

Bowhead whale body condition and links to summer sea ice and upwelling in the Beaufort Sea



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ABSTRACT

We examined the response of bowhead whale (*Balaena mysticetus*) body condition to summer sea ice conditions and upwelling-favorable winds. We used a long-term dataset collected from whales of the Bering–Chukchi–Beaufort Seas (BCB) stock to estimate various body condition indices (BCI's) for individual whales that were harvested by Alaskan Eskimos. A series of offshore regions frequented by bowhead whales in summer were delineated and used to quantify interannual summertime environmental conditions including: (a) mean open water fraction, (b) duration of melt season, (c) date of continuous freeze-up, and (d) mean upwelling-favorable wind stress. Body condition was analyzed relative to these metrics for both the preceding summer feeding season and the previous three seasons combined. Our analysis indicates a significant increase in the long-term trend in an axillary girth-based body condition index (BCI_G) over the study period (1989–2011). The increase in BCI_G is likely associated with the trend in overall reduction of sea ice, including increased duration of open water, changes in upwelling potential (wind stress), and possibly higher primary production in the Pacific Arctic marine ecosystem favoring water-column invertebrates. We found strong significant positive correlations between BCI_G and late summer open water fraction in the Beaufort Sea and smaller nearshore areas off the Mackenzie Delta and west of Banks Island. Additionally, BCI_G was positively and significantly correlated with duration of melt season, later date of freeze-up in the Beaufort Sea, and upwelling-favorable winds on the Mackenzie shelf and west of Banks Island. A strong seasonal difference in BCI's was noted for subadult bowheads, presumably associated with summer feeding; however, yearlings were found to drop in BCI over at least the first summer after weaning. Our results indicate an overall increase in bowhead whale body condition and a positive correlation with summer sea ice loss over the last 2.5 decades in the Pacific Arctic. We speculate that sea ice loss has positive effects on secondary trophic production within the BCB bowhead's summer feeding region. While not part of this study, the abundance of BCB bowheads increased markedly over the same period.

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1. Introduction

The bowhead whale (*Balaena mysticetus*) is an ice-associated mysticete that lives entirely in high-latitude circumpolar arctic seas. In Alaska, bowheads begin life in spring within the subzero (°C) waters of the ice-lead systems of the northern Bering, Chukchi and western Beaufort Seas. They may exceed 19 m in body length and 80 metric tons in body mass. The bowhead whale exhibits a number of superlatives among Cetacea, including the thickest blubber layer, the greatest known longevity of any mammal, the longest baleen, the lowest body core temperatures, and the

largest head-to-body length ratio (Haldiman and Tarpley, 1993; George, 2009).

The Bering–Chukchi–Beaufort Seas (BCB) population of bowheads spends the summer months in the Chukchi and Beaufort Seas (Fig. 1). It is estimated that at the end of Yankee commercial whaling in 1910 (Bockstoe, 1986; Woodby and Botkin, 1993) the BCB bowhead whale population increased from a few thousand animals to nearly 17,000 individuals by 2011 (Givens et al., 2013). This increase is accredited to the cessation of commercial whaling, low natural mortality, a well-managed subsistence hunt, and relatively pristine habitat (George et al., 2004). Today, bowheads remain an important subsistence species for many coastal native communities in Russia, Alaska, and Canada.

Coincident with a growing population, the summer and fall habitats of the BCB stock have seen dramatic reductions in sea

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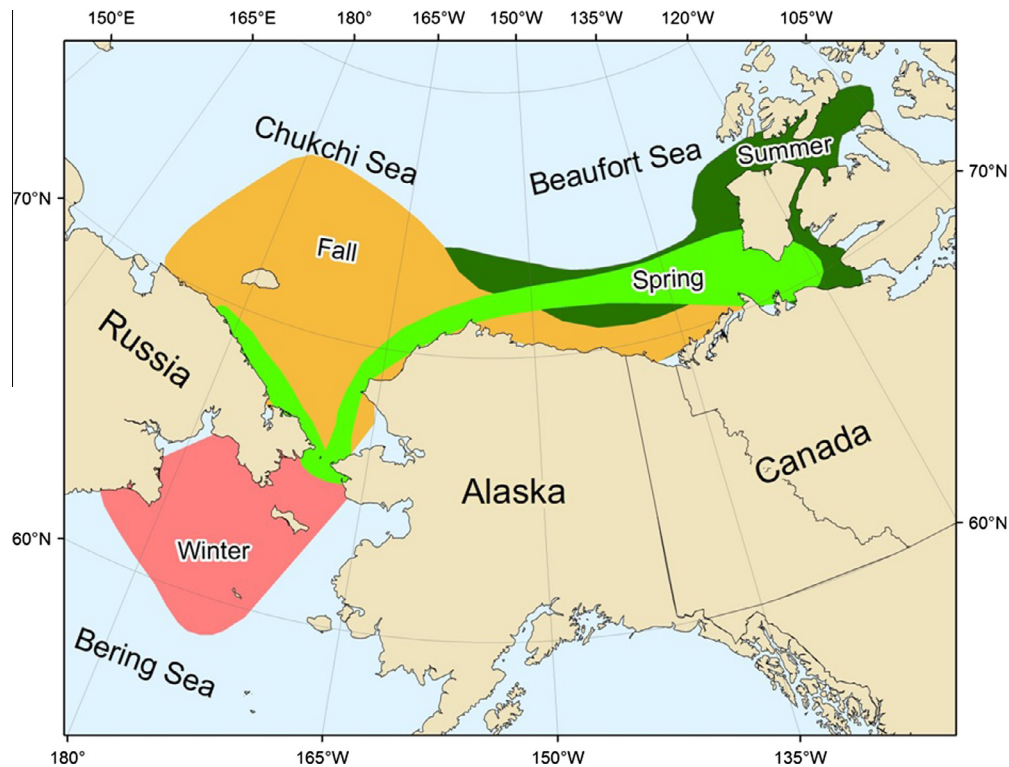


Fig. 1. Seasonal range map of the BCB bowhead whales based on satellite telemetry data (Quakenbush et al., 2012). Bowheads are also known to occur in regions outside these general boundaries.

ice. Since the start of the satellite record in 1979 Arctic summer sea ice extent has declined by 10.2% per decade (Comiso et al., 2008). The summer ice extent in September 2012—the lowest on record—was 49% below the 1979–2000 mean (NSIDC, 2012). Over this same time period, the Arctic melt season has also lengthened by about 20 days (Markus et al., 2009). These changes carry implications for both the pelagic and benthic components of the Arctic marine food web. Bowheads feed primarily on zooplankton (copepods and euphausiids), which are closely coupled to primary production. Thus, the bowhead whale serves as an important indicator species of Arctic environmental change (Moore and Laidre, 2006).

It is not entirely clear how loss of Arctic sea ice will impact bowhead whales over the long term, but there have been hypothesized trade-offs between loss of sea ice habitat and potential increases in food availability (Moore and Laidre, 2006; Laidre et al., 2008). Arctic summer sea ice retreat may drive increased phytoplankton blooms in the Arctic Ocean (see Arrigo and van Dijken, 2015), which may in turn promote greater zooplankton production. Ice algae and phytoplankton collectively provide an extended period of support to pelagic zooplankton, such as copepods and euphausiids (Jin et al., 2012). Reductions in summer sea ice that lead to generally ice-free conditions over the continental shelves may also act to support zooplankton production by creating more opportunity for upwelling events (Pickart et al., 2009), which may bring nutrients to the euphotic zone to be used in primary production. This is especially important later in the summer after nutrients are depleted near the surface. In addition, these same continental-shelf upwelling events may act to advect and aggregate zooplankton, which may also benefit the feeding effectiveness of bowhead whales (Moore and Laidre, 2006). In general, for zooplankton communities to benefit from increased primary production, their grazing periods must match phytoplankton blooms (Kahru et al., 2011; Grebmeier et al., 2015). With increases in

zooplankton production and aggregation, we may expect bowhead whales to feed more effectively during the summer and fall seasons in the Beaufort and Chukchi Seas and thus have improved body condition. In fact some preliminary analyses seemed to suggest a positive relationship between low sea ice densities and bowhead body condition (George et al., 2006).

The North Slope Borough Department of Wildlife Management, a municipal government in northern Alaska, has maintained an extensive dataset from postmortem examinations of bowhead whales harvested by Inupiat subsistence hunters. The dataset includes morphometric measurements from individual whales, which can be used to derive various metrics to monitor body condition changes across years, seasons, and age categories. This dataset is one of the most comprehensive datasets on Arctic cetacean body condition available. It also overlaps with a period of substantial environmental change in the Arctic making the data uniquely suited for analyses of the effects of sea ice loss on bowhead whales.

