TRENDS IN SEA ICE COVER WITHIN HABITATS USED BY BOWHEAD WHALES IN THE WESTERN ARCTIC

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Abstract. We examined trends in sea ice cover between 1979 and 2002 in four months (March, June, September, and November) for four large (~100 000 km^2) and 12 small (~10 000 km^2) regions of the western Arctic in habitats used by bowhead whales (*Balaena mysticetus*). Variation in open water with year was significant in all months except March, but interactions between region and year were not. Open water increased in both large and small regions, but trends were weak with least-squares regression accounting for ≤34% of the total variation. In large regions, positive trends in open water were strongest in September. Linear fits were poor, however, even in the East Siberian, Chukchi, and Beaufort seas, where basin-scale analyses have emphasized dramatic sea ice loss. Small regions also showed weak positive trends in open water and strong interannual variability. Open water increased consistently in five small regions where bowhead whales have been observed feeding or where oceanographic models predict prey entrainment, including: (1) June, along the northern Chukotka coast, near Wrangel Island, and along the Beaufort slope; (2) September, near Wrangel Island, the Barrow Arc, and the Chukchi Borderland; and (3) November, along the Barrow Arc. Conversely, there was very little consistent change in sea ice cover in four small regions considered winter refugia for bowhead whales in the northern Bering Sea, nor in two small regions that include the primary springtime migration corridor in the Chukchi Sea. The effects of sea ice cover on bowhead whale prey availability are unknown but can be modeled via production and advection pathways. Our conceptual model suggests that reductions in sea ice cover will increase prey availability along both pathways for this population. This analysis elucidates the variability inherent in the western Arctic marine ecosystem at scales relevant to bowhead whales and contrasts basin-scale depictions of extreme sea ice retreats, thinning, and wind-driven movements.

Key words: Balaena mysticetus; *Beaufort Sea; Bering Sea; bowhead whale; Chukchi Sea; climate change; ecological scale; sea ice.*

INTRODUCTION

A critical challenge in applied ecology is "interfacing phenomena that occur on different scales of space, time, and ecological organization" (Levin 1992). Physical measures of climate change are commonly examined broadly to detect the effects of shifts in environmental norms on ecosystems or communities (e.g., Forchhammer et al. 2002). While informative on a large scale, this approach may fail to detect changes at the life history scale of individual species, which may confound interpretations about how individuals or populations detect and respond to altered habitats (e.g., Post and Forchhammer 2002, Root et al. 2003). Correlations between climate change and life history events, such as migration or reproduction, provide a basis to model the mechanisms by which natural selection influences phenology (Post et al. 2001). Additionally, when

evaluated at local to regional scales, correlations between climate-induced changes in habitat and long-term population dynamics can help to refine modeling of exogenous influences on life history events (Johnston et al. 2005). Such an approach may be especially important for highly specialized species in extreme environments, such as Arctic marine mammals.

Rapid and dramatic climate change has been reported for the circumpolar High Arctic (ACIA 2004). Specifically, extreme summertime retreats of sea ice (Maslanik et al. 1996, Parkinson et al. 1999, Vinnikov et al. 1999, Parkinson and Cavalieri 2002), a decline of perennial ice cover by 7–9% per decade since 1978 (Comiso 2002, Johannessen et al. 2004), a reduction in sea ice thickness (Yu et al. 2004), impacts of surface winds on movements of thin ice (Rigor and Wallace 2004), and predictions of ~20% reduction in annual ice extent by 2050 (Vinnikov et al. 1999, Serreze et al. 2003) represent a large and growing suite of evidence that global climate warming is rapid and perhaps amplified in the western Arctic (Rigor et al. 2000, IPCC 2001, Johannessen et al. 2004). Reductions of sea ice result in the immediate loss of

critical habitat for ice-obligate marine mammals such as polar bears (*Ursus maritimus*), walruses (*Odobenus rosemarus*), and ice seals (e.g., Stirling 2002, Ferguson et al. 2005). However, impacts on cetaceans are more difficult to gauge (Tynan and DeMaster 1997) because the effects of sea ice loss on polar marine food webs are uncertain (e.g., Tremblay et al. 2002, Arrigo and van Dijken 2004).

