results have since been thoroughly discussed by the Scientific Committee of the International Whaling Commission because of the potential importance of the findings. Some had suggested that the sampling heterogeneity in the JARPA data was so substantial that generalised linear models (GLMs) with interaction terms and random-effects terms should be explored. For the present article, five response variables related to energy storage and the variable 'stomach content weight' are systematically analysed using GLMs. For all five energy storage variables, the results show declines in the interval 3% to 9% over the JARPA period, all significantly different from zero at the 5% level, but no later decline. The weight of sieved stomach contents declined by 25% over the same period. The coefficients of the decline and the coefficients for most other independent variables were similar to values obtained by simple linear regression, but in some cases the standard errors were larger. The results indicate that important changes took place in the Antarctic ecosystem during the 1990s. It is hypothesised that the most important cause of the changes was the simultaneous increase in numbers of other krill feeders, especially humpback whales.

KEYWORDS: MINKE WHALES, ENERGY STORAGE, STOMACH FULLNESS, ECOSYSTEM CHANGES, JARPA, INTERSPECIES COMPETITION, ANTARCTIC

INTRODUCTION

Konishi *et al.* (2008) reported a substantial decline in energy storage in Antarctic minke whales sampled during the 18 years (1987/88–2004/05) of the Japanese Whale Research Programme under Special Permit in the Antarctic (JARPA). Sampling took place during the austral summer each year, typically from early December to late March, in the area 35°E to 145°W and south of 58°S. The western and eastern areas, split at 130°E, were surveyed in alternate years so that the entire 180° survey area was covered every two years. Three variables were used as proxies for energy storage: blubber thickness carefully measured at a mid-lateral point at the level of the dorsal fin; the half girth measured at the level of the umbilicus; and the total weight of the fat dissected from the whale (blubber + intestinal fat). Only data from sexually mature males and pregnant females were used in the investigation. Blubber thickness and girth data were available from about 4,700 whales, while fat weight was available only from the first whale caught each day, altogether 740 whales. Details on the sampling and measurement procedures are given in Konishi (2006) and Konishi *et al.* (2008) (see also Fig. 1).

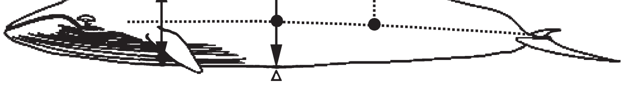

Fig. 1. Position of blubber thickness and half girth measurements. Closed circles = lateral points for blubber thickness measurements; open triangle = position of the umbilicus; arrows: half girth at the levels of the axilla and the umbilicus.

The analyses were carried out using stepwise linear regression (step forward procedure by Wald). The best model was selected using the Bayesian information criterion, BIC (Schwarz, 1978), even when the regression based on *p*-values included more independent variables. The main continuous independent variables were 'year' (1987/88 = year 1), 'body length' (m), 'date' (1 December = day 1), 'longitude' (in degrees east), 'latitude' (degrees) and 'diatom' (scale 1–5). The degree of diatom coverage is believed to be a measure of the time the whale has spent in cold water (Lockyer, 1981). The two sexes were analysed both separately and combined. When they were analysed in combination, 'sex' was used as a categorical variable. The regression analyses showed that blubber thickness, girth and fat weight had been decreasing over the JARPA period. The decrease per year was estimated at 0.02cm for mid-lateral blubber thickness and 17kg for fat weight, corresponding to about 9% for both measurements over the 18-year period. Furthermore, 'date', 'extent of diatom adhesion', 'body length', 'longitude', 'latitude' and 'sex' were identified as partially independent predictors of 'blubber thickness', 'girth' and 'fat weight' (see Konishi *et al.*, 2008).

At the 2011 meeting of the Scientific Committee of the IWC (International Whaling Commission), a paper was presented stating that the particular multiple regression model used by Konishi *et al.* (2008) might have been inappropriate (de la Mare, 2011) and suggesting that mixed-effects models should be fitted to the data to account for various forms of heterogeneity. In response (e.g. see discussions in IWC, 2012; 2013; 2014; 2015a), a large number of mixed-effects models

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were analysed. Two new dependent variables were added to these analyses; (1) 'blubber thickness' at another well-defined lateral point at the level of the umbilicus; and (2) 'half girth' at the level of the axilla.

Konishi *et al.* (2014) hypothesised that the decline in energy storage observed during the JARPA period might indicate that food availability had also declined. To test this hypothesis, the authors used catch data from the 15 years of JARPA during which forestomach contents were weighed and the first five years (2005/06–2009/10) of JARPA II in a linear mixed-effects analysis that showed a 31% decrease in sieved stomach content weight from the research catch of Antarctic minke whales between 1990/91 and 2009/10. Their analyses included 'Local time of day' as an additional explanatory variable because stomach fullness varies with time of day.

At the 2014 IWC Scientific Committee meeting, the model selection procedure used by Konishi *et al.* (2014) was also criticised (IWC, 2015a). The Committee agreed on the model selection procedure described below. These analyses were carried out and subsequently accepted by the Committee as final during the meeting (IWC, 2015b). In the present paper, these analyses have been repeated and extended somewhat. The authors considered this to be an important element of quality assurance for the analyses. However, the main results are unchanged from those presented to the Scientific Committee in 2014.

The energy storage variables have also been analysed for the first six years of JARPA II (2005/06–2010/11) and the results indicate no further decline during these years (Konishi and Walløe, 2014). The data on sieved stomach content weight have therefore also been reanalysed for the JARPA period only for the present paper. For this variable, preliminary analyses showed a small increase in the period 2005/06–2010/11. Thus all analyses described below were of data from the JARPA period only (Fig. 2).

METHODS

In addition to the six continuous response variables and the continuous explanatory variables mentioned above, a number of categorical variables, interaction terms and random-effects terms were used in the analyses. Table 1 contains a list of all response and explanatory variables.

Preliminary model runs with 'DateNum' as a quadratic term always gave a better model fit than the same models run with 'DateNum' as a linear term. Thus in the model runs explored in this article, 'DateNum' has always been used as a quadratic term. For other variables (e.g. 'YearNum', 'Diatom' and 'LtimeNum'), preliminary analyses indicated that linear terms were most appropriate.

The general advice for the exploration of general linear models with possible interaction and random-effects terms is to start from a 'full model' and then add and subtract interaction terms and random-effects terms in a systematic

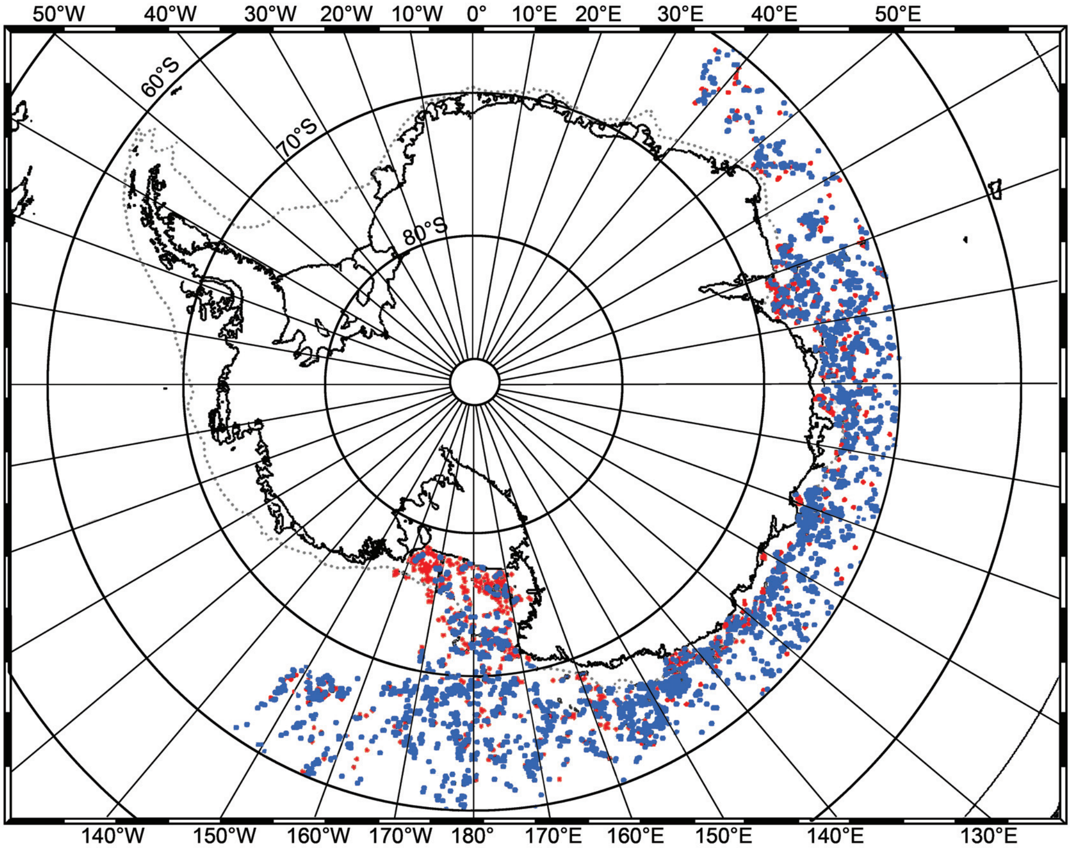

Fig. 2. Map of the Southern Ocean, modified from Konishi *et al.* (2014). The study area for the research programmes is the longitudinal sector between 35°E and 145°W in the Pacific and Indian Ocean sectors of the Southern Ocean. Dots show positions where the Antarctic minke whales used in this study were sampled during JARPA period (1987/88–2004/05) survey seasons (blue male, red female). The grey dotted line shows the 1,000m depth contour, which roughly indicates the edge of the continental shelf. The SCAR Antarctic Digital Database was used for the illustration of Antarctic coastline with extended ice shelves.