The objectives of this study were to: (1) define a body condition metric for harvested bowhead whales from the BCB population based on morphometric data; (2) quantify seasonal differences in body condition for different age classes; (3) examine trends in body condition over time (1989–2011, based on data availability); and (4) relate body condition trends to summer sea ice conditions, including open water fraction, duration of the melt season, and the onset of freeze-up, and the occurrence of upwelling-favorable winds.

2. Methods

2.1. Bowhead whale harvest data

We reviewed data from over 1200 individual harvested bowhead whales from the Alaskan communities of Kaktovik, Nuiqsut,

Barrow, Pt. Lay, Wainwright, Point Hope, Kivalina, Wales, Savoonga, and Gambell. For each animal, data relevant to this study included harvest date, location, sex, pregnancy status, total body length (referred to hereafter as length), length of longest baleen plate, girths at axilla, umbilicus, anus, and peduncle, dorsal and ventral blubber thicknesses at axilla, and ventral blubber thicknesses at umbilicus (Fig. 2). Not all measurements were made on every whale, so sample sizes differ for the various analyses and body condition metrics. The subsample of the larger dataset used in this study ($n = 298$) were those records with high data quality scores for non-pregnant whales landed at Barrow for which both axillary girth and baleen length measurements were made. Data quality was scored based on the consistency, which included a criterion related to the presence of experienced examiners, and completeness of the measurements.

We defined four age classes based on the length of the longest baleen plate as follows: *yearlings*¹ (age 1.0–1.5 yrs) were classified by baleen length >50 to <90 cm; *postweaning* (age ~2–5 yrs) were classified by baleen length between 90 and 140 cm, *subadults* (age ~6–20) were classified by baleen length between 140 and 250 cm, and *adults* (age ~20+ yrs) were classified by baleen length >250 cm (following Lubetkin et al., 2008, 2012). Ages should be considered as approximations given the uncertainty in estimating age from baleen length, particularly for subadult and adult whales.

2.2. Modeling approach for body condition indices

Four body condition indices were developed based on axillary girth (BCI_C), body volume (BCI_V), dorsal blubber thickness (BCI_{DB}), and ventral blubber thickness (BCI_{VB}). BCI_C was the primary index used in this analysis as axillary girth measurements were collected for most whales. The practice of taking girth measurements at four locations (required to compute body volume) started in 1996, and consistent dorsal and ventral blubber thicknesses measurements² were available only since 2003. Therefore different subsets of the dataset, and hence different time-periods, were used for the various analyses.

Whale body volume was computed by approximating body volume as a series of four frustums. The volume of a frustum V_f is given by:

$$V_f = \frac{\pi l}{12} (d_1^2 + d_1 d_2 + d_2^2),$$

where l is the length and d_1 and d_2 are the diameters of the wider and narrower ends, respectively. An estimated snout diameter of 50 cm together with the four diameters³ at the locations of the girth measurements (axilla, umbilicus, anus, and peduncle) were used to estimate volume (see Appendix A). The lengths of the body sections between girth measurements were calculated using total body length and body proportions reported in George (2009).

We used RStudio (2012) to conduct multiple regression analyses on the data. Models were developed using stepwise multiple linear regressions. The following are the most parsimonious models selected on the basis of Akaike information criterion (AIC) scores.

A body condition index based on axillary girth (BCI_C) was computed for individual whales taken in the spring and fall harvests in order to analyze the relationship between body condition and season. BCI_C was computed as the residuals from the following model, using data from both seasons:

$$\begin{aligned} \text{Girth} = & \text{age class} + \text{length} + \text{season} + \text{age class} : \text{length} \\ & + \text{age class} : \text{season} + \text{error} \end{aligned}$$

BCI_C was also determined using only fall whales in order to be used as the dependent variable in the analysis of a suite of environmental variables calculated for the Beaufort Sea (see Section 2.3). For this analysis, the most parsimonious model based on AIC scores was:

$$\text{Girth} = \text{age class} + \text{length} + \text{season} + \text{age class} : \text{length} + \text{error}$$

For the analysis of body condition indices based on volume (BCI_V), dorsal blubber thickness (BCI_{DB}), and ventral blubber thickness (BCI_{VB}) by season, the most parsimonious model based on AIC scores was the full model:

$$\begin{aligned} V, DB, VB = & \text{age class} + \text{length} + \text{season} + \text{age class} : \text{length} \\ & + \text{age class} : \text{season} + \text{length} : \text{season} \\ & + \text{age class} : \text{length} : \text{season} + \text{error} \end{aligned}$$

The coefficients for the five models presented in this section are reported in Appendix B.

2.3. Environmental data for the Beaufort Sea in summer

The BCB summer bowhead whale habitat was divided into eight regions including the broader Beaufort Sea (to 74.5°N), the Beaufort slope and shelf sub-regions, areas both west and east of the Mackenzie Delta, and the slope and shelf west of Banks Island (Fig. 3). In these regions, environmental data were extracted for the following metrics: (1) monthly open water fraction, (2) duration of the melt season, (3) the onset of freeze-up, and (4) mean monthly upwelling-favorable winds stress. The last metric was used for the slope and shelf sub-regions only.

We utilized the monthly averaged Nimbus-7 Scanning Multi-channel Microwave Radiometer (SMMR) and the Defense Meteorological Satellite Program (DMSP) Special Sensor Microwave Imager (SSM/I) and Special Sensor Microwave Imager/Sounder (SSMIS) passive microwave datasets (Cavaliere et al., 1996) to calculate the fraction of open water (i.e., the inverse of sea ice concentration), following Moore and Laidre (2006). All data, which had been processed using the NASA Team algorithm (Comiso et al., 1997), were accessed from the National Snow and Ice Data Center (Boulder, CO). The data were provided in the polar stereographic projection and with a grid cell size of 25 km × 25 km. Metrics included both monthly and mean summer (July to September) open water fraction.

Dates for the onset of continuous spring melt and continuous fall freeze-up were extracted from a dataset, accessed from NASA's Cryospheric Science Data Portal, that was processed using an algorithm developed by Markus et al. (2009) based on daily averaged brightness temperatures obtained from SMMR and SSM/I passive microwave data. Here, the onsets of continuous spring melt and continuous fall freeze-up were defined as the days of year at which the daily mean temperature remains above freezing and below freezing for the respective seasons. The duration of the melt season was the number of days between these dates.

NOAA's daily NCEP (National Centers for Environmental Prediction) North American Regional Reanalysis (NARR) wind data, based on a physical model that accounts for gaps in available wind station data and time steps, was utilized to analyze the occurrence of upwelling-favorable winds. Data exists for grid points every 0.3 × 0.3 deg. The NARR grid points used for the upwelling-favorable wind analysis in this study were chosen based on their locations over the Beaufort shelf and slope sub-regions (Fig. 3). For the given time periods of analysis (monthly and seasonally), the data from these grid points were averaged to yield a

¹ Whales less than 6 months old were excluded from the analysis ($n = 10$).

² Blubber thickness measurements were made of the dermis only, with the hypodermis excluded (see Fig. 8).

³ Diameters were calculated from girth (circumference) measurements.

