

# Ecosystem regime shifts have not affected growth and survivorship of eastern Beaufort Sea belugas

Sebastián P. Luque · Steven H. Ferguson

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**Abstract** Large-scale ocean-atmosphere physical dynamics can have profound impacts on the structure and organization of marine ecosystems. These changes have been termed “regime shifts”, and five different episodes have been detected in the North Pacific Ocean, with concurrent changes also occurring in the Bering and Beaufort Seas. Belugas from the Eastern Beaufort Sea (EBS) use the Bering Sea during winter and the Beaufort Sea during summer, yet the potential effects of regime shifts on belugas have not been assessed. We investigated whether body size and survivorship of EBS belugas harvested in the Mackenzie River delta region between 1993 and 2003 have been affected by previous purported regime shifts in the North Pacific. Residuals from the relationship between body length and age were calculated and compared among belugas born between 1932 and 1989. Residual body size was not significantly related to birth year for any regime, nor to the age group individuals belonged to during any regime. The percentage deviation in number of belugas born in any given year that survived to be included in the hunt (survivorship) did not show any significant trend within or between regimes. Accounting for lags of 1–5 years did not reveal any

evidence of delayed effects. Furthermore, neither population index was significantly related to changes in major climatic variables that precede regime shifts. Our results suggest that EBS beluga body size and survivorship have not been affected by the major regime shifts of the North Pacific and the adjacent Bering and Beaufort Seas. EBS belugas may have been able to modify their diet without compromising their growth and survivorship. Diet and reproductive analyses over large and small time scales can help understand the mechanisms enabling belugas to avoid significant growth and reproductive effects of past regime shifts.

**Keywords** Aleutian low pressure index · Climate change · Food availability · North Pacific Ocean · Pacific decadal oscillation

## Introduction

Large-scale analyses of the temporal variation in the structure of ecosystems in the North Pacific and North Atlantic have shown major periodic, yet unpredictable, changes in marine communities (Hare and Mantua 2000; Ottersen et al. 2001; Benson and Trites 2002; McGowan et al. 2003). This has given rise to the concept of “regime shift” to describe periods of rapid change in the structure of ecosystems, which are separated by longer periods of relative stability. Although formally defining regime shifts remains controversial because of inconsistent criteria (deYoung et al. 2004; Lees et al. 2006), certain features have been repeatedly found across studies reporting such shifts. Lees et al. (2006) reviewed currently used definitions of regime shifts and found that common key features are the existence of “sudden, high-amplitude, infrequent events” that can be measured in physical and biological variables at the spatial

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S. P. Luque (✉)  
Department of Biology, Memorial University,  
St. John's NL A1B 3X9, Canada  
e-mail: spluque@gmail.com

S. H. Ferguson  
Fisheries and Oceans Canada,  
501 University Crescent, Winnipeg MB R3T 2N6, Canada

scale of entire ecosystems. Physical and biological time series spanning more than 30 years are available for the North Pacific Ocean (McGowan et al. 1998), and they have displayed key features of regime shifts, such as rapid and infrequent changes in ecosystem structure (Wu et al. 2005; Watanabe and Kawaguchi 2003; Benson and Trites 2002). Since recording began, five regime shifts are thought to have occurred in the North Pacific: 1925, 1947, 1977, 1989, and 1998 (Mantua 2004), with detectable effects from the Bering Sea to southern California, and from coastal to oceanic habitats. Identifying what specific changes occurred in animal populations of this region, in association with the purported regime shifts, can help to understand the mechanisms linking large-scale ecosystem processes to population well-being (Hanks and Smith 1981).

Several populations of marine mammals, including Steller sea lions (*Eumetopias jubatus* Schreber, 1776), northern fur seals (*Callorhinus ursinus* Linnaeus, 1758), and harbour seals (*Phoca vitulina* spp.), have declined considerably in western Alaska between the mid 1970s and early 1990s (Merrick et al. 1987; Rosen and Trites 2000; Pitcher 1990). Two contrasting hypotheses have been proposed to explain these declines: (1) top-down factors, such as predation and hunting pressure from top predators, have driven marine mammal abundance below pre-1970s levels, independently of food and other resources; or (2) bottom-up factors, such as changes in prey quality and availability, have limited the predators' ability to stabilize or increase their numbers. The argument in favour of the top-down hypothesis is mostly based on evidence of increased predation rates of killer whales (*Orcinus orca* Linnaeus, 1758) on sea otters (*Enhydra lutris* Linnaeus, 1758), and presumably pinnipeds, in response to reductions in whale populations due to whaling. Under this hypothesis, killer whales began feeding on smaller marine mammals, thereby "fishing-down" their food web (Springer et al. 2003). However, not all pinniped populations have declined in the North Pacific, and some of them have even increased, following the end of commercial whaling (Trites et al. 2007a). Evidence from multidisciplinary studies provide more support for the bottom-up hypothesis, i.e. changes in a combination of multiple physical factors have benefited populations of prey species with low fat content (Trites and Donnelly 2003), negatively affecting the energy balance of marine mammals.