Table 1

Names of variables and terms used in the regression analyses.

Response variable (with sample size)	
BT11 (*n* = 4,727)	Blubber thickness at mid-lateral point on the vertical axis of the dorsal fin (in cm)
BT7 (*n* = 4,739)	Blubber thickness at a mid-lateral position on the vertical axis of the umbilicus (in cm)
UmbilicusGirth (*n* = 4,719)	Half girth at the level of the umbilicus (in cm)
AxillaryGirth (*n* = 3,870)	Half girth at the level of the axilla (in cm)
FatWeight (*n* = 738)	Weight of subcutaneous fat (blubber) + weight of intestinal fat (in metric tons)
FirstS (*n* = 3,622)	Sieved stomach content weight from forestomach (in kg)
Explanatory variable (continuous)	
YearNum	Year as a continuous variable (87/88 = year #1)
BLm	Body length (in m)
DateNum	Date number (1 December = day 1)
LongNum	Longitude in degrees E (170°W = 190°E)
LatNum	Latitude in degrees S
Diatom	Degree of diatom coverage (scale 1 to 5)
LtimeNum	Local time of day
Explanatory variable (categorical)	
YearCat	Year as a categorical variable (87/88 = reference level)
LatCat11	Latitude divided into 11 intervals
LongCat11	Longitude divided into 11 sectors
LonSect	Longitude divided into 6 IWC sectors (IIIE = reference level)
Ice	Categorical variable (near ice edge = 1, far from ice edge = 0)
TrackLine	Categorical variable, each straight part of a track line has a different name
Sex	Categorical variable for Sex (female = 0; male = 1)
Interaction and random effects	
YearNum:Sex	Interaction between YearNum and Sex
(1|YearCat)	Random effects of year on the model Intercept
(YearNum | Ice)	Random effects of YearNum partitioned by Ice
(DateNum^2|LonSect)	Random effects of DateNum^2 partitioned by LonSect
(DateNum^2|LatCat11)	Random effects of DateNum^2 partitioned by LatCat11
(DateNum^2|TrackLine)	Random effects of DateNum^2 partitioned by TrackLine

Table 2

Model selection with fat weight as the response variable during the JARPA period.

Model no.	BIC	Models
1	–283	Full.BC<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
2	–110	Full.BC.re1<–lmer(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LonSect))
3	–102	Full.BC.re2<–lmer(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LatCat11))
4	–135	Full.BC.re3<–lmer(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|TrackLine))
5	–114	Full.BC.re4<–lmer(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(YearNum|Ice))
6	–150	Full.BC.re5<–lmer(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat))
7	–278	Full.BC.1<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11)
8	**–332**	**Full.BC.2<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex)**
9	–290	Full.BC.3<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongCat11+Sex)
10	–290	Full.BC.4<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+LongCat11+Sex)
11	–239	Full.BC.5<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex)
12	–159	Full.BC.6<–lm(FatWeight~YearNum:Sex+BLm+Diatom+LatNum+LongNum+LongCat11+Sex)
13	165	Full.BC.7<–lm(FatWeight~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
14	–290	Full.BC.8<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
15	–326	Full.BC.2.1<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum)
16	–338	Full.BC.2.2<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+Sex)
17	–336	Full.BC.2.3<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+Sex)
18	–291	Full.BC.2.4<–lm(FatWeight~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex)
19	–203	Full.BC.2.5<–lm(FatWeight~YearNum:Sex+BLm+Diatom+LatNum+LongNum+Sex)
20	118	Full.BC.2.6<–lm(FatWeight~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+Sex)
21	**–338**	**Full.BC.2.7<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex)**
22	–302	Full.BC.2.7.1<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum)
23	**–344**	**Full.BC.2.7.2<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LatNum+Sex)**
24	–343	Full.BC.2.7.3<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LongNum+Sex)
25	–298	Full.BC.2.7.4<–lm(FatWeight~YearNum+BLm+DateNum^2+LatNum+LongNum+Sex)
26	–209	Full.BC.2.7.5<–lm(FatWeight~YearNum+BLm+Diatom+LatNum+LongNum+Sex)
27	112	Full.BC.2.7.6<–lm(FatWeight~YearNum+DateNum^2+Diatom+LatNum+LongNum+Sex)
28	–307	Full.BC.2.7.2.1<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+LatNum)
29	**–349**	**Full.BC.2.7.2.2<–lm(FatWeight~YearNum+BLm+DateNum^2+Diatom+Sex)##BESTMODEL**
30	–304	Full.BC.2.7.2.3<–lm(FatWeight~YearNum+BLm+DateNum^2+LatNum+Sex)
31	–214	Full.BC.2.7.2.4<–lm(FatWeight~YearNum+BLm+Diatom+LatNum+Sex)

manner (Zuur *et al.*, 2009). The authors tested a 'full model' with biologically plausible variables, including an interaction term. Five potential random-effects terms were then added, one at a time, including a random effect for year treated as a categorical variable. The random-effects term was included if the model run resulted in a lower BIC value than the 'full model'. Finally, the fixed effects, which did not contribute sufficiently to the model, were deleted based on BIC (IWC, 2015b). This is exactly the same procedure as that recommended by the JARPA II review panel (IWC, 2015a).

At each step the model selected should be the one which gives the lowest BIC value (Schwarz, 1978), formulated as:

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

where L is likelihood and K is the number of parameters. However for complex situations, such as the ones investigated here, even the choice of a 'full model' is difficult and the number of possible interaction terms is extremely large. The choices made were based on experience of the models published previously (Konishi *et al.*, 2014; Konishi *et al.*, 2008) and on discussions in the relevant IWC SC sub-committees during its 2014 meeting. Table 2 illustrates the

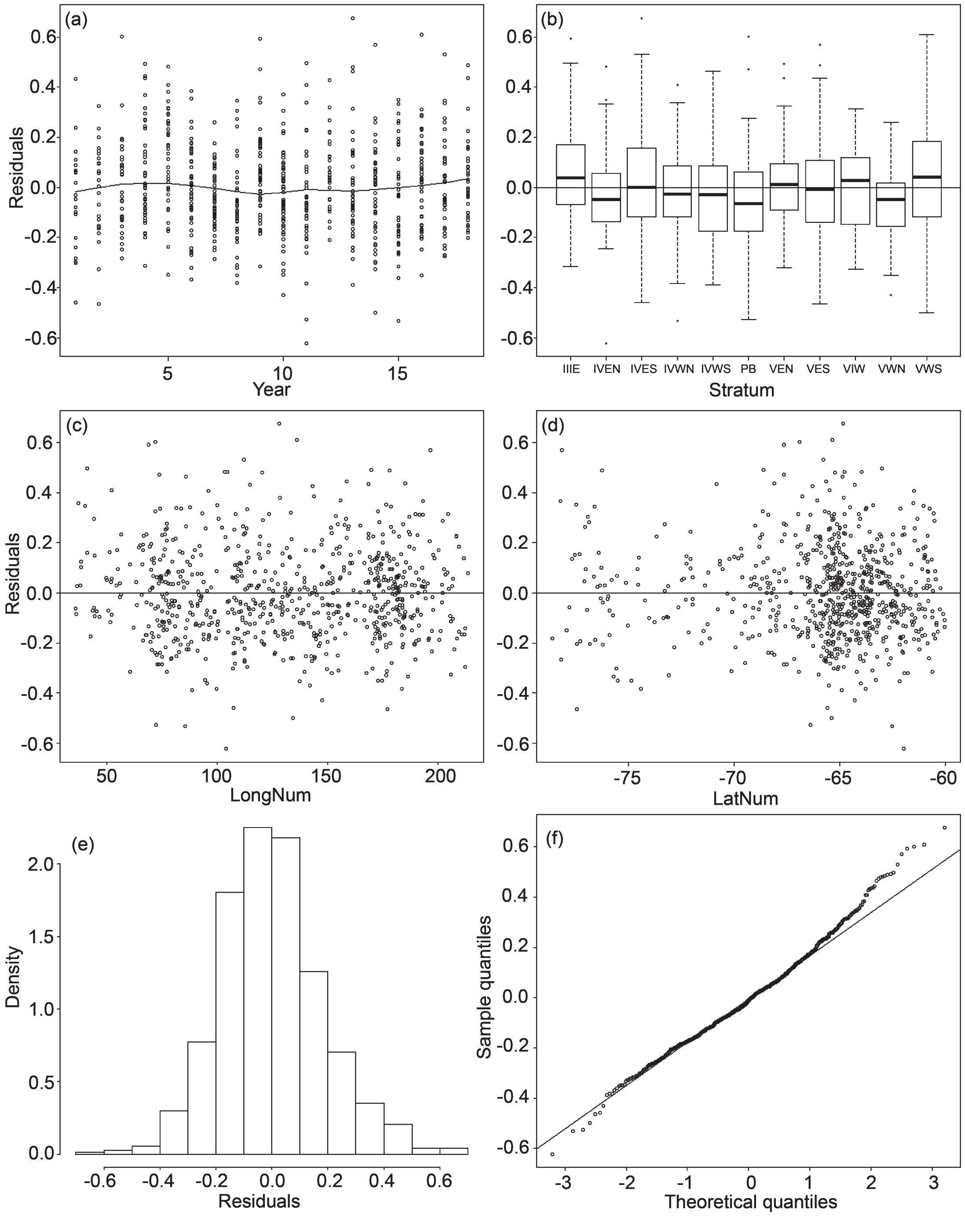

Fig. 3. Diagnostic plots for the best model with FatWeight as the response variable. (a) residual plots against year with spline curve; (b) residual box plots against Stratum from Indian Ocean to Pacific Ocean based on IWC defined areas (Donovan, 1991) with bearing small areas (N, S, E, W); (c) residual plots against longitude (degrees East: LongNum); (d) residual plots against latitude (degrees South: LatNum); (e) distribution of residuals in the best model; and (f) Q-Q plots for the best model.