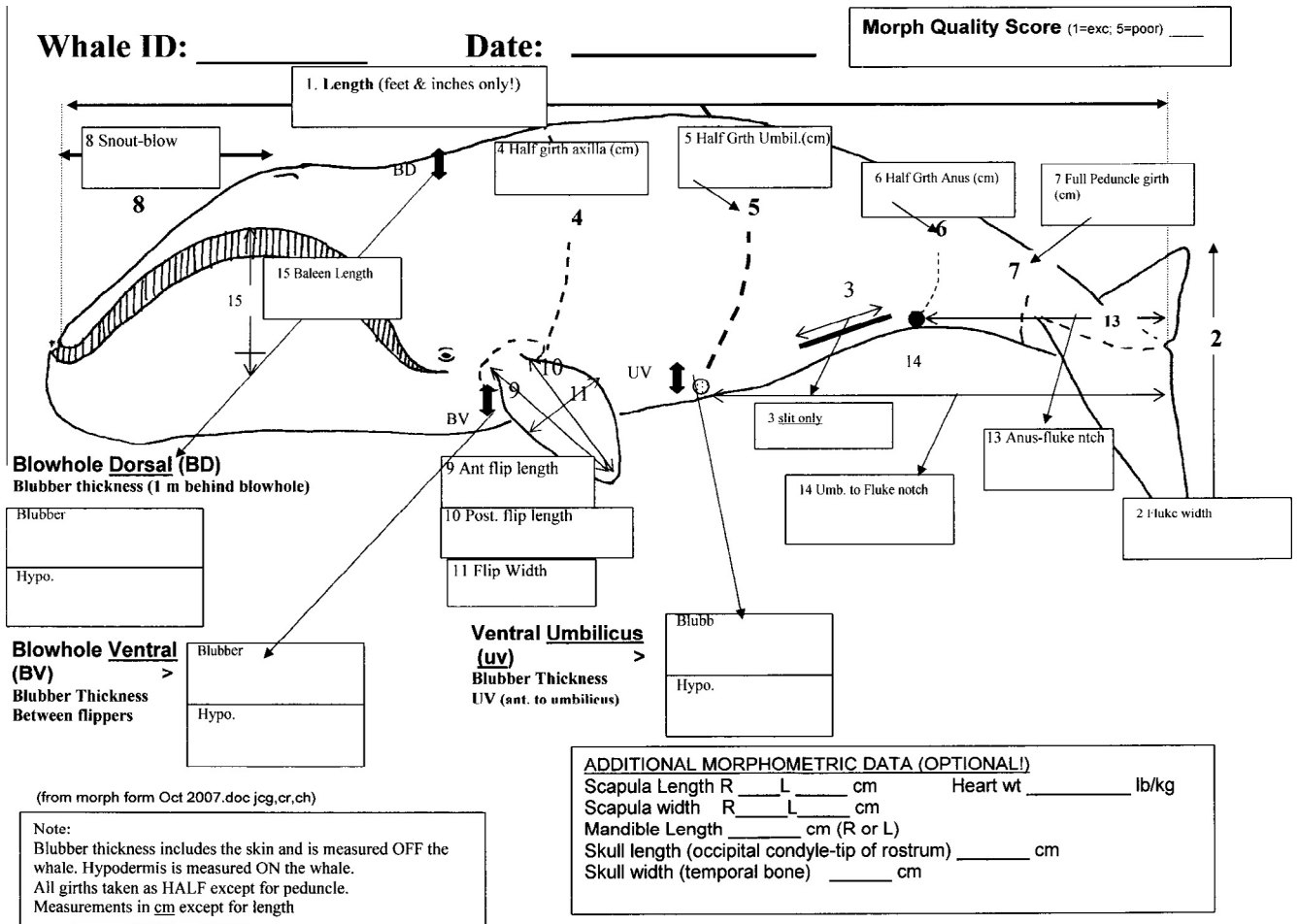


Fig. 2. Diagram of postmortem morphometric measurements for bowhead whales harvested in the Alaskan subsistence hunt.

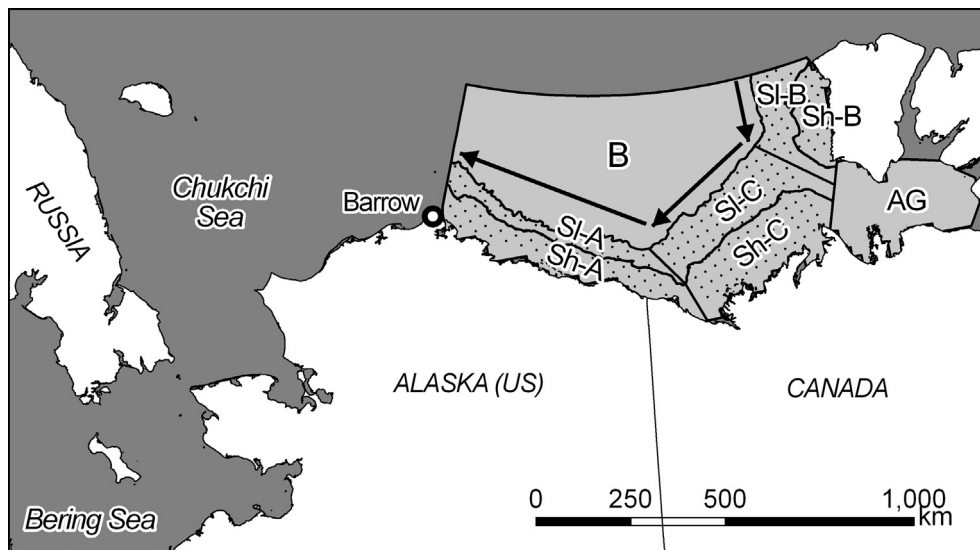


Fig. 3. Map of the eight regions used in this analysis. The larger Beaufort Sea region (B) extends west-to-east from the longitude at Point Barrow to the eastern edge of Amundsen Gulf proper, and south-to-north from the continental coastline to 74.5°N. The Beaufort Shelf (Sh) (waters depths from 0 to 200 m) was divided amongst the shelf that is mostly along the Alaska coast and west of the Mackenzie Delta (Sh-A), the shelf along the Canadian coast and east of the Mackenzie Delta (Sh-C), and the shelf west of Banks Island (Sh-B). The Beaufort Slope (SL) (water depths from 200 to 2000 m) was divided in a similar manner to yield sub-regions SL-A, SL-C, and SL-B. Sub-region AG represents Amundsen Gulf. The black dots represent NARR grid points used for the upwelling wind analysis. Black arrows represent the along-shelf/slope wind component vectors analyzed for each of the shelf/slope pairs.

single regional wind vector in the along-slope directions as indicated by the black arrows in Fig. 3.

In addition to considering the impact of the environmental conditions from a single preceding summer on fall body condition, we used the concept of exponential decay to consider the influence of the three preceding summers combined. With this approach, the environmental influence in a given year is equal to the exponential of years before the present year (0, –1, and –2), such that the three preceding summers were weighted 1, 0.37, and 0.14, respectively. The weighted composite variable, V_C , was calculated as:

$$V_C = 0.67 * V_0 + 0.24 * V_1 + 0.09 * V_2,$$

where V_0 , V_1 , and V_2 represent the variables for 0, 1, and 2 years before present.

3. Results

3.1. Body condition indices

The body condition indices were normally distributed suggesting that standard statistical models were appropriate. BCI_G and BCI_V were significantly influenced by age class, total body length, and season and the interactions between age class and length and age class and season were also statistically significant (Table 1). The significant interaction between age class and season for both axillary girth and volume was most strongly driven by the yearling age class (Fig. 4). The influence of season, as well as the interaction terms, was generally not significant for BCI_{DB} and BCI_{VB} (see Section 3.2).

There was a strong relationship between BCI_G and BCI_V ($r = 0.85$) indicating that axillary girth may serve as a good proxy measurement for volume. Because volume measurements were only available starting in 1996, and very highly correlated with girth, we used BCI_G as the primary BCI for examining longer-term changes in body condition and the influence of environmental variables (Section 3.4).

3.2. Seasonal and age differences in body condition

The results for BCI_G and BCI_V analyses indicate that body condition across all age classes, except yearlings, increased between spring and fall over the summer feeding season (Fig. 5 top panels). The greatest difference between spring and fall BCI_G occurred for post-weaning whales, followed by subadults, and then adults. For adults, the difference in BCI_G and BCI_V between spring and fall, however, was not statistically significant (Table 2). The seasonal difference in blubber thickness (BCI_{DB} and BCI_{VB} ; Fig. 5 bottom panel) was not significantly different for any age class (Table 2).

3.3. Long-term trends in body condition

The analysis of body condition for subadult whales⁴ relative to summer environmental conditions included data from 1989 to 2011.⁵ As noted earlier, we focused on subadults because they showed a marked significant increase in body condition between spring and fall (see Fig. 5) and, unlike yearlings, had been weaned for at least two years. Subadults were also selected because they tend to spend more time in the Beaufort Sea. Subadults are often the leaders in the spring migration arriving first in the Beaufort Sea, and trail during the fall migration being the last to leave the Beaufort Sea (Koski et al., 2006; Suydam and George, 2004). Therefore, subadults likely spend a greater proportion of their time

Table 1

ANOVA tables for body condition models (see Section 2.2) for landed spring and fall bowhead whales at Barrow.

	df	Sum Sq	Mean Sq	F-statistic	p-value [†]
<i>Axillary girth (years 1981–2011; n = 298)</i>					
age class	3	324	108	458.39	<0.001***
length	1	143	143.5	608.86	<0.001***
season	1	4	4.1	17.41	<0.001***
age class:length	3	4	1.4	5.94	<0.001***
age class:season	3	4	1.5	6.27	<0.001***
residuals	286	67	0.2		
<i>Body volume (years 1996–2011; n = 198)</i>					
age class	3	16,963	5654	851.11	<0.001***
length	1	5601	5601	843.14	<0.001***
season	1	99	99	14.96	<0.001***
age class:length	3	495	165	24.81	<0.001***
age class:season	3	115	38	5.77	<0.001***
length:season	1	0	0	0.01	0.905
age class:length:season	3	67	22	3.37	0.020*
residuals	182	1209	7		
<i>Dorsal blubber thickness (years 2003–2011; n = 115)</i>					
age class	3	690	230	36.1	<0.001***
length	1	542	542	85.13	<0.001***
season	1	5	5	0.74	0.392
age class:length	3	53	18	2.77	0.045*
age class:season	3	47	16	2.45	0.068
length:season	1	1	1	0.15	0.695
age class:length:season	3	51	17	2.67	0.052
residuals	99	631	6		
<i>Ventral blubber thickness (years 2003–2011; n = 88)</i>					
age class	3	337	112.5	39.38	<0.001***
length	1	191	190.9	66.83	<0.001***
season	1	5	4.6	1.6	0.21
age class:length	3	12	4.2	1.46	0.23
age class:season	3	10	3.4	1.2	0.32
length:season	1	5	5.5	1.91	0.17
age class:length:season	3	100	33.5	11.72	<0.001***
residuals	72	206	2.9		