The 1977 regime shift is considered to be the strongest event of this kind in the North Pacific, and was associated with a persistent warming of sea surface water. It involved a change from predominantly negative to positive values of two important indices of atmospheric and oceanographic conditions: the Aleutian Low Pressure Index (ALPI), and the Pacific Decadal Oscillation index (PDO). The ALPI measures the intensity of a low pressure system (Beamish et al. 1997), and the PDO measures sea surface

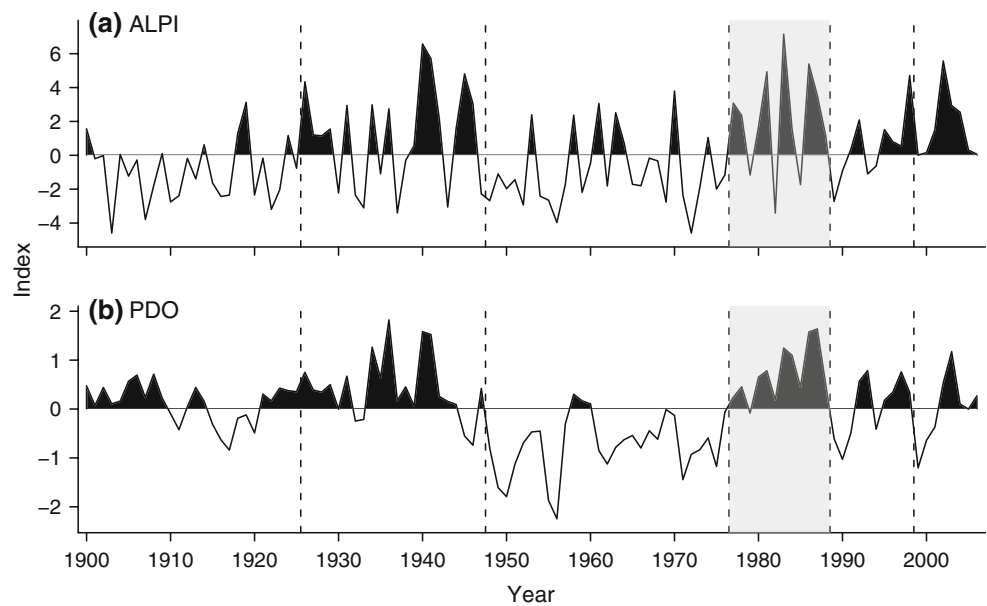
temperature (Mantua et al. 1997) over a defined region of the North Pacific (Fig. 1). Variation in both indices, in turn, is associated with changes in other physical characteristics, and eventually with the biological organization and structure of ecosystems (Collie et al. 2004; Lees et al. 2006). Thus, under the bottom-up hypothesis, the 1977 regime shift had its origins on a change in the physical dynamics between ocean and atmosphere.

Efforts to understand the decline of Steller sea lions in western Alaska, suggest that the rate and magnitude of the physical changes of the mid 1970s were large enough to alter major trophic relationships (Trites et al. 2007b). However, spatial differences in the temporal variability of sea surface temperatures indicate that physical changes following the regime shift were not uniform across the region (Bograd et al. 2005). The temporal pattern of sea surface temperature over the North Pacific shows that the western part of the Gulf of Alaska and southern Bering Sea was significantly different from that of the eastern Gulf of Alaska (see Bograd et al. 2005, Fig. 3). Although the precise mechanism by which Steller sea lions may have increased in number in eastern Alaska and decreased in western Alaska is not clear, pinnipeds, and possibly other marine mammals inhabiting the southern Bering Sea, were negatively affected by this regime shift.

The Bering Sea is an important habitat for four beluga (*Delphinapterus leucas* Pallas, 1776) stocks (from north to south): Eastern Beaufort Sea (EBS), eastern Chukchi Sea, Norton Sound, and Bristol Bay (O'Corry-Crowe et al. 1997). All four stocks are considered to be in healthy condition (Harwood et al. 2002; Angliss and Outlaw 2007; Grebmeier et al. 2006), and they have been harvested commercially and traditionally by native communities. Consistent with this assessment, there has not been any reduction in the availability of old and large individuals from 1980 to 2000, for the EBS stock (see "Results"). Belugas from these four stocks migrate offshore and into the Bering Sea during autumn and winter, and return to their summering grounds during the rest of the year for molting and calving (Richard et al. 1997). Furthermore, animal density is higher during the winter as beluga habitat is reduced in size (S. P. Luque, S. H. Ferguson and P. Richard, unpublished data). Thus, belugas spend part of their lives in an area where the effect of regime shifts in the North Pacific has been strong, and where intraspecific competition may be high.

A shift from arctic to subarctic community structure during the last decade has also been documented in the northern Bering Sea (Grebmeier et al. 2006). These changes were associated with increased air and water temperatures, leading to reduced ice cover and a northward shift in the distribution of pelagic fish. Grebmeier et al. (2006) suggest that benthic prey populations have been

**Fig. 1** Changes in the **a** Aleutian low pressure index (ALPI) and **b** Pacific decadal oscillation (PDO) reflect purported ecosystem regime shifts (vertical dashed lines). Regimes are characterized by periods of mostly positive (filled regions under the curve) or negative indices. **a, b** The shaded rectangle represents the regime following the strongest shift



reduced, as a result of higher carbon consumption by the larger pelagic populations throughout the water column, compared to previous conditions. Species which depend on benthic prey, such as gray whales (*Eschrichtius robustus* Lilljeborg, 1861) and walrus (*Odobenus rosmarus* Linnaeus, 1758), apparently responded to the changes by shifting their distribution further north (Moore et al. 2003; Laidre et al. 2008). Evidence for documented regime shifts in the Bering Sea have shown concurrent changes in the Beaufort Sea including freshwater runoff (Macdonald et al. 1999), polar bear and ringed seal reproductive failure (Stirling 2002), sea bird demographics (Lovvorn et al. 2003), and associated changes in sea ice (Drobot 2003). Despite the magnitude of the 1977 regime shift in the North Pacific, and the recent changes observed in the northern Bering Sea, there are no studies documenting the response of belugas to this event, which also affected the Beaufort and Chukchi Seas (Drobot 2003).