Table 3

Summary for the best model using FatWeight as the response variable (Full.BC.2.7.2.2 in Table 2).

Coefficients	Estimate	Std. error	*t* value
(Intercept)	–2.1510	0.1494	–14.40
YearNum	–0.0083	0.0014	–5.87
BLm	0.4262	0.0166	25.65
DateNum^2	2.97E–05	2.17E–06	13.69
Diatom	0.0414	0.0058	7.12
Sex	–0.1365	0.0171	–7.99

systematic procedure in the simplest case of the six which were investigated. In this case the best model did not include any interaction terms or random-effects terms. Table 6 illustrates the procedure in one of the more complex of the six cases investigated. In this case, the best model included two random-effects terms.

The use of Maximum Likelihood (ML) or Restricted Maximum Likelihood (REML) can be explained as follows (see also Zuur *et al.*, 2009).

(1) Decide which random effects to include and fit the models using REML.

(2) Systematically try to eliminate some of the fixed effects then fit the models using ML.

(3) When the best model has been identified in step (2), fit it using REML.

The R-programs 3.0.2 (R Development Core Team, 2013) were used for all calculations and package ‘lme4’ version 1.0.4 (Bates *et al.*, 2014) was used for linear mixed-effects models.

RESULTS

Table 2 shows the model selection procedure for the dependent variable ‘FatWeight’. Model 1 shows the basic full model. Models 2–6 show the basic model with five different random-effects terms added one at a time. None of these models resulted in lower BIC values than the basic model. Thus none of these random effects were included in the final model. Models 7–31 show the systematic reduction of explanatory variables from the basic model (No 1). Model 29 gave the lowest BIC value. No further reduction in independent variables gave lower BIC values (not shown in the table). Table 3 presents the statistical parameters of this best model for ‘FatWeight’. It can be seen that the total weight of fat in the whales declined over the 18 JARPA years by 8.3 ± 1.4kg yr^{-1}. The weight of fat was 137 ± 17kg higher in females than in males. The weight of fat also increased with body length, with the date during the feeding season and with extent of diatom adhesion, which is believed to be a measure of the time the animal has spent in cold water. All the regression coefficients are statistically highly significant. Fig. 3 shows six diagnostic plots of the fit of this model.

Table 4 illustrates the model selection for blubber thickness at the mid-lateral point below the dorsal fin (BT11). Again, none of the models with random effects added (Models 2–6) resulted in lower BIC values than the basic model (No. 1). Systematic reduction of independent variables resulted in model 21, which gave the lowest BIC value and thus was considered to be the best fit. Table 5 shows the regression results for this model. The blubber thickness declined by 0.019 ± 0.002cm yr^{-1} over the JARPA period. Blubber thickness, like fat weight, was dependent on body length, extent of diatom adhesion, date during the feeding season and sex. In addition, blubber thickness increased from west to east and decreased from south to north. All coefficients are statistically highly significant. Fig. 4 shows six diagnostic plots for the model fit.

Table 6 illustrates the model selection for blubber thickness at the level of the umbilicus (BT7). When year was added to the basic model as a random categorical variable,

Table 4

Model selection with blubber thickness (BT11) as the response variable during the JARPA period.

<table>
<tr><th>Model no.</th><th>BIC</th><th>Models</th></tr>
<tr><td>1</td><td>10,794</td><td>Full.BC<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)</td></tr>
<tr><td>2</td><td>10,948</td><td>Full.BC.re1<–lmer(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LonSect))</td></tr>
<tr><td>3</td><td>10,920</td><td>Full.BC.re2<–lmer(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LatCat11))</td></tr>
<tr><td>4</td><td>10,816</td><td>Full.BC.re3<–lmer(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|TrackLine))</td></tr>
<tr><td>5</td><td>10,948</td><td>Full.BC.re4<–lmer(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(YearNum|Ice))</td></tr>
<tr><td>6</td><td>10,797</td><td>Full.BC.re5<–lmer(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat))</td></tr>
<tr><td>7</td><td>10,837</td><td>Full.BC.1<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11)</td></tr>
<tr><td>8</td><td>10,772</td><td>Full.BC.2<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex)</td></tr>
<tr><td>9</td><td>10,787</td><td>Full.BC.3<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongCat11+Sex)</td></tr>
<tr><td>10</td><td>10,801</td><td>Full.BC.4<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+LongCat11+Sex)</td></tr>
<tr><td>11</td><td>11,377</td><td>Full.BC.5<–lm(BT11~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex)</td></tr>
<tr><td>12</td><td>11,640</td><td>Full.BC.6<–lm(BT11~YearNum:Sex+BLm+Diatom+LatNum+LongNum+LongCat11+Sex)</td></tr>
<tr><td>13</td><td>10,803</td><td>Full.BC.7<–lm(BT11~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)</td></tr>
<tr><td>14</td><td>10,787</td><td>Full.BC.8<–lm(BT11~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)</td></tr>
<tr><td>15</td><td>10,821</td><td>Full.BC.2.1<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum)</td></tr>
<tr><td>16</td><td>10,817</td><td>Full.BC.2.2<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+Sex)</td></tr>
<tr><td>17</td><td>10,781</td><td>Full.BC.2.3<–lm(BT11~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+Sex)</td></tr>
<tr><td>18</td><td>11,367</td><td>Full.BC.2.4<–lm(BT11~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex)</td></tr>
<tr><td>19</td><td>11,756</td><td>Full.BC.2.5<–lm(BT11~YearNum:Sex+BLm+Diatom+LatNum+LongNum+Sex)</td></tr>
<tr><td>20</td><td>10,781</td><td>Full.BC.2.6<–lm(BT11~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+Sex)</td></tr>
<tr><td>21</td><td>10,767</td><td>Full.BC.2.7<–lm(BT11~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex)##BESTMODEL</td></tr>
</table>

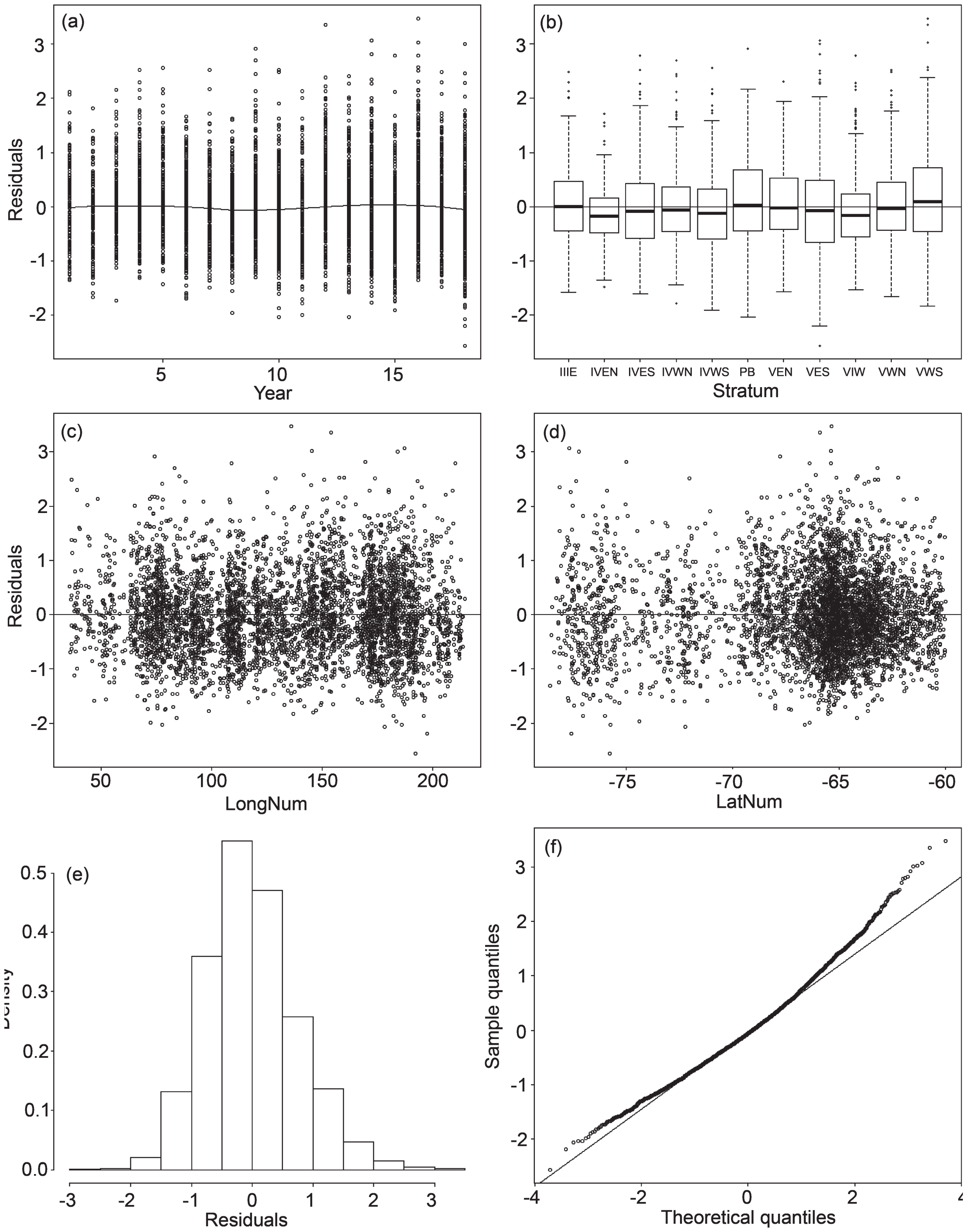

Fig. 4. Diagnostic plots for the best model with blubber thickness (BT11) as the response variable. For further explanation, see the caption for Fig. 3.