[†] Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

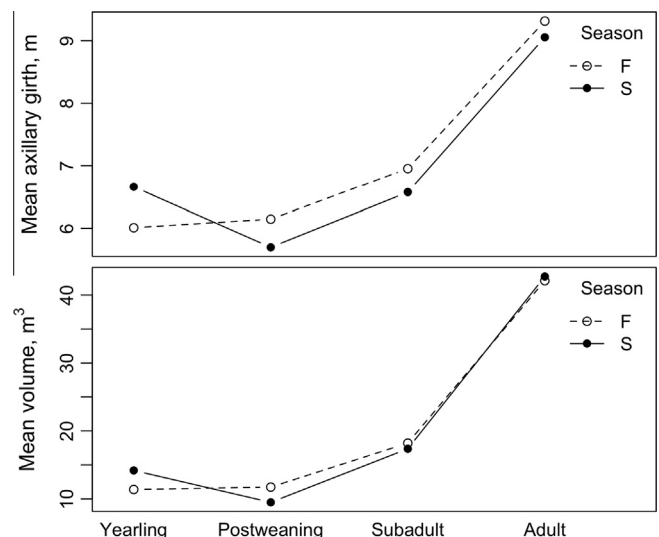


Fig. 4. Interaction plots showing axillary girth (top) and volume (bottom) as a function of age class and season (F = fall, S = spring). Note that the fall animals are on average 'fatter' and more massive except for yearling whales, which lose girth and volume (mass) over their first summer.

within the regions used for our analysis of environmental variables (refer to Fig. 3). Lastly, the subadult age class provided the greatest samples size ($n = 100$) compared with yearlings ($n = 16$), postweaning whales ($n = 39$), and adults ($n = 33$).

⁴ Whales harvested at Barrow in fall with high data quality scores.

⁵ During the early to mid-1980s, the harvest quotas were low (<5/yr) at Barrow and most strikes were used in the spring hunt leaving few or none for the fall hunt.

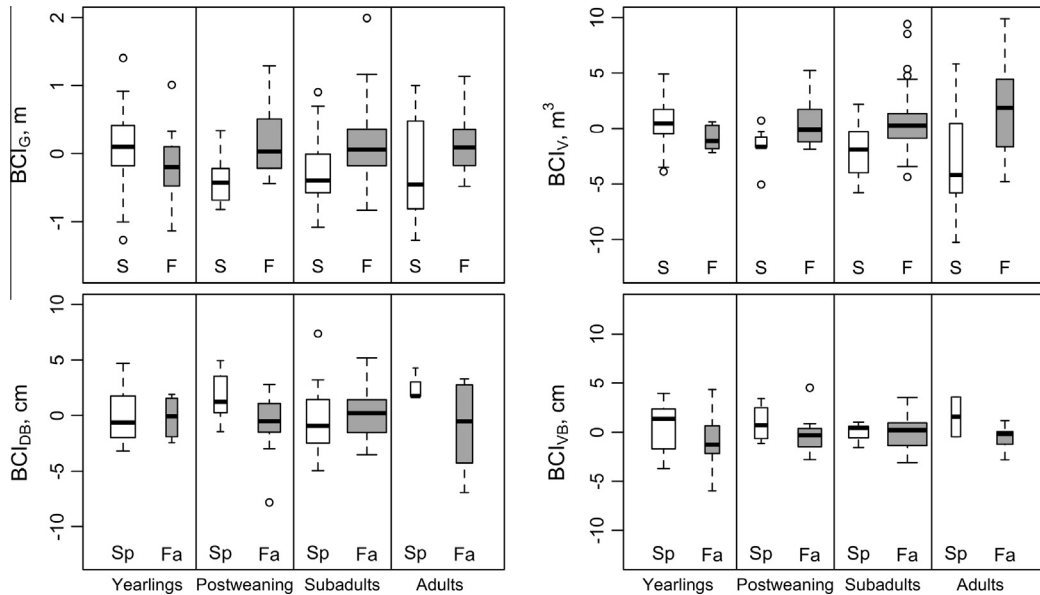


Fig. 5. Seasonal comparisons (S = spring, F = fall) of the BCI's for different age classes and life stages. Box widths are proportional to the square-roots of the number of observations in the groups. BCI = body condition index (subscripts: G = girth, V = volume, DB = dorsal blubber, VB = ventral blubber). Note that blubber thickness does not change significantly ($p > 0.05$) between seasons, however girth and volume increase after the summer feeding season. Yearlings are an exception and lose weight after weaning and leaving their mother.

Table 2

Results of seasonal comparisons of various body condition metrics by age class (also see Fig. 5). BCI = body condition index; G = girth, V = volume, DB = dorsal blubber, VB = ventral blubber.

	<i>t</i>	df	<i>p</i> -value
<i>BCI_G</i>			
Yearlings	1.7	32	0.11
Postweaning	-5	46	<0.001***
Subadult	-4	64	<0.001***
Adult	-1.6	21	0.13
<i>BCI_V</i>			
Yearlings	2.3	29	0.028*
Postweaning	-2.5	9.5	0.032*
Subadult	-4	27	<0.001***
Adult	-2	13	0.061
<i>BCI_{DB}</i>			
Yearlings	0.18	5	0.87
Postweaning	1.7	7.1	0.13
Subadult	-0.61	19	0.55
Adult	2.1	9	0.063
<i>BCI_{VB}</i>			
Yearlings	0.66	5.6	0.53
Postweaning	1.1	4.6	0.34
Subadult	-0.23	22	0.82
Adult	1	1.2	0.48

Over the period of 1979–2011, the open water fraction in the Beaufort Sea (region B) increased by approximately 9% and 11% per decade for summer (July to September) and September, respectively (see Fig. 6; Druckenmiller unpublished data). Over the shorter time period of 1989–2011 (the period in which reliable body condition data were available for subadult whales), BCI_G for subadult whales demonstrated a marked significant increase of 2.7% per decade, with a noticeable reduction in the size of the 95% confidence interval of BCI_G in recent years (Fig. 6). We initially suspected the reduction in uncertainty was due to a refinement in how axillary girth measurements were taken; however data quality scoring was consistent through this period. We suspect the reduction in uncertainty (BCI_G) after 2000 may be due to larger sample sizes (more whales landed), less variation in body

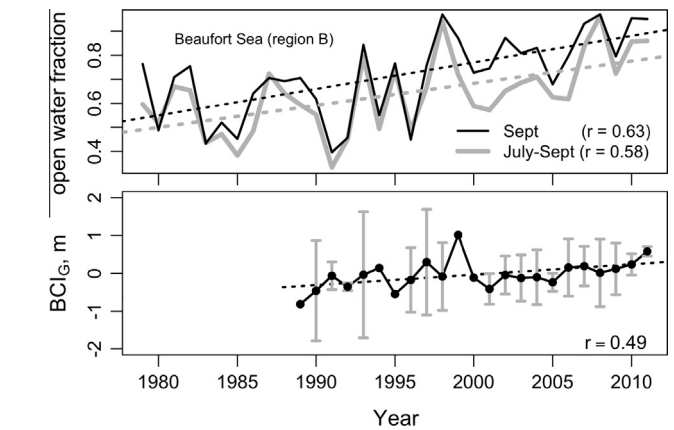


Fig. 6. Top: Plot of the mean open water fraction during summer (July to September) and September (month of the sea ice minimum) for the Beaufort Sea (region B in Fig. 3) from 1979 to 2011. Bottom: Trend in BCI_G (body condition index based on axillary girth only) for fall subadult bowhead whales (1989–2011; $n = 100$). Each annual data point is a mean for all whales caught in a given fall season. Error bars represent the 95% confidence interval for the whales taken each year. The *r*-values for the respective linear regressions are provided for each data series.

condition between whales, and less interannual variability in sea ice conditions.

3.4. Influence of Beaufort Sea summer conditions on fall body condition

We examined correlations between BCI_G of fall subadult whales (taken at Barrow) and a range of independent environmental variables including, open water fraction (Table 3), the duration of the melt season and the onset of continuous freeze-up (Table 4), and upwelling-favorable winds (Table 5). The results for analyses of the preceding summer and the previous three summers were highly correlated. Therefore, for brevity we mainly focused on the results using data from the preceding summer. However, it is

Table 3

Linear regression results of BCI_G against mean open water fraction for the preceding summer and the three previous summers combined for each region (see Fig. 3).