Limited data from other cetaceans include a survey of the western Arctic bowhead whale population that reports an annual increase of 3.4% between 1978 and 2001 (George et al. 2004), notwithstanding ecosystem changes. Environmental maternal effects in large-bodied mammals, such as cetaceans, result in delayed life history effects and require consideration of lags in demographic testing (Beckerman et al. 2002; Owen-Smith 2005; Räsänen and Kruuk 2007). To investigate whether any effects of previous regime shifts can be detected for EBS beluga, our objectives were to: (1) compare the body size at age of individuals born in years corresponding to different regimes with respect to the overall growth curve previously estimated for this stock; and (2) test whether the number of belugas born in certain years that were included in the hunt,

or survivorship, was higher or lower than expected during periods of regime shift, at various temporal lags.

The relationship between both relative indices (body size and survivorship) and environmental indices (ALPI and PDO) was also analysed to test for potential association between climate change and beluga population parameters. If food resources for belugas have been negatively affected following the 1977 regime shift, as they have for other marine mammals, we predicted that body growth of young belugas should have been reduced, resulting in smaller adult body size. We also expected survivorship to be reduced following this strong regime shift.

## Materials and methods

Age and morphometric data from EBS belugas were collected and maintained by the Fisheries Joint Management Committee (Box 2120, Inuvik, Canada) and Fisheries and Oceans Canada, in collaboration with hunters and members of local Inuvialuit and Hunters and Trappers Associations (Fig. S1, Electronic supplementary material). Data from EBS belugas harvested from 1988 to 2003 were available, representing catches reported from nine communities and hunting camps (Table 1).

### Body size and growth measurements

Morphometric measurements including body mass, body length and girth were obtained from whale carcasses, following procedures described elsewhere (Stewart 1994; Sergeant and Brodie 1969; Brodie 1971; Doidge 1990). Because body mass may change dramatically depending on

**Table 1** Summary of samples analysed from beluga harvested in the eastern Beaufort Sea

Community <sup>a</sup>	Females	Males	Capture years	Birth years
1 Shingle point	16	20	1995–1999	1932–1983
2 West Whitefish	2	7	1993–1999	1933–1977
3 Kendall Island	21	51	1995–2002	1940–1988
4 Aklavik	8	17	1998–2002	1941–1982
5 Inuvik	29	112	1998–2003	1935–1988
6 East whitefish	6	52	1993–1999	1936–1982
7 Hendrickson Island	43	151	1993–2002	1939–1984
8 Tuktoyaktuk	11	43	1994–2003	1942–1989
9 Paulatuk	5	31	1993–2000	1935–1983
All	141	484	1993–2003	1932–1989

<sup>a</sup> Numbers for communities correspond to those in Fig. S1 in the Electronic supplementary material

the nutritional status of the individual (Peters et al. 1983; LaBarbera 1989), we used standard length as an index of body size for belugas in this study.

To estimate the age of individual beluga in the sample, dentine growth layer groups (GLG) were counted in a tooth extracted from the lower mandible. The lower jaw was boiled in water to facilitate extraction, and the tooth was cast in resin for longitudinal sectioning and counting of GLG. Ages were assigned to animals assuming one GLG per annum i.e. age equals the GLG count for any given individual (Stewart et al. 2007; Luque et al. 2007). Only belugas aged by the same experienced reader were used, resulting in data from 625 EBS belugas captured from 1993 to 2003 for subsequent analyses (Table 1).

#### Relative body size during different regimes

We used a Gompertz growth model to define the relationship between body length and age (Fig. 2):

$$l_t = Ae^{-be^{-kx}} \quad (1)$$

where  $l_t$  represents length-at-age  $t$  (years),  $A$  represents asymptotic length;  $k$  represents the rate of exponential

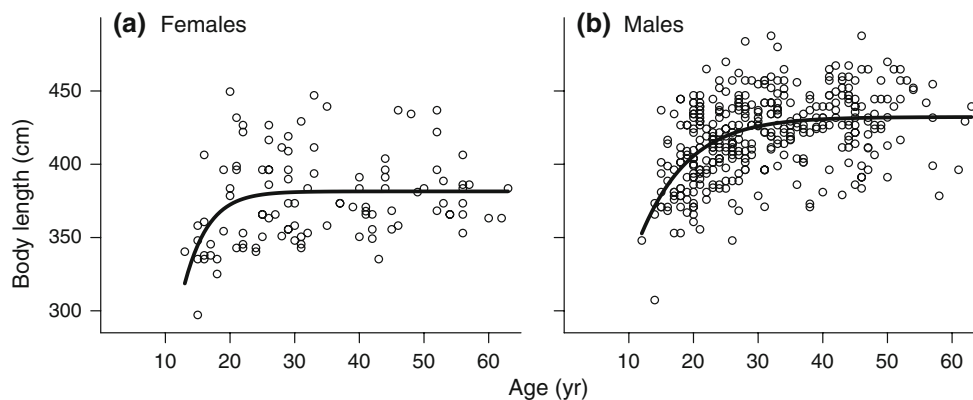
growth decay, and  $b$  is a constant describing initial growth (Windsor 1932; Winship et al. 2001), and  $x$  is observed age. Using a von Bertalanffy model and a linear model on the semi-log-transformed relationship revealed indistinguishable fits for the Gompertz and von Bertalanffy models, whereas the semi-log relationship did not accurately describe the growth data, as linearity assumptions were violated (Zar 1996). For comparison with previously published reports, we chose the Gompertz model to describe growth for each sex.