The bowhead (*Balaena mysticetus*) is the only baleen whale endemic to the Arctic (see Plate 1). This species is highly adapted to ice-covered seas and can easily navigate through extensive areas of nearly solid sea ice cover (Ellison et al. 1987, George et al. 1989, Mate et al. 2000, Heide-Jørgensen et al. 2003, 2006, Heide-Jørgensen and Laidre 2004). Although capable of navigating dense pack ice, bowhead whales often inhabit open water habitats. For example, they frequently occur in polynyas (recurrent localized areas of open water surrounded by sea ice) and along the marginal ice zone in winter and early spring (Moore and Reeves 1993, Bogoslovskaya 2003) and, in summer and autumn, select open water or light (<40%) to moderate (<70%) sea ice cover (Moore et al. 2000). Bowheads feed on a variety of pelagic and epibenthic zooplankton that are produced in, or advected to, Arctic feeding areas (e.g., Finley 2001, Lowry et al. 2004).

The Bering–Chukchi–Beaufort (BCB) population of bowhead whales, also known as the western Arctic stock (defined here as Arctic and subarctic seas west of 110° W and east of 140° E), is the best-studied of five extant populations (Burns 1993, Moore and Reeves 1993). The BCB population overwinters in the northern Bering Sea and migrates north and east through the Chukchi and Beaufort seas in April–May (Fig. 1). Whales reach feeding grounds in the Canadian Beaufort Sea by June, and migrate west and south across the Alaskan Beaufort and Chukchi seas between August and October. The autumn migration bifurcates at Barrow, with some whales swimming due west toward Wrangel Island (Mate et al. 2000) and others southwest across the Chukchi Sea to the northern Chukotka coast, where feeding has been observed (Miller et al. 1986, Moore et al. 1995). Whales pass south through Bering Strait and return to the northern Bering Sea in November and December (Moore and Reeves 1993, Bogoslovskaya 2003), although specific migration routes remain undefined. Shore-based counts of bowheads migrating along the southeast Chukotka Peninsula and long-term observations (Bogoslovskaya 2003, Melnikov et al. 2004) indicate some deviations from the annual cycle (depicted in Fig. 1). Some whales remain in the Gulf of Anadyr through May and migrate through Bering Strait in June, with the timing of the migration shifted by ≥30 days between cold and mild years. These late-migrating whales may swim north from Bering Strait to an area of varied topography in the Arctic basin called the Chukchi Borderland (Melnikov et al. 1998, Shimada et al. 2004), where copepod biomass (~300 mg/m^3) peaks in June

PLATE 1. Bowhead whales are the only baleen whale endemic to the Arctic. They can live over 100 years, reach 19 m in length, and can be identified by white scars and natural markings, as on this indiviual photgraphed in the Beaufort Sea near Barrow, Alaska. Photo credit J. C. George.

(Kolosova and Melnikov 2001, Ashjian et al. 2003). Furthermore, there is a regular summer occurrence of bowheads reported along the north coast of the Chukotka Peninsula (Bogoslovskaya 2003).