Region and time period		Mean open water fraction (1 year)			Mean open water fraction (3 year)		
		Slope	Std error	p-value	Slope	Std error	p-value
B	July	0.393	0.269	0.1500	0.740	0.343	0.0330*
	August	0.775	0.320	0.0170*	1.046	0.400	0.0100*
	September	0.722	0.268	0.0084**	0.879	0.350	0.0140*
	Summer	0.718	0.306	0.0210*	1.022	0.390	0.0100*
Sh-A	July	0.392	0.222	0.0800	0.621	0.277	0.0270*
	August	0.892	0.451	0.0510	1.512	0.590	0.0120*
	September	0.808	0.471	0.0890	1.001	0.683	0.1500
	Summer	0.840	0.395	0.0360*	1.284	0.511	0.0140*
SI-A	July	0.314	0.188	0.0970	0.506	0.231	0.0310*
	August	0.591	0.314	0.0630	0.956	0.400	0.0190*
	September	0.552	0.336	0.1000	0.743	0.460	0.1100
	Summer	0.572	0.293	0.0540	0.881	0.372	0.0200*
Sh-C	July	0.269	0.313	0.3900	0.652	0.450	0.1500
	August	0.932	0.483	0.0570	1.410	0.680	0.0410*
	September	0.689	0.363	0.0610	0.886	0.563	0.1200
	Summer	0.978	0.493	0.0500	1.629	0.727	0.0270*
SI-C	July	0.219	0.184	0.2400	0.515	0.266	0.0550
	August	0.639	0.222	0.0049**	0.922	0.302	0.0029**
	September	0.543	0.191	0.0055**	0.786	0.274	0.0050**
	Summer	0.551	0.220	0.0140*	0.894	0.309	0.0047**
Sh-B	July	0.278	0.157	0.0800	0.461	0.198	0.0220*
	August	0.378	0.148	0.0120*	0.509	0.188	0.0080**
	September	0.532	0.157	0.0010**	0.718	0.204	0.0007***
	Summer	0.438	0.162	0.0083**	0.602	0.204	0.0040**
SI-B	July	0.295	0.192	0.1300	0.546	0.251	0.0320*
	August	0.408	0.178	0.0240*	0.594	0.227	0.0100*
	September	0.469	0.167	0.0059**	0.699	0.220	0.0019**
	Summer	0.456	0.190	0.0190*	0.686	0.243	0.0058**
AG	July	0.337	0.343	0.3300	0.839	0.466	0.0750
	August	1.670	1.210	0.1700	3.050	1.750	0.0850
	September	1.650	1.060	0.1200	2.530	1.660	0.1300
	Summer	1.182	0.803	0.1400	2.388	1.106	0.0330*

Table 4

Linear regression of BCI_G against the duration of melt season and the date of continuous freeze-up. Independent variables are from the (A) preceding summer and (B) preceding three summers. Note that the 3-yr previous summer composite variable improves the overall correlation; especially for the duration of melt season.

Sub-region and variable	Duration of melt season			Date of continuous freeze-up		
	Slope	Std error	p-value	Slope	Std error	p-value
<i>(A) Preceding summer</i>						
B	0.007	0.003	0.0130*	0.010	0.004	0.0093**
Sh-A	0.006	0.003	0.0240*	0.007	0.003	0.0470*
SI-A	0.006	0.002	0.0160*	0.007	0.003	0.0093**
Sh-C	0.004	0.002	0.1100	0.007	0.004	0.0860
SI-C	0.005	0.002	0.0073**	0.009	0.003	0.0020**
Sh-B	0.005	0.002	0.0240*	0.009	0.003	0.0055**
SI-B	0.004	0.002	0.0640	0.008	0.003	0.0250*
AG	0.003	0.002	0.1900	0.005	0.004	0.2600
<i>(B) Preceding three summers</i>						
B	0.012	0.004	0.0021**	0.014	0.005	0.0035**
Sh-A	0.011	0.004	0.0058**	0.009	0.004	0.0320*
SI-A	0.010	0.003	0.0033**	0.010	0.003	0.0043**
Sh-C	0.006	0.003	0.0380*	0.010	0.005	0.0500
SI-C	0.008	0.002	0.0009***	0.013	0.004	0.0004***
Sh-B	0.006	0.002	0.0095**	0.011	0.004	0.0028**
SI-B	0.006	0.003	0.0150*	0.012	0.004	0.0048**
AG	0.006	0.003	0.0560	0.008	0.006	0.1500

worth noting that some of the strongest correlations between body condition and environmental metrics were for the preceding 3-years (e.g., Table 3, Sh-B in September).

Statistically significant correlations were found between fall sub-adult BCI_G and mean open water fraction over most of the summer periods in several regions (Table 3). The strongest correlations occurred in September in the Beaufort Sea region (B), the Canadian slope (SI-C), and the regions west of Banks Island (SI-B and Sh-B). Significant positive correlations were found for BCI_G versus the duration of melt season and the onset of freeze-up in all regions except for the Canadian shelf (Sh-C) and Amundsen Gulf (AG) (Table 4; Fig. 7). The date of continuous freeze up showed a higher correlation with BCI_G than did the duration of melt season. Significant correlations between BCI_G and mean upwelling-favorable wind stress were scattered amongst the regions but were highest for the Canadian shelf and slope waters (Sh-C and SI-C) in August (Table 5). The Alaskan shelf (Sh-A) and SI-B showed the least correlations between BCI_G and upwelling wind.

While not reported here, we examined the interaction between open water fractions and upwelling-favorable winds given that a reduced sea ice cover increases the coupling between atmosphere and ocean. We found significant interactions were limited to the Canadian shelf (Sh-C) and the Canadian and Alaskan slopes (SI-C and SI-A) during the early summer (July).

4. Discussion

We analyzed morphometric data from harvested bowhead whales and physical environmental parameters to explore both seasonal and long-term changes in bowhead whale body condition. These data comprise one of the few comprehensive and long-term

Table 5

Linear regressions of BCI_G against mean upwelling wind stress for the preceding summer and the three previous summers combined for each region (see Fig. 3). A negative slope for mean along shelf/slope wind stress suggests a positive correlation between upwelling-favorable wind and BCI since a negative wind leads to upwelling.

Sub-region and time period		Mean along shelf/slope wind stress (1 year)			Mean along shelf/slope wind stress (3 year)		
		Slope	Std error	p-value	Slope	Std error	p-value
Sh-A	July	-4.8	3.4	0.1600	-7.2	4.1	0.0810
	August	-6.9	3.6	0.0580	-10.2	5.0	0.0440*
	September	-0.6	1.6	0.7300	-2.6	2.2	0.2300
	Summer	-4.4	3.4	0.2000	-7.5	4.0	0.0640
SI-A	July	-4.2	3.3	0.2100	-6.8	4.0	0.0970
	August	-7.2	2.7	0.0095**	-10.9	4.0	0.0073**
	September	-1.5	1.5	0.3200	-4.0	2.1	0.0580
	Summer	-6.4	3.1	0.0410*	-10.1	3.8	0.0099**
Sh-C	July	-3.4	7.5	0.6500	-10.1	11.9	0.4000
	August	-22.8	6.0	0.0002***	-30.9	7.9	0.0002***
	September	-3.7	2.3	0.1000	-6.1	3.0	0.0430*
	Summer	-14.6	5.6	0.0100*	-19.1	6.8	0.0059**
SI-C	July	-0.3	8.2	0.9700	-5.3	13.8	0.7000
	August	-23.2	6.5	0.0006***	-29.1	8.4	0.0008***
	September	-5.8	2.5	0.0210*	-9.0	3.3	0.0081**
	Summer	-19.1	6.2	0.0026**	-25.8	7.8	0.0014**
Sh-B	July	-4.9	4.5	0.2800	-8.8	5.8	0.1300
	August	-10.5	5.1	0.0410*	-14.8	6.9	0.0340*
	September	-8.9	5.7	0.1200	-15.1	6.9	0.0300*
	Summer	-14.8	6.9	0.0340*	-19.8	8.1	0.0160*
SI-B	July	-4.8	6.2	0.4400	-10.4	8.0	0.1900
	August	-14.4	8.4	0.0920	-22.0	11.2	0.0520
	September	-9.9	7.4	0.1800	-19.3	8.9	0.0320*
	Summer	-16.1	9.7	0.0990	-25.1	11.2	0.0280*