Using the corresponding predictive equations for males and females (Fig. 2), we calculated the standardized residuals for each observation. We considered belugas with positive residuals as being larger than average, and those with negative residuals as smaller than average, at any given age. To investigate whether growth was affected by the conditions experienced by belugas during different regimes and age classes, we grouped residuals according to the regime in which belugas were born. Additionally, to account for delayed effects of changes in environmental conditions, we classified belugas according to the age class they belonged to during each year of their lives. We considered belugas as calves if they were 2 years old or younger [i.e. the duration of lactation (Brodie 1971)], as juveniles if they had between 3 and 10 years of age, and as adults if they were older than 10 years of age (Robeck et al. 2005). Thus, we compared the residuals observed when whales were harvested among these groups for each regime they experienced.

#### Survivorship index

Relatively large and old belugas have been consistently available from EBS beluga harvests (Harwood et al. 2002; Luque and Ferguson 2006). The distribution of birth years of belugas harvested should reflect the distribution of births in the population in this case. Consequently, EBS belugas represent an ideal population in which to investigate whether birth year is related to their probability of survival and inclusion in the harvest. Therefore, we

**Fig. 2** Relationship between body length and age for **a** female and **b** male Eastern Beaufort Sea (EBS) belugas. The predictive equation for females is  $381.5e^{-7.56e^{-0.29x}}$  and for males is  $432.2e^{-1.16e^{-0.15x}}$ , where  $x$  is age. Yr Year



modelled the number of belugas born in any given year as a function of their year of birth. We calculated the year of birth of each whale by subtracting their age from the year in which they were captured, and constructed a histogram of the number of whales born every year. If Inuit harvests represented the majority of beluga mortality and only the oldest and largest individuals are targeted by hunters, the number of whales would be expected to increase as a function of the year of birth, up to the year of birth of whales deemed to be too young to be hunted. However, younger and smaller belugas are hunted, and other mortality factors are not age-selective (e.g. ice entrapment) for EBS belugas, and thus the number of whales born after a certain year of birth is expected to decline. We excluded the decreasing right side of the histogram from our analyses because it represents whale cohorts that had not lived long enough to become selected by hunters (Fig. S2, Electronic supplementary material).

Birth years of EBS belugas harvested ranged from 1932 to 1989. We defined the beginning of the decline in numbers of belugas born as the first year after which numbers declined for more than 2 consecutive years after the maximum. Using this criterion, the number of belugas born after 1979 declined, so we excluded whales born after this date from the model for the reason outlined above (Fig. S2, Electronic supplementary material). We used a backward stepwise procedure to fit a polynomial model:

$$y_i = b_0 + b_1x + b_2x^2 + b_3x^3 + \dots + b_{kx}^k + \varepsilon_i \quad (2)$$

where  $y_i$  is the number of whales born in year  $i$ ,  $b_0$  is the intercept,  $b_1$  to  $b_k$  are regression coefficients,  $x$  is year of birth, and  $\varepsilon_i$  is an error term associated with each observation, to the number of belugas born from 1932 to 1979 with the remaining sample. We used the fitted model to predict the number of belugas born each year, and calculated a survivorship index as  $100 \times \text{residuals/predicted}$ . This index has been previously used to estimate recruitment and study its relationship to climate change in ringed seals (Ferguson et al. 2005). We interpreted years with positive residuals as years in which the observed number of belugas born exceeded the expected value; those with negative residuals as years in which this number was below the expected value. We compared the survivorship index between periods before and after known regime shifts at various temporal lags.

We began the backward stepwise polynomial regression with a fifth degree polynomial, and based the model selection on the Akaike information criterion (Kiesseppä 1997). We performed all data manipulation and statistical procedures in the GNU R system (R Development Core Team 2007), and values are presented as mean  $\pm$  SE, unless stated otherwise.

## Results

### Body growth comparisons

The residuals from the body length-at-age relationship, classified by the age group belugas belonged to during different regimes did not show that particular age groups were affected during any particular regime (Fig. 3). The interquartile range of the distribution of residuals included zero for all age groups during the five regimes studied. In female and male belugas, variation in residuals between different regimes was independent of age group (ANOVA  $F_{4,5} = 0.26$  and  $F_{4,5} = 1.24$ , respectively,  $P > 0.1$  both sexes), and there were no significant effects of regime, nor age group ( $P > 0.1$  for both effects and sexes). Therefore, we pooled residuals from both sexes for the analysis of their relationship with ALPI and PDO.