Table 5

Summary for the best model using blubber thickness (BT11) as the response variable (Full.BC.2.7 in Table 4).

Coefficients	Estimate	Std. error	*t* value
(Intercept)	0.9766	0.3481	2.81
YearNum	–0.0190	0.0022	–8.65
BLm	0.1142	0.0273	4.19
DateNum^2	0.0001	0.0000	33.19
Diatom	0.2281	0.0092	24.79
LatNum	–0.0151	0.0036	–4.14
LongNum	0.0021	0.0003	7.44
Sex	–0.3329	0.0297	–11.19

the BIC value decreased (Model 6). The next four model runs (7–10) show that another random effect should also be added. Systematic reduction of the linear terms in the basic model showed that model 28 resulted in the lowest BIC value. Table 7 shows the statistical parameters of the random and fixed effects. Blubber thickness at this lateral point declined by 0.015 ± 0.008cm yr^{-1}. This decline is only marginally significant at the 5% level. The other explanatory variables were roughly of the same magnitude as for the other blubber thickness variable, the only exception being that 'LongNum' was not included in the best model. All these variables were statistically highly significant. Fig. 5

Table 6

Model selection with blubber thickness (BT7) as the response variable during the JARPA period.

Model no.	BIC	Models
1	9,153	Full.BC<–lm(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
2	9,317	Full.BC.re1<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LonSect))
3	9,286	Full.BC.re2<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LatCat11))
4	9,222	Full.BC.re3<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|TrackLine))
5	9,316	Full.BC.re4<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(YearNum|Ice))
6	**9,149**	**Full.BC.re5<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat))**
7	9,174	Full.BC.re5.1<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|LonSect))
8	9,173	Full.BC.re5.2<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|LatCat11))
9	**9,135**	**Full.BC.re5.3<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine))**
10	9,174	Full.BC.re5.4<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(YearNum|Ice))
11	9,008	Full.BC.re5.3ML<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
12	9,093	Full.BC.re5.3ML.1<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
13	**8,954**	**Full.BC.re5.3ML.2<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)**
14	9,002	Full.BC.re5.3ML.3<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
15	9,043	Full.BC.re5.3ML.4<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
16	9,559	Full.BC.re5.3ML.5<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
17	9,313	Full.BC.re5.3ML.6<–lmer(BT7~YearNum:Sex+BLm+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
18	9,023	Full.BC.re5.3ML.7<–lmer(BT7~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
19	9,000	Full.BC.re5.3ML.8<–lmer(BT7~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
20	9,045	Full.BC.re5.3ML.2.1<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
21	8,948	Full.BC.re5.3ML.2.2<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
22	8,995	Full.BC.re5.3ML.2.3<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
23	9,508	Full.BC.re5.3ML.2.4<–lmer(BT7~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
24	9,283	Full.BC.re5.3ML.2.5<–lmer(BT7~YearNum:Sex+BLm+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
25	8,968	Full.BC.re5.3ML.2.6<–lmer(BT7~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
26	**8,946**	**Full.BC.re5.3ML.2.7<–lmer(BT7~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)**
27	9,233	Full.BC.re5.3ML.2.7.1<–lmer(BT7~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
28	**8,940**	**Full.BC.re5.3ML.2.7.2<–lmer(BT7~YearNum+BLm+DateNum^2+Diatom+LatNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)##BESTMODEL**
29	8,987	Full.BC.re5.3ML.2.7.3<–lmer(BT7~YearNum+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
30	9,500	Full.BC.re5.3ML.2.7.4<–lmer(BT7~YearNum+BLm+DateNum^2+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
31	9,274	Full.BC.re5.3ML.2.7.5<–lmer(BT7~YearNum+BLm++Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
32	8,961	Full.BC.re5.3ML.2.7.6<–lmer(BT7~YearNum+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)

shows the six diagnostic plots indicating that the model fit is good.

Table 8 illustrates the model selection for half girth at the level of the umbilicus. As for BT7, two random effects had to be added to the basic model (Model 9). Table 9 shows the regression coefficients for the best model. 'Half girth' declined by 0.406 ± 0.136cm yr^{-1} over the JARPA period, so that total girth declined by 0.81 cm yr^{-1}. The independent variables body length, extent of diatom adhesion, date during the feeding season and sex influenced girth in the same manner as they did the other dependent variables, but girth decreased from west to east. All coefficients were statistically different from zero. Fig. 6 shows the diagnostic plots.

Table 7

Summary for the best model using blubber thickness (BT7) as the response variable (Full.BC.re5.3ML.2.7.2 by REML in Table 6).

Random effects			
Groups	Name	Std. dev.	
TrackLine	(Intercept)	9.33E–02	
	DateNum^2	1.62E–05	
YearCat	(Intercept)	1.59E–01	
Residual		6.04E–01	
Fixed effects	Estimate	Std. error	*t* value
(Intercept)	0.7281	0.3268	2.23
YearNum	–0.0149	0.0076	–1.96
BLm	0.1049	0.0223	4.70
DateNum^2	0.0001	0.0000	23.83
Diatom	0.1831	0.0076	24.04
LatNum	–0.0277	0.0035	–7.82
Sex	–0.4345	0.0249	–17.45

The model with the lowest BIC value was selected at each step, even if the reduction in BIC was small. However, it may be argued that very small BIC differences have no real significance and that in such cases the simpler of the two models should be selected. The model selection for umbilicus half girth is one such case (Table 8). The introduction of the second random effect term (DateNum^2|TrackLine) in Model 9 results in only a slightly lower BIC value than that for Model 6, but Model 8 is more complex. Therefore, the consequences of using the simpler model as basis for further selection were explored. The coefficients for the fixed effects for the resulting final model were very close to the values listed in Table 9 (difference of less than 1%).

Table 10 illustrates the model selection for axillary half girth. For this model, there was only one random term involving year. Table 11 shows the estimated coefficients from the best model. Total girth declined by 0.90 cm yr^1 or 16cm over the JARPA period. The coefficients for the other explanatory variables had the same sign and were of similar magnitude to the coefficients for girth at the umbilicus. All

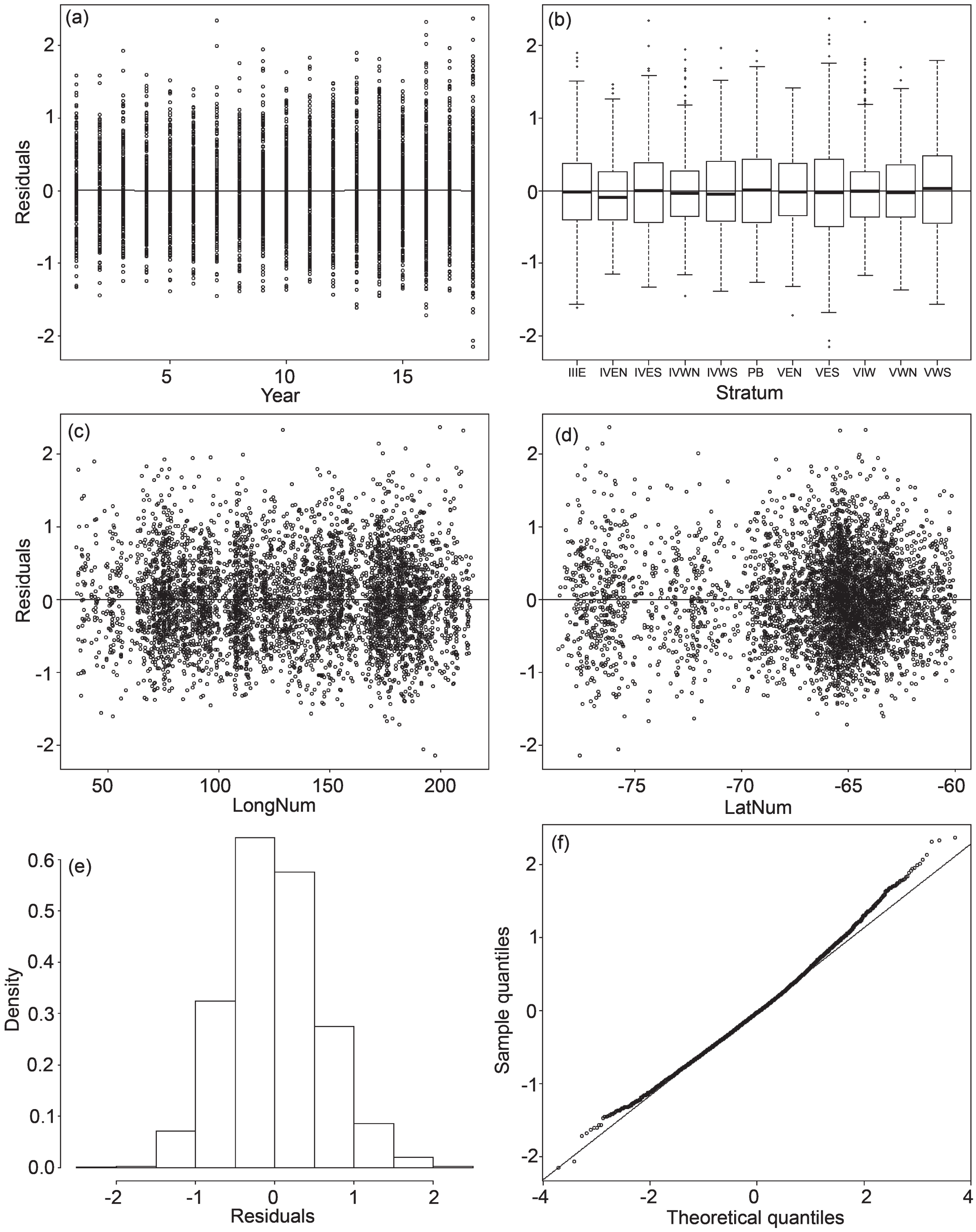

Fig. 5. Diagnostic plots for the best model with blubber thickness (BT7) as the response variable. Descriptions for each plot are same as written in the caption of Fig. 3.

coefficients were statistically different from zero. Fig. 7 shows the diagnostic plots.