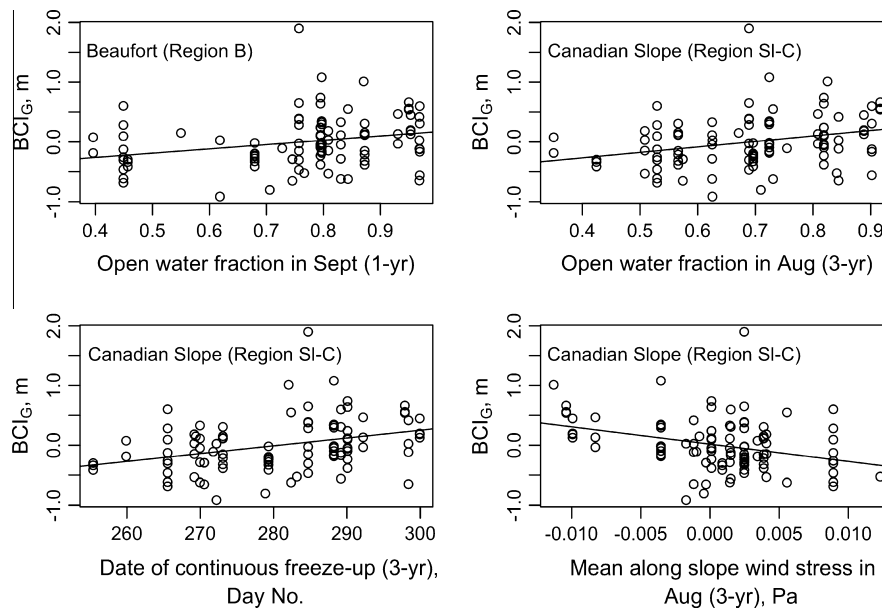


Fig. 7. Scatter plots and linear models of selected environmental metrics against body condition for specific regions examined in this study. See Section 4.3 for a full discussion of these plots. These time series indicate a positive response in bowhead body condition to these environmental metrics. Note that negative wind stress indicates upwelling-favorable easterly winds.

datasets on Arctic cetacean body condition available and spans a period of extensive environmental changes in the Arctic. This allowed us to analyze the relationship between body condition and ecosystem variability.

4.1. Utility of the body condition index

The girth-based body condition index for bowheads provides a relatively robust metric for estimating body condition. The error in our measurements is on the order of ± 10 cm, which results in low

relative error (~ 1 – 2%) since bowheads are large animals (NSB unpublished data). A concern was that whales harvested in fall, which tend to have more engorged stomachs than those harvested in spring (Lowry et al., 2004; NSB unpublished data), could lead to a positive bias on body condition indices. However, axillary girth (BCI_G) is taken anterior to the gut and is not affected by stomach volume; thus avoiding possible bias (Fig. 8). Additionally, bowheads have relatively small stomachs so we suspect that bias in body volume (BCI_V) estimates, which rely on girth measurements at the umbilicus, is small.

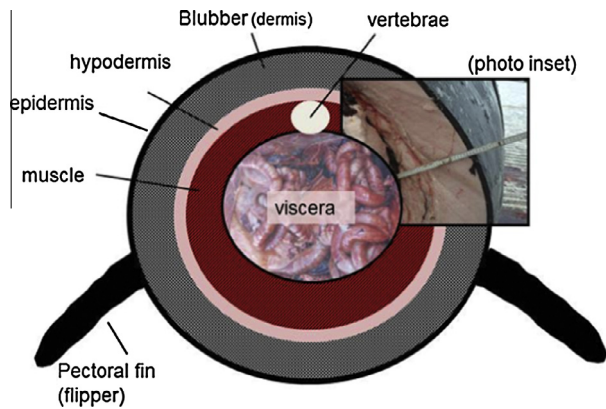


Fig. 8. Diagram of a cross section of a bowhead whale at the level of the umbilicus. Changes in body girth (and mass) are likely driven by the amount of hypodermis, visceral fat and perhaps muscle mass. Note the inset photograph of a cross section of a yearling (“ingutuk”) bowhead showing the epidermis (skin), dermis (blubber), thick hypodermis (fat underlying the blubber) and skeletal muscle.

While differences in blubber thickness between seasons do not appear to be significantly different, there could be small changes (ca ± 2 cm) that go undetected with our methods. However, for body girth measurements, even a small increase in muscle mass, hypodermis, and/or visceral fat (i.e., “body radius”) results in a 6-fold (2π) increase in girth which can be detected and measured using our methods.

4.2. Seasonal changes in body condition

Bowhead whales exhibit seasonal changes in body condition (BCI_G and BCI_V ; see Fig. 5) depending on age class. This was particularly true for subadult whales, which had a significantly higher BCI_G and BCI_V in fall than in spring. We presume this fattening is due to summer feeding opportunities. Subadults are likely dependent on summer feeding more than other age classes due to the fact they have recently become independent. Freshly weaned yearlings lose body condition through their first summer and likely for several subsequent seasons (2–3 years). This is probably because their baleen rack is under-developed and does not allow for effective feeding after they have left their mother. Thus, sufficient baleen length is likely a prerequisite for growth in body length (e.g., Lubetkin et al., 2008; George, 2009), as well as summertime fattening.

As is the case with gray whales (*Eschrichtius robustus*), bowhead whales’ blubber thickness does not significantly differ between seasons (Rice and Wolman, 1971; George, 2009) (BCI_{DB} and BCI_{VB} ; see Fig. 5). This does not appear to be true for fin whales (*Balaenoptera physalus*), which show seasonal differences in both blubber thicknesses and body girths (Lockyer, 1987). Gray whales show a dramatic seasonal change in body girth (Rice and Wolman, 1971), while adult bowheads appear to stay at a fairly high level of nutrition throughout the year and do not show such dramatic differences (Table 2; George, 2009). However, this is not the case for subadult bowhead whales for the reasons described earlier. The reason for a detectable difference in girth without a measureable difference in blubber thickness in bowhead whales is in part due to changes in the thickness of the hypodermis layer (fat layer between the muscle and the blubber layer), visceral fat (fat associated with the internal organs and gut, generally around the kidneys, stomach and intestines), and possibly also overall muscle mass (Fig. 8). Further, blubber has an important structural function and changes little in dimension between seasons while lipid densities do vary – at least for bowheads (Mau, 2004) and gray whales.

Table 6

Correlation matrix for open water fraction by month. Note that the Beaufort region (B) as a whole is strongly correlated with the sub regions.

	B	Sh-A	SI-A	Sh-C	SI-C	Sh-B	SI-B	AG
July								
B	1.00							
Sh-A	0.85	1.00						
SI-A	0.88	0.99	1.00					
Sh-C	0.72	0.63	0.66	1.00				
SI-C	0.89	0.71	0.76	0.83	1.00			
Sh-B	0.80	0.59	0.63	0.54	0.83	1.00		
SI-B	0.85	0.59	0.64	0.58	0.88	0.95	1.00	
AG	0.63	0.39	0.41	0.27	0.43	0.53	0.53	1.00
August								
B	1.00							
Sh-A	0.76	1.00						
SI-A	0.84	0.97	1.00					
Sh-C	0.63	0.55	0.55	1.00				
SI-C	0.84	0.62	0.67	0.84	1.00			
Sh-B	0.69	0.32	0.39	0.57	0.82	1.00		
SI-B	0.79	0.39	0.45	0.60	0.86	0.94	1.00	
AG	0.57	0.41	0.41	0.65	0.64	0.65	0.61	1.00
September								
B	1.00							
Sh-A	0.74	1.00						
SI-A	0.81	0.96	1.00					
Sh-C	0.74	0.69	0.69	1.00				
SI-C	0.88	0.68	0.71	0.87	1.00			
Sh-B	0.74	0.45	0.49	0.65	0.84	1.00		
SI-B	0.77	0.39	0.42	0.56	0.79	0.91	1.00	
AG	0.60	0.44	0.53	0.84	0.72	0.53	0.46	1.00

4.3. Environmental factors affecting body condition

Our results indicate an overall increase in bowhead whale body condition (BCI_G) and a positive correlation with summer sea ice loss over the last 2.5 decades (Fig. 6). We speculate that sea ice loss has positive effects on secondary trophic production within the bowhead’s summer feeding regions in the BCB, which may lead to increases in the densities of bowhead prey such as copepods and euphausiids. The long-term increase in BCI_G is likely associated with reduced ice cover, duration of open water, upwelling potential (wind stress), and a more productive arctic marine ecosystem favoring the types of water-column invertebrates which constitute the main bowhead prey species.

Bowhead whale body condition (BCI_G) was correlated to broad scale environmental conditions within the Beaufort Sea (B) region, including open water fraction, duration of the melt season, and date of continuous freeze-up. Highly significant correlations were also found for these variables, along with upwelling favorable winds, in smaller sub-regions that are important to bowhead whales. The highest correlations between BCI_G and environmental conditions in sub-regions during the preceding summer were on the slope and shelf waters off the Mackenzie River Delta and shelf waters west of Banks Island (Tables 3–5). While our results correspond well with the regions used by bowhead whales that have been tracked with satellite telemetry, the sub-region west of Banks Island (Sh-B) was not determined to be a bowhead feeding “hot spot” based on radio telemetry analysis (Quakenbush et al., 2012; Citta et al., 2015), nor by limited aerial surveys (Moore and Reeves, 1993). Quakenbush et al. (2012) report the late spring and early summer eastward migration of bowhead whales through our study region as, in progressive order, through SI-A, SI-C, Sh-C and AG, while Citta et al. (2015) report bowheads lingering on the Canadian Shelf (Sh-C) and the western portion of Amundsen Gulf (AG) from early May through late-September. It is likely that the sub-region Sh-B was identified as significant in this study because ice conditions within these sub-regions are highly

correlated (see Table 6) due to the nature of sea ice patterns in the eastern Beaufort.