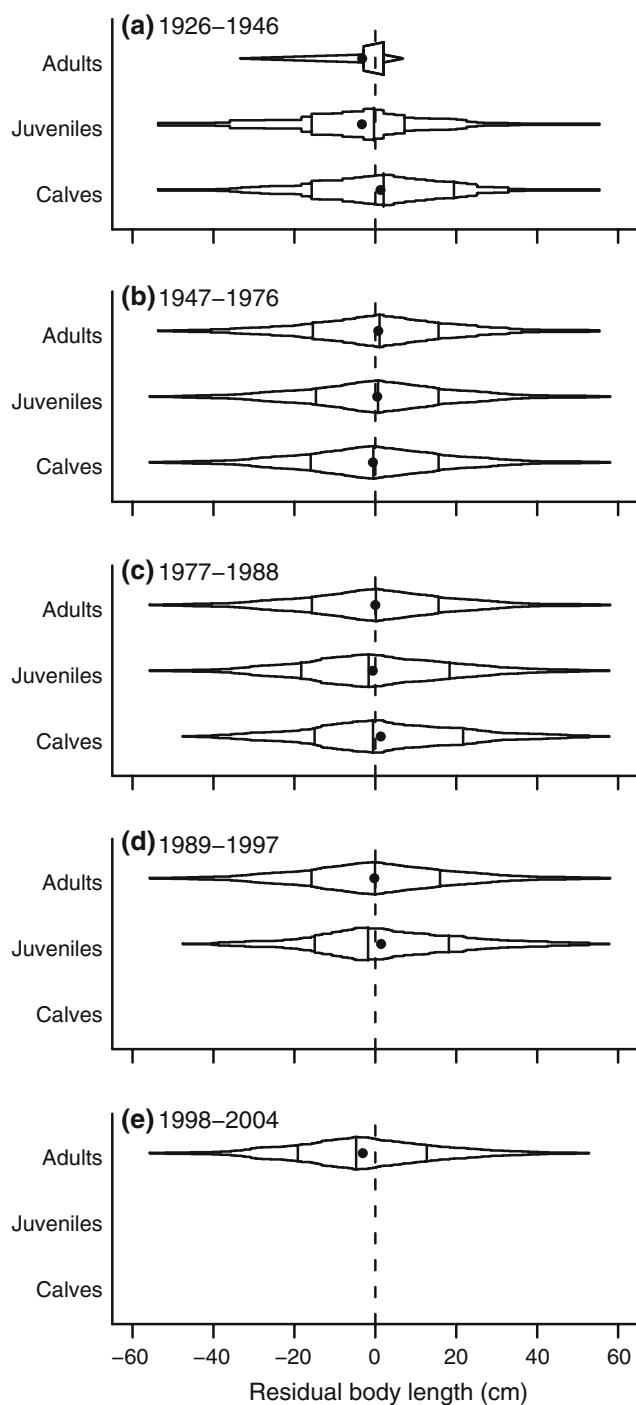
The residual body length-at-age of belugas was neither significantly related to the ALPI ( $r = 0.001$ ,  $P = 0.4$ ) nor to the PDO ( $r < 0.001$ ,  $P = 0.9$ ) indices at birth (Fig. 4a, b). Introducing lags to the indices, so that they correspond to the indices from 1 to 5 years of age produced similar results, with  $r$  ranging from  $< 0.001$  to 0.11. The weak relationship with both indices suggests that growth of belugas was not significantly affected by major environmental changes induced by regime shifts in the North Pacific and Bering Sea.

### Survivorship

For belugas born between 1932 and 1979, there was a significant relationship between the number of belugas born in any given year and their year of birth ( $r = 0.78$ ,  $P < 0.001$ ). A second-degree polynomial, as in Eq. 2, was the best model chosen to describe the relationship (Table 2), using a backward stepwise regression procedure ( $r^2 = 0.78$ ,  $P < 0.001$ ). The parameters of the model were (estimate and SE in parenthesis):  $b_0 = 1.0614 \times 10^4$  ( $1.2138 \times 10^4$ ),  $b_1 = -1.1356 \times 10$  ( $-1.2412 \times 10$ ), and  $b_2 = 3.0345 \times 10^{-3}$  ( $3.1726 \times 10^{-3}$ ) (Fig. 5a).

There was no relationship between the survivorship index calculated from the model and year of birth ( $r = 0.001$ ,  $P = 0.8$ ). The index did not vary between regimes, although there was considerable variation between years (Fig. 5b). Approximately 43% of the indices were negative during the 1926–1946 regime, while 50% were negative during the 1948–1976 regime, consistent with the lack of relationship between the survivorship index and year of birth.

The survivorship index was neither significantly related to the ALPI ( $r = 0.01$ ,  $P = 0.4$ ) nor to the PDO ( $r = 0.02$ ,  $P = 0.4$ ) environmental indices at birth (Fig. 6). Introducing lag effects in the indices, to test for effects from 1 to



**Fig. 3** Residual body length-at-age of EBS belugas was not related to the age category (adults, juveniles, and calves) they belonged to during the five purported regime shifts in the North Pacific Ocean: **a** 1926–1946, **b** 1947–1976, **c** 1977–1988, **d** 1989–1997, and **e** 1998–2004. Shape of the box-percentile represents all quantiles from first through 99th, the mean (*circle*), median, and 25th and 75th quantiles (*solid vertical reference lines*) of the distributions

5 years, did not result in any significant relationships between these variables. Therefore, variability in the number of belugas born and surviving to be included in the

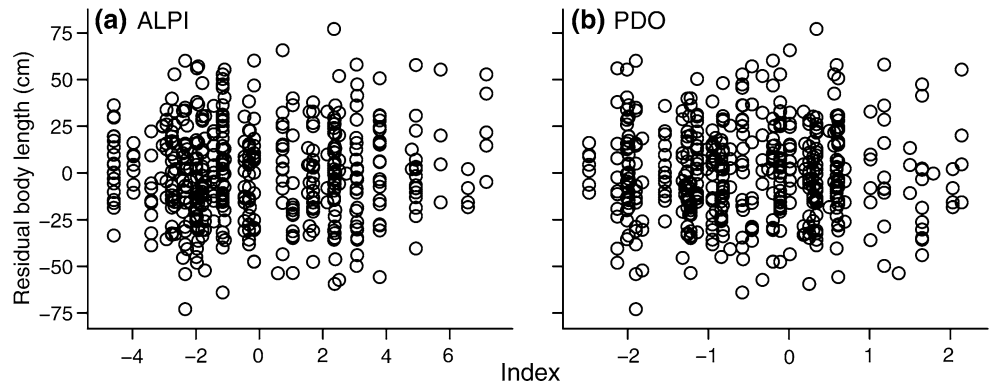
hunt was not directly related to the main regime shift signals.