A circumpolar commercial harvest of bowhead whales reduced the species to extremely low numbers by the early 20th century (Bockstoce and Burns 1993, Ross 1993). A periodic springtime census of the BCB population conducted from sea ice pressure ridges at Barrow, Alaska since the mid-1970s estimated the population at 10 470 whales (SE = 1351) and a 3.4%
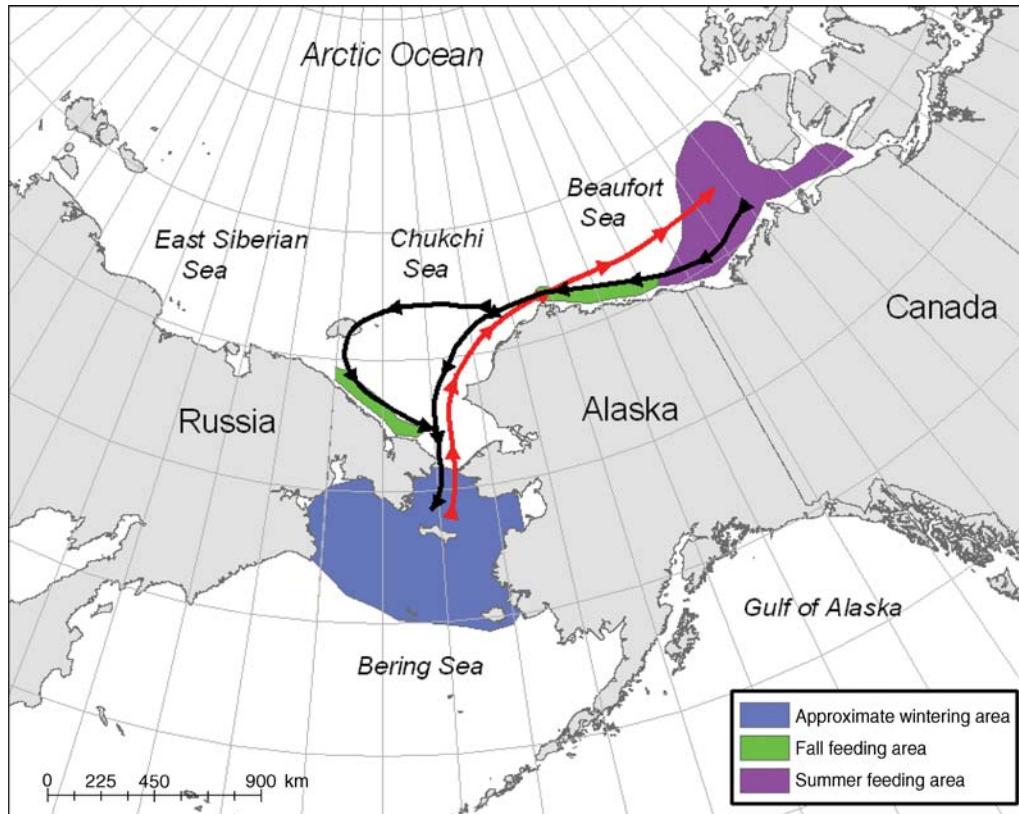
Fig. 1. Generalized Bering–Chukchi–Beaufort (BCB) bowhead whale migration route, feeding areas, and approximate overwintering region. Red line with arrows shows spring migration north and east; black line with arrows shows autumn migration west and south.

annual rate of increase for the period 1978–2001 (George et al. 2004). This population growth was attributed to low anthropogenic mortality, a relatively pristine habitat, and a well-managed subsistence hunt. Concerns for the population are now focused on ecosystem perturbations due to climate change (e.g., loss of sea ice) and accompanying anthropogenic activities (e.g., commercial shipping, fishing and oil development) (George et al. 2004). These concerns underscore the need to delineate habitats key to bowhead whale survival and recruitment and to assess ecological effects of climate change at temporal and spatial scales important to, and perceived by, the population.

In Arctic marine ecosystems, resources are patchy (Ainley and DeMaster 1990), and measurement of habitat features by direct observation is often impossible. In the case of climate change, satellite-based observation of key variables (i.e., sea ice) provides a means to examine habitat changes or habitat loss over a large spatial and regular temporal scale. We used satellite-based observations of sea ice concentration to examine trends in ice cover in 16 regions delineated by seasonal occurrence of BCB bowhead whales, together comprising the full range of the population. Given the

dramatic reductions in sea ice reported for the western Arctic (Comiso 2002, Johannessen et al. 2004) and the potential for sea ice to affect localized prey production (Tremblay et al. 2002, Arrigo and van Dijken 2004), our purpose was to investigate changes in habitats linked to the pattern of seasonal occurrence of BCB bowhead whales and to develop a conceptual model of how sea ice changes could impact their access to prey.