Table 12 illustrates the model selection for the log-transformed weight of the sieved contents of the forestomach. Model 25 was the best model; it did not include any interaction terms or random-effects terms. Table 13 shows the regression coefficients for the best model. Stomach content weight decreased by 25% (95%CI 10–37%) over the JARPA period, excluding the first three years when the contents of the forestomach were not weighed. All the listed coefficients are statistically highly significant. Fig. 8 shows the diagnostic plots. Since the distribution of residuals showed a large deviation from a normal distribution, different transformations of the primary data were tested. To examine the effect of the skewness of the distribution of data for the log-transformed stomach content weight, these data were also Box-Cox transformed and model selection was conducted again. The selected best model was same as for log-transformed stomach content weight, showing a significant decline (Table 14 and Fig. 9). The Box-Cox transformed data showed an approximately symmetrical distribution, but with lighter tails than a normal distribution. Thus the real significance probabilities can be assumed to be smaller than the probabilities calculated from normal distributions.

DISCUSSION

The results show that all the five dependent variables related to energy storage declined substantially in Antarctic minke whales in the eastern (Pacific) half of the Antarctic Ocean

Table 8

Model selection with umbilicus half girth as the response variable during the JARPA period.

Model no.	BIC	Models
1	36,745	Full.BC<–lm(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
2	36,793	Full.BC.re1<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LonSect))
3	36,795	Full.BC.re2<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LatCat11))
4	36,711	Full.BC.re3<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|TrackLine))
5	36,797	Full.BC.re4<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(YearNum|Ice))
6	**36,651**	**Full.BC.re5<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat))**
7	36,665	Full.BC.re5.1<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|LonSect))
8	36,671	Full.BC.re5.2<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|LatCat11))
9	**36,647**	**Full.BC.re5.3<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine))**
10	36,676	Full.BC.re5.4<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(YearNum|Ice))
11	36,631	Full.BC.re5.3ML<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
12	36,641	Full.BC.re5.3ML.1<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
13	**36,575**	**Full.BC.re5.3ML.2<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)**
14	36,623	Full.BC.re5.3ML.3<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
15	36,629	Full.BC.re5.3ML.4<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
16	36,987	Full.BC.re5.3ML.5<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
17	36,846	Full.BC.re5.3ML.6<–lmer(UmbilicusGirth~YearNum:Sex+BLm+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
18	38,018	Full.BC.re5.3ML.7<–lmer(UmbilicusGirth~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
19	36,629	Full.BC.re5.3ML.8<–lmer(UmbilicusGirth~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
20	36,587	Full.BC.re5.3ML.2.1<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
21	36,593	Full.BC.re5.3ML.2.2<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
22	**36,574**	**Full.BC.re5.3ML.2.3<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)**
23	36,931	Full.BC.re5.3ML.2.4<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
24	36,795	Full.BC.re5.3ML.2.5<–lmer(UmbilicusGirth~YearNum:Sex+BLm+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
25	37,961	Full.BC.re5.3ML.2.6<–lmer(UmbilicusGirth~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
26	36,574	Full.BC.re5.3ML.2.7<–lmer(UmbilicusGirth~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
27	36,582	Full.BC.re5.3ML.2.3.1<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
28	36,605	Full.BC.re5.3ML.2.3.2<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+Diatom+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
29	36,933	Full.BC.re5.3ML.2.3.3<–lmer(UmbilicusGirth~YearNum:Sex+BLm+DateNum^2+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
30	36,794	Full.BC.re5.3ML.2.3.4<–lmer(UmbilicusGirth~YearNum:Sex+BLm+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
31	37,977	Full.BC.re5.3ML.2.3.5<–lmer(UmbilicusGirth~YearNum:Sex+DateNum^2+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)
32	**36,573**	**Full.BC.re5.3ML.2.3.6<–lmer(UmbilicusGirth~YearNum+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat)+(DateNum^2|TrackLine),REML=F)##BESTMODEL**

during the JARPA period (1987/88 to 2004/05). The variable fat weight is perhaps most directly related to energy storage, but was available for about 15% of the whales only. Its value is given by the sum of the weights of the intestinal fat and blubber in the animal. Naturally other parts of the whale body also contain fat, but intestinal fat and subcutaneous fat are the two fat stores which in most mammals increase during fattening and decrease during starvation (Christiansen *et al.*, 2013; Miller *et al.*, 2012; Miller *et al.*, 2011; Williams *et al.*, 2007). The results indicate that these two fat stores decreased by about 9% (95% CI 6%–12%) during the JARPA years. The decreases in this section were calculated as difference of estimated first and last year's value using mean value and the coefficients; see also the example in Konishi *et al.* (2014).

Table 9

Summary for the best model using umbilicus half girth as the response variable (Full.BC.re5.3ML.2.3.6 by REML in Table 8).

Random effects

Groups	Name	Std. dev.
TrackLine	(Intercept)	2.59E+00
	DateNum^2	1.05E–05
YearCat	(Intercept)	2.83E+00
Residual		1.13E+01

Number of obs: 4,711, groups: TrackLine, 720; YearCat, 18

Fixed effects	Estimate	Std. error	*t* value
(Intercept)	75.4200	4.2620	17.69
YearNum	–0.4059	0.1364	–2.98
BLm	17.0500	0.4203	40.57
DateNum^2	0.0012	0.0001	17.41
Diatom	2.4730	0.1430	17.29
LongNum	–0.0559	0.0088	–6.39
Sex	–1.5270	0.4448	–3.43

In most mammals, the thickness of subcutaneous fat in the middle part of the body is another good measure of energy storage. In whales, the girth is mainly a measure of the amount of blubber and intestinal fat, but it also depends on other anatomical factors, e.g. the size of the foetus in female whales. This applies particularly to the girth at the level of the umbilicus. Both blubber thickness measurements and both girth measurements declined during the JARPA period.

One difficulty involved in using all five variables as proxies for measurements of energy storage is that it is known that the fat content of fat tissue can vary. The measurements would have been easier to interpret if the percentage of fat in the tissues had also been measured. Analysis of a limited volume of data from JARPA showed a positive correlation between blubber thickness and lipid content (IWC, 2015a). Even though the fat content of the blubber tissue was not measured, the results for all five variables indicate an important negative trend in energy storage.