Sea ice interacts with the primary production of the Arctic Ocean in at least two ways. The structural layer at the bottom of the ice provides a substrate for ice algae, and ice thickness and snow cover can limit light penetration/availability to both ice algae and phytoplankton (Smetacek and Nicol, 2005; Søreide et al., 2010). The ice algae growing season is restricted to the period when the ice cover is consolidated and when there is enough light reaching the bottom of the ice. Phytoplankton production is restricted to the euphotic zone and mostly begins after the breakup of ice (Søreide et al., 2010). Arrigo et al. (2012), however, suggest that the shift toward seasonal ice, which is thinner than multi-year ice, and the associated decrease in the albedo of melt ponds (Perovich and Polashenski, 2012) supports under-ice phytoplankton blooms at a scale that was once believed to only occur in open water. As the Arctic sea ice cover is thinned and reduced in extent and temporal coverage, more solar energy enters the ocean, adding heat to the upper layer and increasing the availability of photosynthetically active radiation (PAR) for primary production (Pabi et al., 2008).

Several studies have investigated the effect of reduced sea ice cover on primary production. Arrigo and van Dijken (2004) found that the most intense phytoplankton blooms occurred when the water column was stratified in late spring through warming and ice melt, prior to nutrient depletion, while later summer blooms (August and September) benefited from mixing that replenished nutrients. Using ocean color data spanning 1998 through 2009, Arrigo and van Dijken (2011) found that the annual net primary production in the Arctic Ocean increased by 20% from 441 to

585 Tg C yr⁻¹ due to a 27% decrease in sea ice concentration and a 45 day increase in the growing season. Arrigo et al. (2008) concluded that continental shelves in the Pacific Arctic experienced the largest recent increases in annual net primary production (NPP) because they are more susceptible to nutrient replenishment by advection and vertical mixing processes. The sea ice cover also acts to decouple ocean dynamics from atmospheric forcing. With sea ice retreating beyond shelf breaks, more storms and upwelling may bring nutrient rich Atlantic water onto the shelves (Carmack and Chapman, 2003; Tremblay et al., 2008; Pickart et al., 2009).

Ashjian et al. (2010) and Okkonen et al. (2011) have shown that euphausiids that are advected northward from the Bering Sea are often concentrated locally in the waters near Point Barrow (“Barrow krill trap”) as a result of bathymetry, geography and particular wind driven oceanographic processes. It is likely that several other reoccurring and persistent prey traps exist along the Beaufort Sea coast that are responsible for bowhead aggregations (e.g., north of the Tuktoyaktuk Peninsula; Quakenbush et al., 2012; Moore and Reeves, 1993). The significance of the onset of freeze-up in nearly all regions of the Beaufort Sea may be a trigger for bowheads to depart from the productive summer feeding waters and to begin their fall migration toward the Bering Sea.

Søreide et al. (2010) identified a coupling between the relative timing of ice algae and phytoplankton blooms and the reproduction and ontogenic development of *Calanus glacialis*—an arctic grazer that accounts for up to 80% of the secondary biomass in the arctic shelf seas and an important prey species for bowhead whales. If phytoplankton blooms occur earlier due to an earlier ice break-up or thinning ice, then the time lag between the ice algae bloom, which is largely fixed based on the solar cycle, and

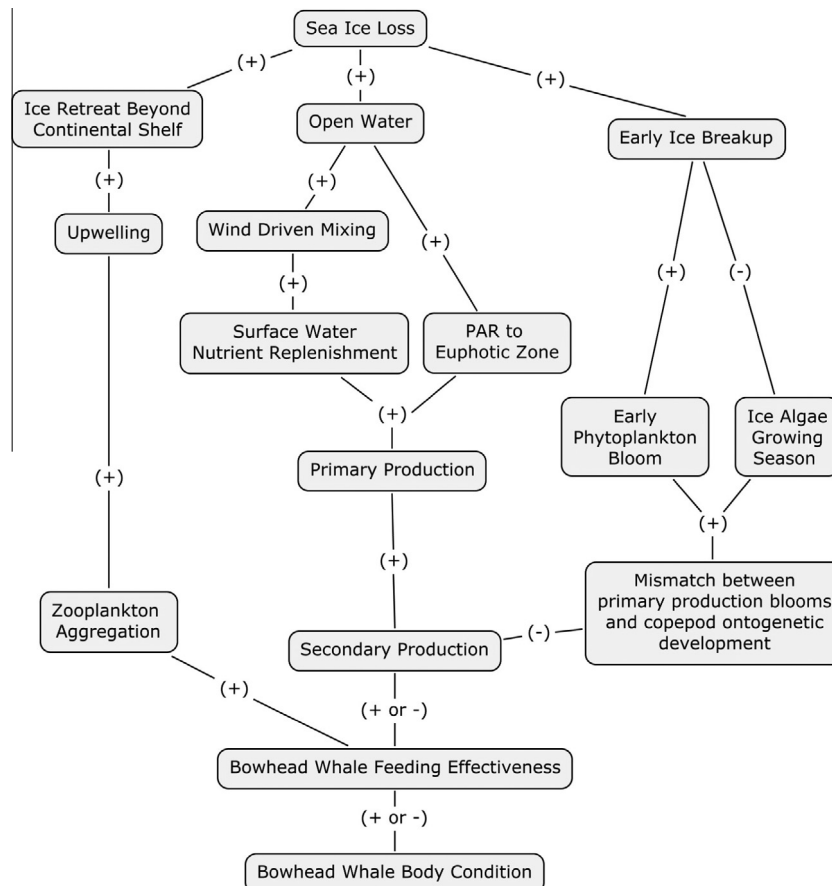


Fig. 9. Conceptual model for how changes in Arctic sea ice may have (a) positive or (b) negative impacts on bowhead whale body condition. The model begins at the top of the figure and the “+” and “-” signs indicate possible positive or negative effects. PAR = photosynthetically active radiation.

the phytoplankton bloom will shorten (Søreide et al., 2010). This may have consequences for the development of *C. glacialis* as female reproduction benefits from the ice algae bloom, while the first feeding nauplii stages benefit from the later phytoplankton bloom (Søreide et al., 2010). The adaptability of *C. glacialis* to take advantage of changes in the timing of blooms remains unknown (Søreide et al., 2010).

Our conceptual model shown in Fig. 9 summarizes the possible links between sea ice loss and bowhead whale body condition as discussed in this paper. The loss of sea ice and hence the general increase in open water may lead to greater mixing and, as a result, provide a means for the replenishment of nutrients to surface waters. This, accompanied with increased PAR to the euphotic zone, may increase primary production, which in turn supports increased secondary production. Sea ice loss that results in greater open water over the continental shelves may support increased upwelling at the shelf breaks, providing the occurrence of upwelling favorable winds, which may aggregate zooplankton. In general, an increase in secondary production, which implies an increase in bowhead prey, together with greater aggregation of that prey may increase the effectiveness of bowhead feeding in the region, which would serve to increase body condition on a seasonal basis. Fig. 9 also highlights the importance of timing within the Arctic food web by including the role an early ice break-up may potentially play in leading to a mismatch between peaks in primary production and the reproductive and ontogenetic development of copepods (Søreide et al., 2010). Such a mismatch may reduce overall secondary production, which would have a negative influence on bowhead feeding effectiveness simply by less food being available.

The relationship between body condition for Arctic marine mammals and loss of sea ice is complicated and likely a function of the position the species occupies in the food web, the influence of sea ice on foraging patterns and prey availability, and regional differences in productivity (Moore et al., 2014). At shorter time scales, there is increasing evidence that Arctic marine mammals demonstrate variability in ecological responses to climate change, which means that some populations are doing well (according to demographic or body condition metrics) despite sea ice decline (see Divoky et al., 2015; Crawford et al., 2015; Harwood et al., 2015). In Alaska for instance, body condition of polar bears in the Chukchi Sea has been high between 2008 and 2011 when compared to historic data, and higher than that of the neighboring southern Beaufort Sea subpopulation where body condition is declining (Rode et al., 2013). In the Bering and Chukchi seas, growth rate, age of maturation, pregnancy rate, blubber thickness, and the proportion of pups in the samples from harvested ringed seals are similar or better in the 2000s than during the 1960s and 1970s (Quakenbush et al., 2011).