## Discussion

We tested whether previous large-scale ecosystem changes (regime shifts) in the Bering and Beaufort Seas affected growth and survival of EBS belugas. The main motivation for this study was that EBS belugas migrate to the Bering Sea during winter, when they presumably consume a significant proportion of their annual energy intake, as demonstrated for their closest relatives, the narwhals (*Monodon monoceros* Linnaeus, 1758) (Laidre and Heide-Jørgensen 2005). In particular, we expected to find negative effects of the strong 1977 regime shift, which is considered to be the origin of sharp declines in several fish-eating pinnipeds in western Alaska (Benson and Trites 2002; Trites and Donnelly 2003), and also affected the adjacent Chukchi and Beaufort Seas. However, our results indicate that body size (length) at the age belugas were harvested, relative to the estimated average of the population, was not affected by the different regimes they lived through. This was true regardless of the age of belugas throughout those regimes. Nor did we detect any trends, positive or negative, in an index of survivorship that could be related to regime shifts. Similarly, we did not find any evidence that the main indicators of physical forcing in the North Pacific and Bering Sea (ALPI and PDO) have influenced these indices of relative body size and survivorship. We examine our assumptions, propose potential explanations for these findings, and identify questions that require more attention to understand the responses of belugas to changes in prey availability.

Statistical power, i.e. our ability to reject a false null hypothesis, is a critical consideration whenever a null hypothesis is not rejected. However, post hoc power analyses may not be meaningful because power is closely related to the observed *P*-value in the traditional frequentist approach (Hoenig and Heisey 2001), so confidence intervals provide a better assessment of effects and effect sizes. In the linear model testing for regime and age group effects on residual body length (Fig. 3), 95% confidence intervals of parameters were consistently symmetrical around zero (the null hypothesis of no difference with respect to the baseline calf beluga and 1926–1946 regime group) ranging from (−7.95, 9.12) to (−35.10, 18.75) for regime effects, and from (−12.83, 9.15) to (−24.50, 30.63) for age group effects. In the model testing for correlations between residual body length and ALPI or PDO indices, the intervals were also symmetrical around zero, ranging from (−0.08, 0.22) for ALPI and from (−0.64, 0.06) for PDO. However, in the model testing for correlations between

**Fig. 4** Residual body length-at-age of EBS belugas was not related to the **a** ALPI, nor to the **b** PDO during their year of birth. Incorporation of lags on both indices also resulted in non-significant relationships (not shown; see text). For abbreviations, see Figs. 1 and 2

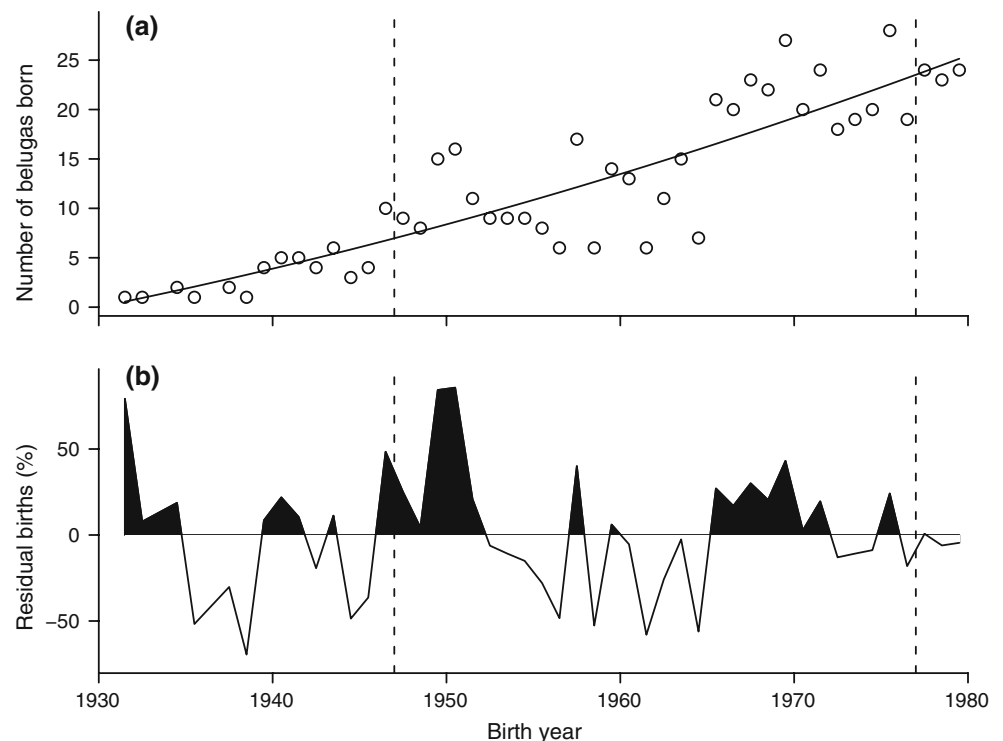


**Table 2** Summary of comparisons between a second-degree polynomial model to predict number of belugas born in particular years (Fig. 5a) with alternative models, up to a fifth-degree polynomial,

chosen through backward stepwise regression. The Akaike Information Criterion (AIC) was used as the main criteria for model selection