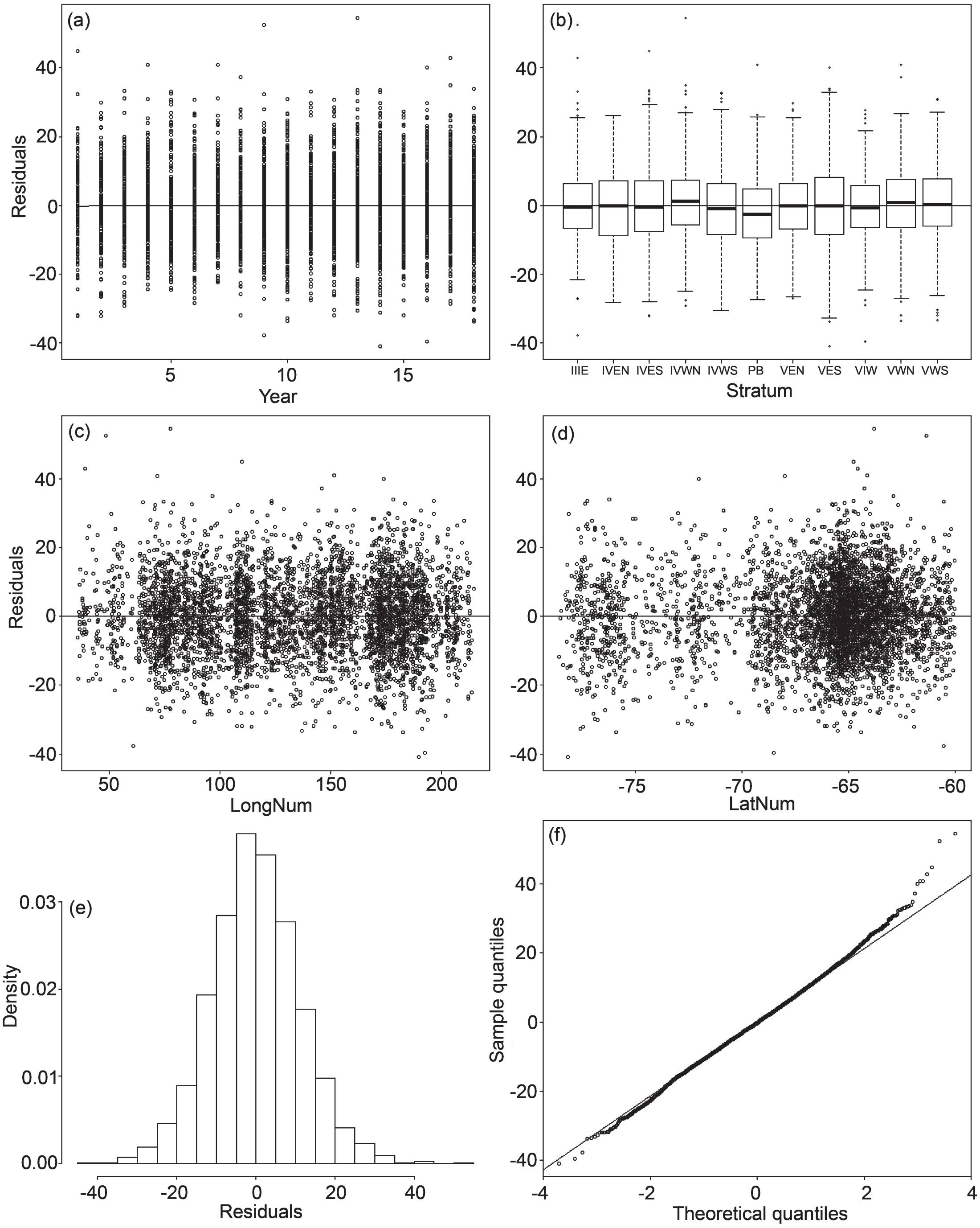

Fig. 6. Diagnostic plots for the best model with umbilicus half girth as the response variable. For further explanation, see the caption for Fig. 3.

The five variables were also significantly related to other independent variables. They all increased with extent of diatom adhesion, which is suggested to be a measure of how long an animal has spent in cold Antarctic waters (Lockyer, 1981). The five variables also increased with time during the feeding season and with body length. The energy stores in females were larger than in males. Other variables, such as longitude and latitude and random-effects variables, were included only in a few of the best models, and did not always have a consistent relationship with the different dependent variables.

The amount of food in the forestomach decreased during the day from the beginning to the end of the sampling period (a linear decrease on the log scale). Sampling started 1 hour after sunrise and ended 1 hour before sunset, but was limited to a maximum of 12 hours per day. On average, the weight of sieved food in the stomach declined during a 12-hour day from 57kg in the morning to 13kg in the evening, a decrease of 77%. An important implication of this finding is that the main feeding period for the Antarctic minke whale must be during the period from evening to early morning. The amount of food in the forestomach decreased substantially during the JARPA period, which indicates that food availability was decreasing and was the reason for the decline in energy storage.

None of five dependent variables showed any further decrease during the JARPA II years (2006/07–2011/12) (Konishi and Walløe, 2014, unpublished results for stomach

Table 10

Model selection with axillary half girth as the response variable during the JARPA period.

Model no.	BIC	Models
1	30,944	Full.BC<-lm(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex)
2	30,988	Full.BC.re1<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LonSect))
3	30,987	Full.BC.re2<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|LatCat11))
4	30,949	Full.BC.re3<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(DateNum^2|TrackLine))
5	30,983	Full.BC.re4<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(YearNum|Ice))
6	**30,907**	**Full.BC.re5<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat))**
11	30,894	Full.BC.re5ML<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
12	30,913	Full.BC.re5ML.1<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+(1|YearCat),REML=F)
13	**30,830**	**Full.BC.re5ML.2<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat),REML=F)**
14	30,886	Full.BC.re5ML.3<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongCat11+Sex+(1|YearCat),REML=F)
15	30,886	Full.BC.re5ML.4<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
16	30,991	Full.BC.re5ML.5<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
17	31,025	Full.BC.re5ML.6<-lmer(AxillaryGirth~YearNum:Sex+BLm+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
18	32,578	Full.BC.re5ML.7<-lmer(AxillaryGirth~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
19	30,888	Full.BC.re5ML.8<-lmer(AxillaryGirth~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+LongCat11+Sex+(1|YearCat),REML=F)
20	30,848	Full.BC.re5ML.2.1<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+LongNum+(1|YearCat),REML=F)
21	30,825	Full.BC.re5ML.2.2<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LatNum+Sex+(1|YearCat),REML=F)
22	**30,823**	**Full.BC.re5ML.2.3<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat),REML=F)**
23	30,930	Full.BC.re5ML.2.4<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex+(1|YearCat),REML=F)
24	30,995	Full.BC.re5ML.2.5<-lmer(AxillaryGirth~YearNum:Sex+BLm+Diatom+LatNum+LongNum+Sex+(1|YearCat),REML=F)
25	32,534	Full.BC.re5ML.2.6<-lmer(AxillaryGirth~YearNum:Sex+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat),REML=F)
26	30,824	Full.BC.re5ML.2.7<-lmer(AxillaryGirth~YearNum+BLm+DateNum^2+Diatom+LatNum+LongNum+Sex+(1|YearCat),REML=F)
27	30,840	Full.BC.re5ML.2.3.1<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+LongNum+(1|YearCat),REML=F)
28	30,820	Full.BC.re5ML.2.3.2<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+Diatom+Sex+(1|YearCat),REML=F)
29	30,922	Full.BC.re5ML.2.3.3<-lmer(AxillaryGirth~YearNum:Sex+BLm+DateNum^2+LongNum+Sex+(1|YearCat),REML=F)
30	31,001	Full.BC.re5ML.2.3.4<-lmer(AxillaryGirth~YearNum:Sex+BLm+Diatom+LongNum+Sex+(1|YearCat),REML=F)
31	32,542	Full.BC.re5ML.2.3.5<-lmer(AxillaryGirth~YearNum:Sex+DateNum^2+Diatom+LongNum+Sex+(1|YearCat),REML=F)
32	**30,817**	**Full.BC.re5ML.2.3.6<-lmer(AxillaryGirth~YearNum+BLm+DateNum^2+Diatom+LongNum+Sex+(1|YearCat),REML=F)##BESTMODEL**

contents). Fat weight was not measured regularly during JARPA II.

The results of sighting surveys indicate that the abundance of Antarctic minke whales in the Eastern Antarctic Ocean has either been constant or possibly declined somewhat during the JARPA years (Hakamada *et al.*, 2013; IWC, 2012, pp.35–39). The results presented here therefore indicate that major changes took place in the eastern Antarctic ecosystem during the 18 JARPA years that reduced the amount of krill available for Antarctic minke whales. Likely explanations could be either a gradual decrease in krill production due to environmental change (e.g. global warming) or increasing competition from other krill-feeding species. No good estimates of krill abundance are available (IWC, 2015a). Regarding other krill feeders, sighting surveys have shown that the abundance of large baleen whales increased substantially during the JARPA period e.g. blue (*B. musculus*) and southern right (*Eubalaena australis*) whales and especially humpback whales (*Megaptera novaeangliae*) (Branch *et al.*, 2004; Branch and Rademeyer, 2003; Matsuoka *et al.*, 2011). Thus it is possible that our results reflect the reverse of Laws' 'krill surplus hypothesis' (Laws, 1977). Although this hypothesis was not universally accepted, Laws claimed that during the first half of the twentieth century, when the large baleen whales were hunted down to low numbers, krill not eaten by these whales became available to Antarctic minke whales and other krill feeders (seals and birds), allowing their numbers to increase. Law's hypothesis presupposes that large baleen whales such as humpback and blue whales are more efficient krill feeders than Antarctic minke whales. Thus there is no contradiction between the increase in humpback whale abundance during the JARPA period and the simultaneous decline in minke whale energy storage, according to the Law's hypothesis.

Table 11

Summary for the best model using axillary half girth as the response variable (Full.BC.re5.3ML.2.3.6 by REML in Table 10).