Coincidental with increases in body condition reported here, BCB bowhead whale abundance has increased at a rate of 3.7% per year since 1978 (Givens et al., 2013) and now stands at about 17,000 whales (95% CI: 15,704–18,928). While recent increases could also be associated with more extensive and productive feeding opportunities in the Beaufort Sea, we recognize that bowheads are still recovering from Yankee commercial whaling one hundred years ago. On the other hand, Brandon and Wade (2006) estimated the pre-exploitation carrying capacity (K) for BCB bowheads at about 14,000 whales which suggests that the carrying capacity of their range may have increased since the mid-1800s when commercial whaling began.

Some of the main findings of this study are well illustrated by the plots in Fig. 7, as follows: (a) we found a positive correlation between BCI_G and open water fraction for the entire Beaufort Sea study region for the previous September. This increase in open water fraction (0.40–0.97) is correlated with an increase in BCI_G

of 0.41 m; (b) there is a strong positive correlation between BCI_G and the previous 3-year open water fraction for August within the Canadian slope (Region SI-C); there is also a strong positive correlation between BCI_G and date of continuous freeze-up within SI-C; and (c) one of the strongest correlations between BCI_G and the environmental variables is the strong negative correlation between BCI_G and the previous 3-year mean upwelling favorable wind stress on the Canadian slope (Region SI-C) for August. Note that a negative wind stress corresponds to upwelling-favorable winds. This range of wind stress is correlated with an increase in BCI_G of 0.67 m. Said another way, upwelling-favorable easterly winds over a 3-year period were strongly correlated with an increase in BCI_G , resulting in a 67 cm increase in mean girth or roughly 2 tons for a 9-m length whale (George, 2009).

4.4. Conclusions

Length-girth measurements of harvested bowhead whales appear to provide a robust index for estimating body condition, which can be used to understand seasonal changes in body condition and for correlating with annual environmental factors in summer (sea ice density, upwelling potential, ice-free period, etc.). In this study we found that bowheads exhibit strong seasonal differences in body condition particularly for the subadult age class, presumably associated with summer feeding. However, blubber thickness did not change seasonally suggesting that increases in girth are associated with increases in hypodermis, visceral fat and possibly muscle mass. We found yearlings drop in BCI over at least their first summer after leaving their mother and do not grow in body length. This is likely associated with an inability to effectively feed with their relatively short (<100 cm) baleen. Finally, we found significant positive correlations between body condition and environmental factors in regions along the Alaskan and Canadian coast. These regions are consistent with regions identified as important for bowhead feeding in other studies (see Lowry et al., 2004; Walkusz et al., 2012; Bradstreet et al., 1987; Citta et al., 2015). The significant long-term increase in bowhead whale body condition is correlated with reductions in sea ice and other environmental factors, which may be associated with higher production in the Pacific-Arctic marine ecosystem (Bering, Chukchi, and Beaufort Seas) favoring increases in water-column invertebrates.

Acknowledgements

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Appendix A. Method for estimating bowhead whale volume (from: George, 2009)

The approach of stacking frustums was used to compute body volume, V_B . The volume of a frustum V_f is given by:

$$V_f = \frac{\pi l}{12} (d_1^2 + d_1 d_2 + d_2^2)$$

where l is the length and d_1 and d_2 are the diameters of the wider and narrower ends, respectively. Assuming that whales have a distal snout diameter of roughly 50 cm (snout girth was not measured), whale body volume is approximated by stacking frustums according to the performed girth measurements.

V_B is given by:

$$V_B = V_{f1} + V_{f2} + V_{f3} + V_{f4}$$

where V_{f1} , V_{f2} , V_{f3} and V_{f4} – the volumes of individual frustums – are respectively defined as:

$$V_{f1} = \frac{\pi l_1}{12} (d_{snout}^2 + d_{snout} d_{axil} + d_{axil}^2)$$

$$V_{f2} = \frac{\pi l_2}{12} (d_{axil}^2 + d_{axil} d_{umb} + d_{umb}^2)$$

$$V_{f3} = \frac{\pi l_3}{12} (d_{umb}^2 + d_{umb} d_{anus} + d_{anus}^2)$$

$$V_{f4} = \frac{\pi l_4}{12} (d_{anus}^2 + d_{anus} d_{ped} + d_{ped}^2)$$

The previous equations are expressed in terms of girth g by substituting $d = g/\pi$:

$$V_{f1} = \frac{l_1}{12\pi} (g_{snout}^2 + g_{snout} g_{axil} + g_{axil}^2)$$

$$V_{f2} = \frac{l_2}{12\pi} (g_{axil}^2 + g_{axil} g_{umb} + g_{umb}^2)$$

$$V_{f3} = \frac{l_3}{12\pi} (g_{umb}^2 + g_{umb} g_{anus} + g_{anus}^2)$$

$$V_{f4} = \frac{l_4}{12\pi} (g_{anus}^2 + g_{anus} g_{ped} + g_{ped}^2)$$

Therefore,

$$V_B = \frac{l_1 (g_{snout}^2 + g_{snout} g_{axil} + g_{axil}^2) + l_2 (g_{axil}^2 + g_{axil} g_{umb} + g_{umb}^2) + l_3 (g_{umb}^2 + g_{umb} g_{anus} + g_{anus}^2) + l_4 (g_{anus}^2 + g_{anus} g_{ped} + g_{ped}^2)}{12\pi}$$

The total length of a whale l_T from snout to fluke is an available measurement for all whales, while measurements of l_1 , l_2 , l_3 , and l_4 are not and must be expressed in terms of the known proportions to l_T (George, 2009):

$$l_1 = 0.39l_T, \quad l_2 = 0.17l_T, \quad l_3 = 0.19l_T, \quad \text{and} \quad l_4 = 0.17l_T$$

Substituting these gives:

$$V_B = \frac{l_T}{12\pi} [0.39(g_{snout}^2 + g_{snout} g_{axil} + g_{axil}^2) + 0.17(g_{axil}^2 + g_{axil} g_{umb} + g_{umb}^2) + 0.19(g_{umb}^2 + g_{umb} g_{anus} + g_{anus}^2) + 0.17(g_{anus}^2 + g_{anus} g_{ped} + g_{ped}^2)]$$

Appendix B. Coefficients from body condition models

See Table A1.

Table A1
Coefficients^a from body condition models (see Section 2.2).

Models from Section 2.2	(1) Axillary girth	Co.	(2) Axillary girth (fall only)	Co.
(1) Axillary girth = age	(Intercept)	-0.7636	(Intercept)	-0.929
class + length + season + age	ageclassPW	0.387	ageclassPW	-1.079
class:length + age class:season + error	ageclassSA	1.9787	ageclassSA	2.208
(2) Axillary girth = age	ageclassA	0.4366	ageclassA	1.356
class + length + season + age	length	0.8595	length	0.88
class:length + error	seasonS	0.3019	ageclassPW:length	0.101
(3–5) Volume, dorsal blubber, and ventral blubber = age class + length + season + age	ageclassPW:length	-0.0746	ageclassSA:length	-0.335
class:length + age	ageclassA:length	-0.308	ageclassA:length	-0.257
class:season + length:season + age	ageclassPW:seasonS	-0.1833		
class:length:season + error	ageclassSA:seasonS	-0.8824		
	ageclassA:seasonS	-0.6583		
		-0.6122		
(3) Volume	(4) Dorsal blubber	Co.	(5) Ventral blubber	Co.
(Intercept)	(Intercept)	-11.304	(Intercept)	-42.45
ageclassPW	ageclassPW	-15.649	ageclassPW	31.74
ageclassSA	ageclassSA	12.126	ageclassSA	46.15
ageclassA	ageclassA	-5.772	ageclassA	35.29
length	length	3.929	length	7.76
seasonS	seasonS	39.242	seasonS	82.24
ageclassPW:length	ageclassPW:length	1.507	ageclassPW:length	-4.32
ageclassSA:length	ageclassSA:length	-1.961	ageclassSA:length	-6.25
ageclassA:length	ageclassA:length	-0.816	ageclassA:length	-5.44
ageclassPW:seasonS	ageclassPW:seasonS	23.402	ageclassPW:seasonS	-41.9
ageclassSA:seasonS	ageclassSA:seasonS	-40.502	ageclassSA:seasonS	-83.56
ageclassA:seasonS	ageclassA:seasonS	-38.535	ageclassA:seasonS	-218.58
length:seasonS	length:seasonS	-4.856	length:seasonS	-10.13
ageclassPW:length:seasonS	ageclassPW:length:seasonS	-2.534	ageclassPW:length:seasonS	5.28
ageclassSA:length:seasonS	ageclassSA:length:seasonS	4.926	ageclassSA:length:seasonS	10.25
ageclassA:length:seasonS	ageclassA:length:seasonS	5.072	ageclassA:length:seasonS	20.31

^a PW, SA, and A amended to ageclass represent postweaning, subadult, and adult age classes respectively. S amended to season represents spring.

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