Model	Deviance	Residual <i>df</i>	$\delta$ AIC	AIC
$y_i = b_0 + b_1x + b_2x^2 + b_3x^3 + b_4x^4 + b_5x^5 + \varepsilon_i$	<0.001	43	0	130.72
$y_i = b_0 + b_1x + b_2x^2 + b_3x^3 + b_4x^4 + \varepsilon_i$	<0.001	43	0	130.72
$y_i = b_0 + b_1x + b_2x^2 + b_3x^3 + \varepsilon_i$	0.005	44	-2	128.72

**Fig. 5 a** The number of EBS belugas born each year based on age of belugas harvested between 1993 and 2004 (survivors). The model does not include belugas born after 1979, the year of birth of belugas deemed to be too young to be harvested. The expected number of surviving belugas (*y*) followed the polynomial model  $y = (1.0614 \times 10^4) - (1.1356 \times 10)x + (3.0345 \times 10^{-3})x^2$ , where *x* is year of birth. **b** The survivorship index ( $100 \times$  residual/predicted; percentage residual births) did not vary systematically with year of birth. Positive residuals in **b** are denoted by the filled regions under the curve, and the vertical dashed lines demarcate regime shifts

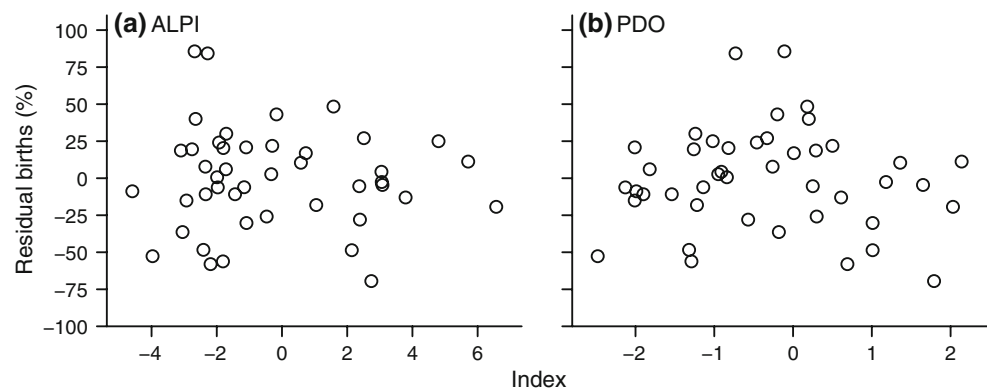


survivorship index and these environmental indices, the intervals were less symmetrical and ranged from (-5.61, 2.39) for ALPI and from (-13.16, 4.99) for PDO, suggesting that a small negative effect may indeed be real with larger sample sizes. Therefore, any real effects of regime shifts on growth do not appear to have been missed in our

study, and a small real negative effect on survivorship may have been detected with larger sample sizes and/or a more accurate survivorship index.

The concept of residuals as an index of the nutritional status of animals, or prey availability, is widely used in research on mammals and birds (e.g. Georges and Guinet

**Fig. 6** Residual number of belugas born (survivorship index) of EBS belugas was not related to **a** ALPI nor to **b** PDO, during the year of birth. Incorporation of lags on both indices also resulted in non-significant relationships (not shown; see text). For abbreviations, see Figs. 1 and 2



2000; Ardia 2005). However, some authors criticize the use of residuals in this context (Green 2001; García-Berthou 2001), arguing that assumptions of independence of residuals from age (in the present study), and that age is measured without error, often are not met, leading to invalid interpretations. Age was measured in three to five blind replicates by a single reader in the present study (Stewart 1994), so any errors in age determination are likely to be small, and much smaller than those in body length measurements. Nonetheless, age cannot be accurately determined for teeth without a visible neonatal line, and is underestimated for worn teeth (Klevezal 1995), further limiting sample sizes. Therefore, our conclusions are only valid within the age range of animals in our sample.

As in Ferguson et al. (2005), we assumed that age structure remained constant, and that variation in the expected number of belugas born and surviving until the harvest resulted from variation in pregnancy rate, neonatal survival, and juvenile recruitment. Variation in the latter three variables was assumed to be associated to changes in belugas' habitat, mainly food resources. These assumptions are rarely met, and the robustness of our model to minor departures from them is difficult to assess with the available data, and highlight the need for independent estimates of abundance (e.g. aerial surveys), and analysis of samples to determine the reproductive status of harvested belugas. However, the best available knowledge of the population indicates that EBS beluga density has remained relatively stable or shown marginal growth over the past 30 years (COSEWIC 2004).

The estimated growth curves represent a cross-sectional description of the variation in body length relative to age for EBS belugas, at the ages they were harvested. Growth in many species is adaptive, changing primarily in response to environmental conditions before maturation (Arendt 1997). Therefore, we assumed the residuals from the growth model reflect the cumulative effect of conditions experienced by belugas before they were harvested, particularly prior to weaning. Rapid and large reductions in

the availability of prey that are rich in energy content, such as those that may occur during regime shifts, can affect milk energy transfer from mother to offspring (Boyd 1999). Dependent offspring often adjust to the reduced energy intake by limiting growth, in favour of development of other physiological functions for survival (Arendt 1997). If the magnitude and duration of the period of nutritional stress are sufficiently large and prolonged, adult body size can be reduced (Metcalf and Monaghan 2001) below the long-term average for the population. EBS belugas of any age at the time regime shifts occurred did not appear to suffer any long-term effects on their body length. Similar evidence from other cetaceans is lacking, but the period of nutritional stress following the 1977 regime shift was sufficiently large and sustained to cause reductions in adult body size of Steller sea lions (Trites and Donnelly 2003). If the dietary changes for belugas in the Bering Sea were similar to those of Steller sea lions, EBS belugas may have avoided the negative effects by feeding more intensively in other areas throughout their annual migration cycle. Beluga movements and diving behaviour in autumn suggest that they spend considerable time foraging outside their wintering areas, for both EBS (Richard et al. 1997, 2001b) and High Arctic stocks (Martin et al. 1998; Richard et al. 2001a). Despite recent beluga diet studies (Loseto et al. 2008), we still do not know when beluga gain most of their energy. However, all areas of the beluga range were affected by the 1977 regime shift including the Chukchi and Beaufort Seas (Macdonald et al. 1999; Stirling 2002; Drobot 2003; Lovvorn et al. 2003).