Random effects			
Groups	Name	Std. dev.	
YearCat	(Intercept)	2.692	
Residual		12.824	
Number of obs: 3,868, groups: YearCat, 14			
Fixed effects	Estimate	Std. error	*t* value
(Intercept)	35.5500	5.3260	6.68
YearNum	–0.4499	0.1867	–2.41
BLm	24.1200	0.5174	46.62
DateNum^2	0.0009	0.0001	13.76
Diatom	1.6650	0.1732	9.62
LongNum	–0.0207	0.0087	–2.39
Sex	–5.2350	0.5251	–9.97

When deciding whether an environmental change or interspecies competition is the explanation for the decline in energy storage in Antarctic minke whales during JARPA period, observations on the stomach content weight of animals taken in the Ross Sea appear to be important. The krill species found above the continental shelf of the Ross Sea (*Euphausia crystallorophias*) is different from the species that lives in the rest of the Antarctic Ocean (*E. superba*). Antarctic minke whales enter the Ross Sea and

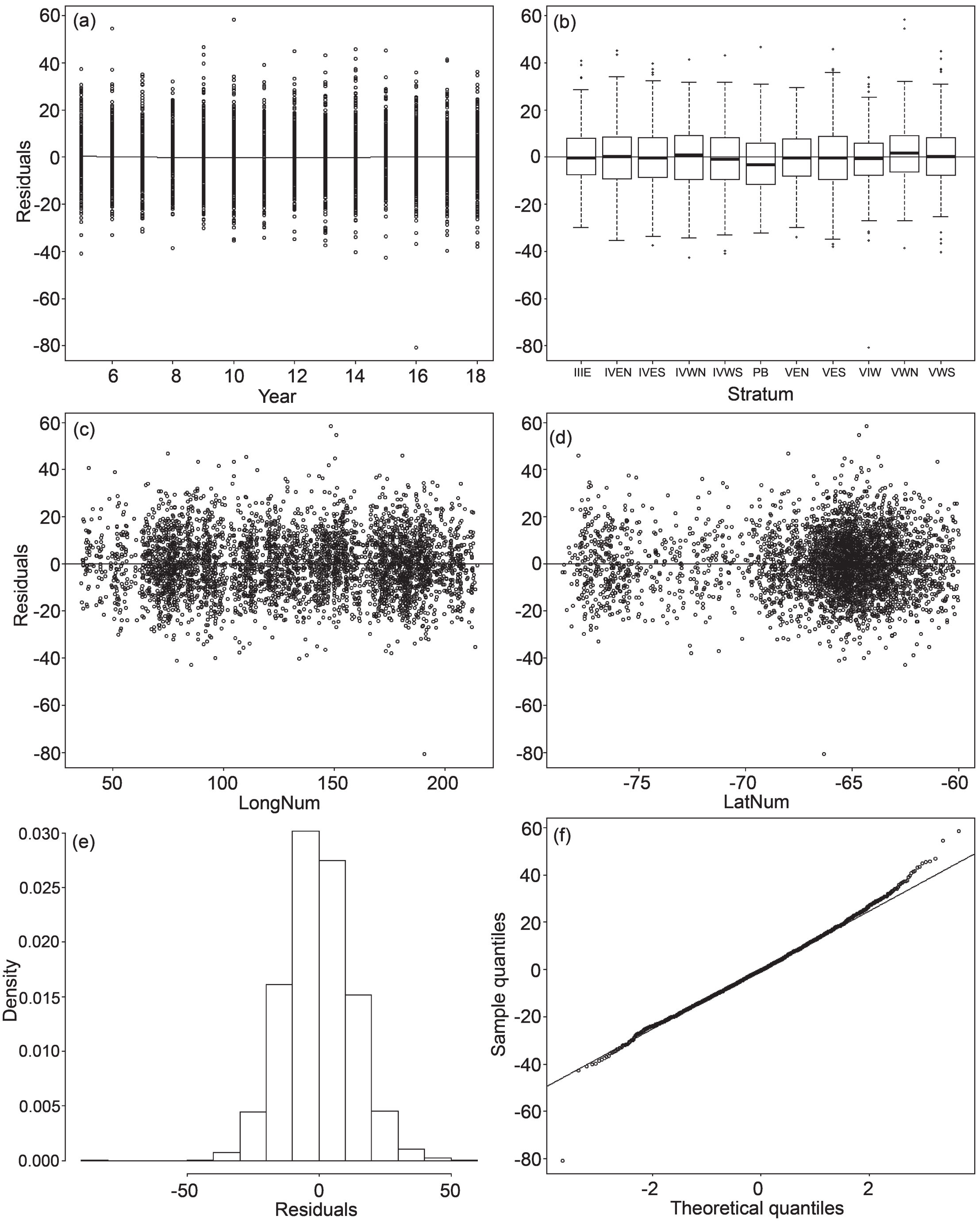

Fig. 7. Diagnostic plots for the best model with axillary half girth as the response variable. For further explanation, see the caption for Fig. 3.

feed on *E. crystallorophias*, whereas humpback whales do not. Thus, there should be no competition between humpback and Antarctic minke whales for *E. crystallorophias* in the Ross Sea. This fits well with the observation that the stomach content weight of whales caught in the Ross Sea did not decline over the JARPA years, in contrast to the decline in the rest of the survey area. For more details on the interpretation of these results, see Konishi *et al.* (2014).

The primary observations for the present investigation were not obtained according to the strict rules laid down originally by Ronald Fisher for experimental design in agricultural research (Fisher, 1935). The deviations are of course explained by the logistics of research vessel movements. Similar logistical limitations are often found in series of observations obtained in environmental and medical epidemiological research, making the exploration of possible models and the corresponding statistical analyses a challenging process. Until quite recently, common practice in such situations was to apply linear regression or analysis of variance, not only to the total available dataset but also to a large number of different subsets of the total material. If all the analyses gave approximately the same results, those results were accepted. The present authors used this approach in the analyses of blubber thickness, girth and fat weight reported in 2008 (Konishi *et al.*, 2008). Today, faster computers and efficient software make it possible to explore a large number of different models, including models with

Table 12

Model selection with sieved stomach content weight as the response variable during the JARPA period.

Model no.	BIC	Models
1	14,041	Full.SCW<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum) #Fullmodel
2	14,163	Full.SCW.re1<–lmer(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum+(DateNum|LonSect))
3	14,149	Full.SCW.re2<–lmer(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum+(DateNum|LatCat11))
4	14,158	Full.SCW.re3<–lmer(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum+(YearNum|Ice))
5	14,084	Full.SCW.re4<–lmer(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum+(1|Year))
6	14,287	Full.SCW.1<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex)
7	14,034	Full.SCW.2<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+LtimeNum)
8	13,985	Full.SCW.3<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+Sex+LtimeNum)
9	14,033	Full.SCW.4<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongCat11+Sex+LtimeNum)
10	14,033	Full.SCW.5<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LongNum+LongCat11+Sex+LtimeNum)
11	14,041	Full.SCW.6<–lm(log(FirstS)~YearNum:Sex+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum)
12	14,052	Full.SCW.7<–lm(log(FirstS)~YearNum:Sex+BLm+LatNum+LongNum+LongCat11+Sex+LtimeNum)
13	14,164	Full.SCW.8<–lm(log(FirstS)~YearNum:Sex+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum)
14	**14,033**	**Full.SCW.9<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum)**
15	14,279	Full.SCW.9.1<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+LongCat11+Sex)
16	14,040	Full.SCW.9.2<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+LongCat11+LtimeNum)
17	**13,977**	**Full.SCW.9.3<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+Sex+LtimeNum)**
18	14,025	Full.SCW.9.4<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongCat11+Sex+LtimeNum)
19	14,025	Full.SCW.9.5<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LongNum+LongCat11+Sex+LtimeNum)
20	14,044	Full.SCW.9.6<–lm(log(FirstS)~YearNum+BLm+LatNum+LongNum+LongCat11+Sex+LtimeNum)
21	14,156	Full.SCW.9.7<–lm(log(FirstS)~YearNum+DateNum^2+LatNum+LongNum+LongCat11+Sex+LtimeNum)
22	14,222	Full.SCW.9.3.1<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+Sex)
23	13,985	Full.SCW.9.3.2<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+LongNum+LtimeNum)
24	13,999	Full.SCW.9.3.3<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LatNum+Sex+LtimeNum)
25	**13,969**	**Full.SCW.9.3.4<–lm(log(FirstS)~YearNum+BLm+DateNum^2+LongNum+Sex+LtimeNum)##BESTMODEL**
26	13,988	Full.SCW.9.3.5<–lm(log(FirstS)~YearNum+BLm+LatNum+LongNum+Sex+LtimeNum)
27	14,111	Full.SCW.9.3.6<–lm(log(FirstS)~YearNum+DateNum^2+LatNum+LongNum+Sex+LtimeNum)

DateNum was replaced by DateNum^2.

Table 13

Summary for the best model using log-transformed stomach content weight as the response variable (Full.SCW.9.3.4 in Table 12).

Residuals				
Min	1Q	Median	3Q	Max
–5.4882	–1.1189	0.3483	1.278	3.6083
Coefficients	Estimate	Std. error	*t* value	
(Intercept)	1.3680	0.2690	5.086	
YearNum	–0.0203	0.0065	–3.103	
BLm	0.3293	0.0271	12.153	
DateNum	0.0000	0.0000	4.452	
LongNum	–0.0040	0.0006	–6.614	
Sex	0.2405	0.0557	4.316	
LtimeNum	–0.1239	0.0077	–16.163	

Table 14

Summary for the best model using Box-Cox transformed stomach content weight as the response variable.

Residuals				
Min	1Q	Median	3Q	Max
–6.3785	–1.9168	0.1629	1.9048	6.7132
Coefficients	Estimate	Std. error	*t* value	
(Intercept)	1.7870	0.4030	4.434	
YearNum	–0.0317	0.0098	–3.234	
BLm	0.5357	0.0406	13.195	
DateNum	0.0001	0.0000	4.965	
LongNum	–0.0060	0.0009	–6.654	
Sex	0.3608	0.0835	4.323	
LtimeNum	–0.1998	0.0115	–17.404	

Table 15

Comparison of year effects from the simple models and the best models.

	Simple models (from equation below)		Best models (from previous tables)	
Response variable	YearNum	SE	YearNum	SE
Fat weight	–0.0083	0.0014	–0.0083	0.0014
BT11	–0.0161	0.0022	–0.0190	0.0022
BT7	–0.0116	0.0019	–0.0149	0.0076
Half umbilicus girth	–0.4596	0.0348	–0.4059	0.1364
Half axillary girth	–0.4433	0.0532	–0.4499	0.1867
log (FirstS)	–0.0256	0.0066	–0.0203	0.0065

Response variable = YearNum+BLm+DateNum^2+Diatom+Sex.
log(FirstS) = YearNum+BLm+DateNum^2+LTimeNum+Sex.

interaction terms and random-effects terms. De la Mare suggested in 2011 that the sampling heterogeneity in the JARPA data made it impossible to draw any conclusions about time trends. Our extensive modelling exercise has shown beyond doubt that it is in fact possible to draw reliable conclusions, and that all six dependent variables showed a large negative trend during the JARPA period. Even the magnitudes of the regression coefficients are similar to those obtained by multiple linear regression in 2008. The standard errors are larger but the results are still significantly different from zero at the 5% level (see also Tables 3, 5, 7, 9, 11, 13 and 15). Results of this kind are not uncommon in other fields of research. For example, results obtained by multiple linear regressions in medical epidemiology have been

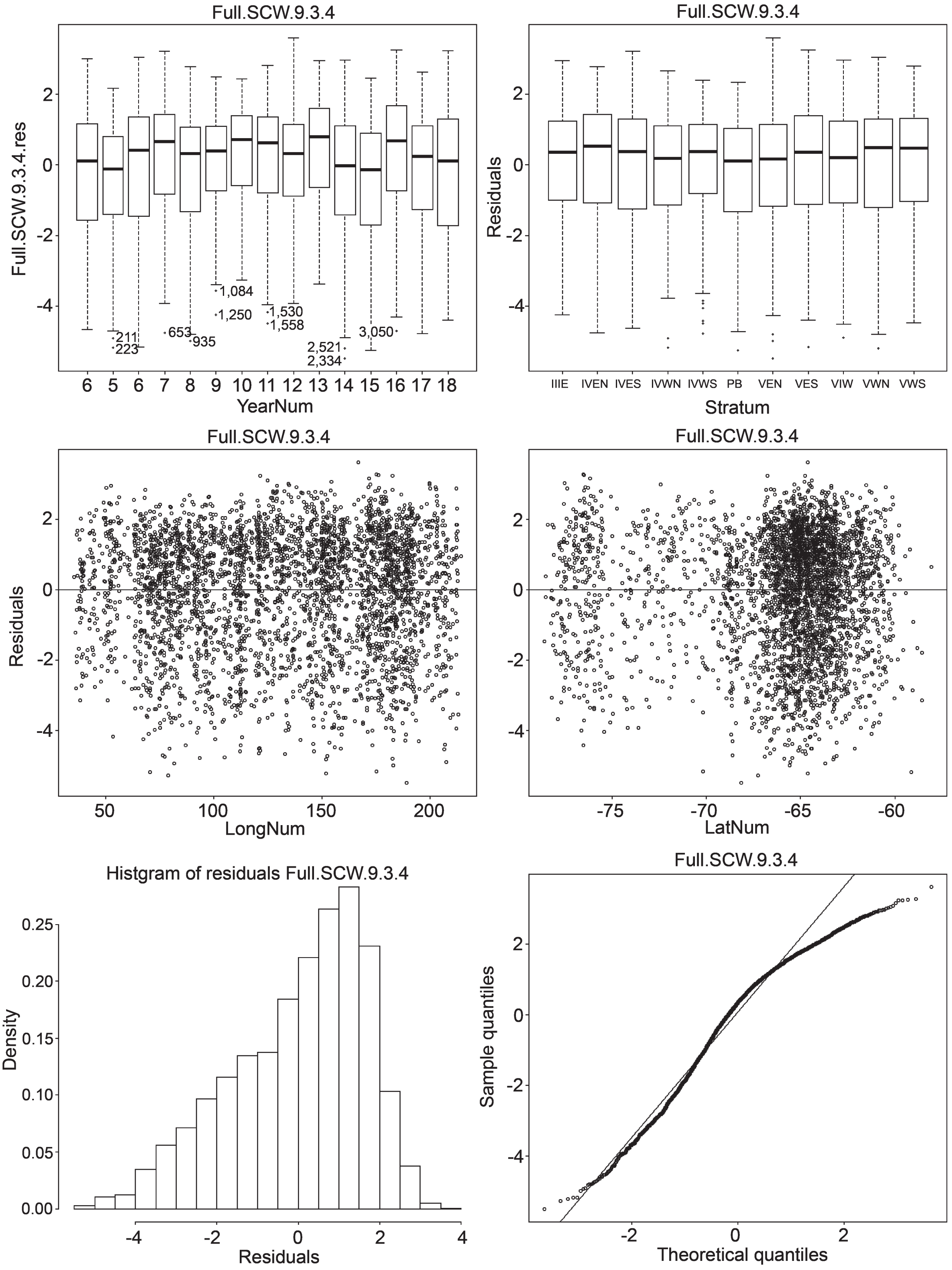

Fig. 8. Diagnostic plots for the best model with log-transformed stomach content weight as the response variable. For further explanation, see the caption for Fig. 3.

confirmed by more sophisticated modern analyses, again usually with somewhat larger standard errors.

For the dependent variable ‘Fat weight’, the best model was a simple linear regression model without interaction or random-effects terms (Tables 2 and 3). To illustrate the points above, this simple model was run for the other four related dependent variables as well, and a similar simple model was run for stomach fullness. In Table 15, the coefficients for the decline over the JARPA period for these model runs are compared to the coefficients from the best models. This table shows that simple linear regression gives much the same results for point estimates of the decline as the more complex models, but the coefficients from the models with random effects have higher standard errors. Thus the decline in energy storage over the JARPA years seems to be robust to the model selection. Similar results were obtained for all the other independent variables in the simple regression model. In this context it should be remembered that the standard errors found using the more complex models may be artificially low, since the error connected with model selection (based on BIC values) is ignored (Efron, 2014).

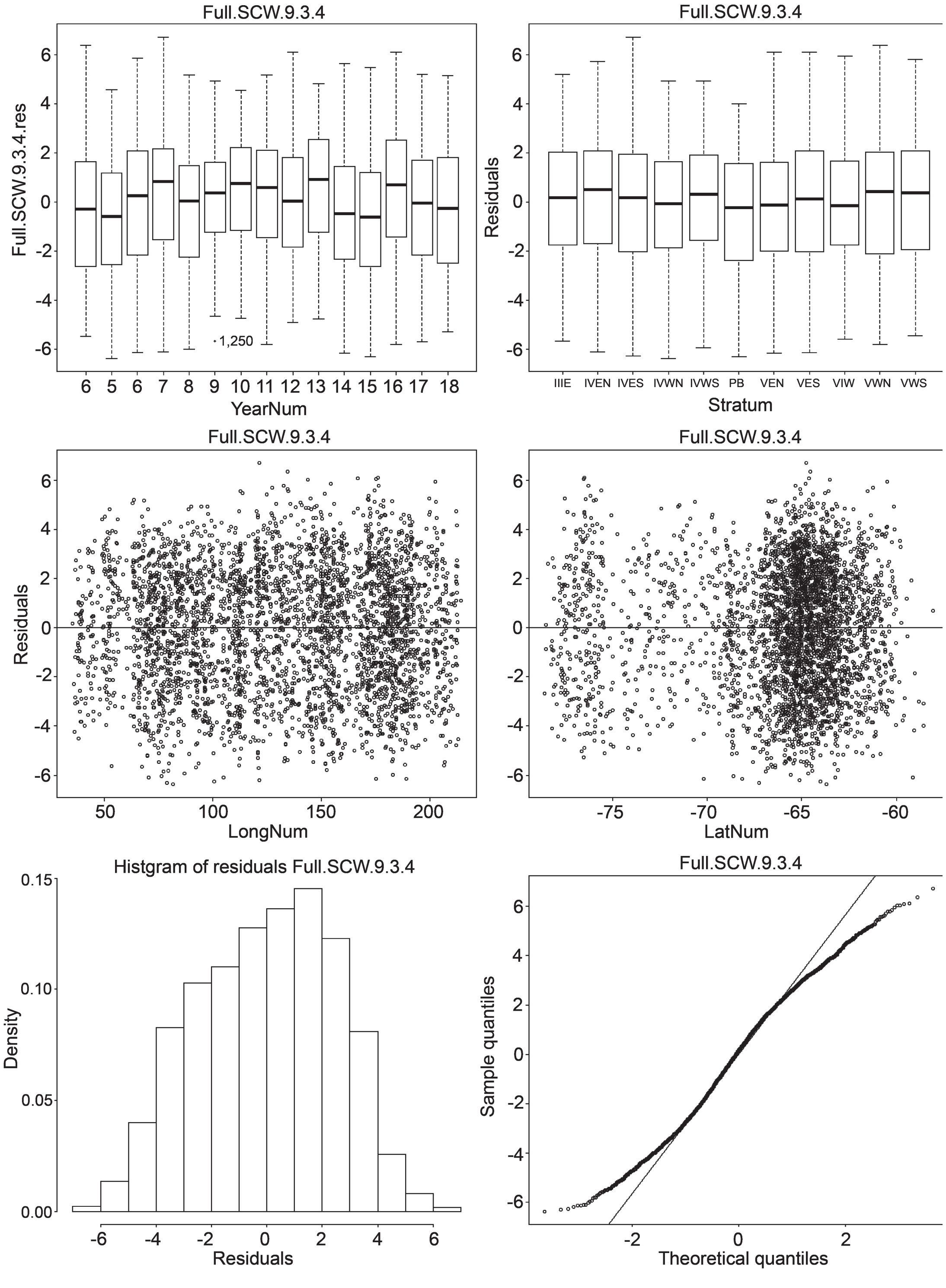

Fig. 9. Diagnostic plots for the best model with Box-Cox transformed stomach content weight as the response variable. For further explanation, see the caption for Fig. 3.

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