We used a survivorship index as an indicator of adult female pregnancy rates and calf survival (Boyd et al. 1999). Pregnant female mammals incur increased energy costs, which they cover through increased food intake or mobilization of body reserves (Young 1976). Therefore, variation in the quality, abundance, and availability of food can have an impact on their reproduction. Evidence for this effect is available for adult female pinnipeds (Boyd et al. 1990; Lunn and Boyd 1993), and indirectly for cetaceans (Greene et al. 2003; Leaper et al. 2006). Although there

was large variation in the survivorship index of EBS belugas, it was not related to the large-scale ecosystem changes resulting from regime shifts in the North Pacific and Bering Sea.

Little is known about the responses of cetaceans to climate change in the North Pacific, and the Bering Sea in particular (George et al. 2004), although declines in primary and secondary production are thought to be occurring (Schell 2000). However, our results suggest that EBS belugas have either: (1) physiologically coped with increased nutritional costs resulting from reductions in food availability or change in diet, following large-scale ecosystem reorganization in the Bering Sea; or (2) modified their diet without significant negative effects on nutrition. Which of these possible explanations is the most plausible requires knowledge of beluga movements and foraging behaviour throughout their annual cycle. EBS belugas remain in the Beaufort Sea during late spring, summer, and early autumn (Richard et al. 1997, 2001b; Loseto et al. 2007), when they use a relatively large area. Data on EBS beluga diet is limited to the summer open-water season (Loseto et al. 2008), but suggest that they feed on Arctic cod (S. H. Ferguson, unpublished data). Additionally, deep-diving behaviour by belugas suggests they feed on benthic prey (Martin et al. 1998; Richard et al. 2001a, b), likely epibenthic Arctic cod. No data are available for periods prior to the strong 1977 regime shift, although structures like teeth may provide insights into past diet (Clementz and Koch 2001). However, the limited time of the year that belugas spend in the Bering Sea may have allowed them to minimize any nutritional deficiencies encountered there.

In contrast to otariid pinnipeds, belugas and most cetaceans are not constrained by the need to return to a fixed location during lactation, so they can forage over larger areas, and can remain in foraging grounds for longer periods. Belugas can also store proportionally larger fat stores in their blubber, compared to smaller marine mammals, allowing them to survive through longer periods of reduced food intake (Evans et al. 2003; Lockyer 2007). Effects of regime shifts on beluga, therefore, may have been subtler physiological and behavioural changes that can be detected with additional data. For instance, fat stores may have allowed belugas to “buy” the time needed to find and begin feeding on new prey, as the ecosystem shifted to new regimes. Such changes, however, occur within the context of predator–prey interactions throughout trophic levels. Recent models and reviews of state-dependent foraging behaviour and risk management by mesopredators (Frid et al. 2007; Heithaus et al. 2008), such as belugas and seals, suggest that mesopredators trade off energy gains for

predator safety, and that the strength of the trade-off is largely determined by the predator’s nutritional state. Regardless of the mechanism causing killer whales to switch to prey of lower trophic level, the consequence for belugas may have been a reduction in predation pressure (Rugh et al. 2000; Shelden et al. 2003), allowing them to access more profitable prey that was otherwise inaccessible due to risk effects. These conjectures highlight the importance of investigating beluga diet profiles. Stable isotope (Peterson and Fry 1987) and fatty acid (Iverson et al. 2004) analysis techniques are now available that can help to address these questions over large and small time scales, respectively.

In summary, our results suggest that EBS belugas have not suffered any long-term effects of regime shifts in the Bering Sea, where they migrate and spend 4 months during the winter and early spring, or the Beaufort Sea, where they migrate in summer and autumn. Belugas born between 1932 and 1989 (killed between 1993 and 2003) were neither larger nor smaller than the overall expected size for whales of this stock when they were harvested. The age group that belugas belonged to during the different regimes did not affect the probability of them being larger or smaller than predicted when they were harvested. The percentage deviation from the predicted number of belugas born in a given year, and surviving to be included in the hunt (survivorship index), did not show any trends within nor between purported regimes. Accounting for 1- to 5-year lagged effects on body length-at-age and survivorship of belugas did not reveal evidence of food limitation. Furthermore, there was no relationship between residual length, survivorship index, and the major climate indices of ecosystem regime shifts (ALPI and PDO). Therefore, beluga growth and survivorship appeared to vary independently of the large-scale ecosystem changes that have affected populations of pinnipeds and marine communities in the region. Belugas occurring at their current density may be resilient to negative effects of ecosystem changes in the Bering Sea by adjusting feeding behaviour in prey, time, or space. For example, the increase in pelagic fish following the strong 1977 regime shift and increased temperatures may have caused a change in beluga diet, without growth and survival costs for the EBS population.

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