METHODS

Study area and region designations

Trends in sea ice cover were calculated for 16 regions in each of four seasons. Regions were delineated by the seasonal occurrence of bowhead whales and known areas of occupation (Fig. 2). Large regions encompassed >100 000 km² and included seas or ocean basins, such as the Bering Sea (occupied by bowheads in winter), the Chukchi Sea (occupied during spring and autumn migrations), and the Beaufort and East Siberian Seas (occupied during summer and autumn feeding). Small regions were ~10 000 km² and were directly linked to winter refugia (i.e., polynyas), spring and autumn migration corridors, or summer and autumn feeding areas. This included wintertime polynyas near Nunivak Island, St. Matthew Island, St. Lawrence Island/
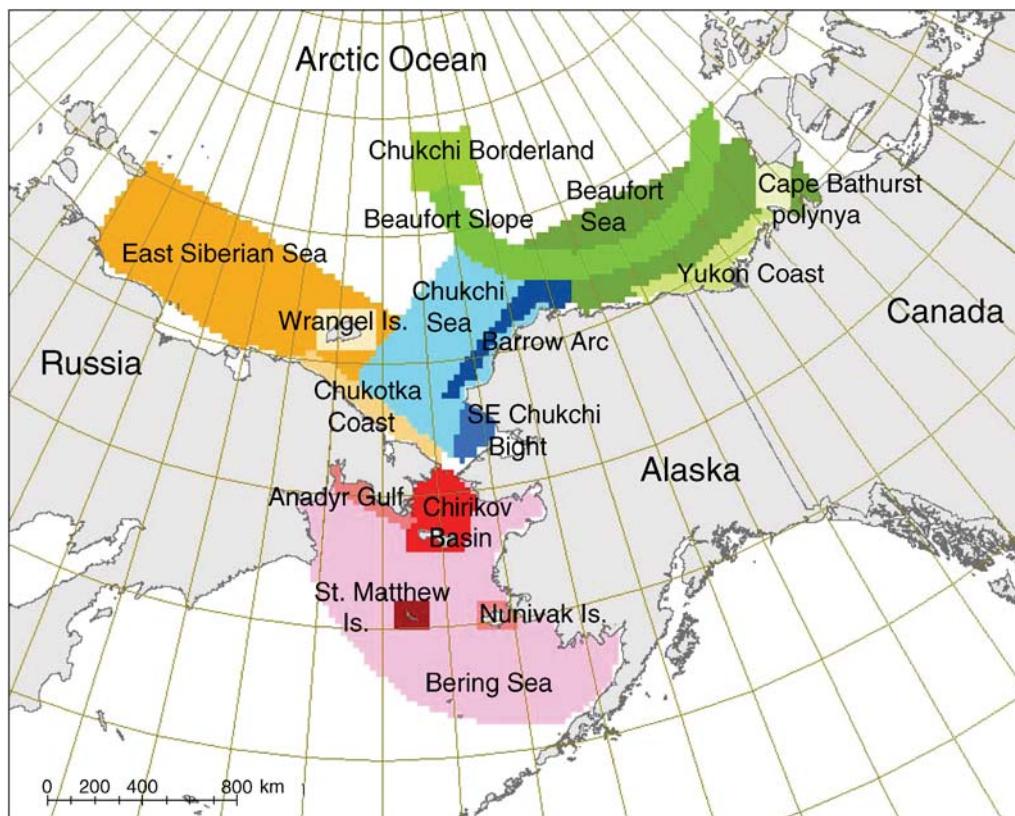
FIG. 2.   Regions used for sea ice cover trend analysis: Bering Sea (red), Chukchi Sea (blue), East Siberian Sea (gold), and Beaufort Sea (green).

Chirikov Basin, and the Northern Gulf of Anadyr, migratory corridors such as the southeast bight of the Chukchi Sea (Chukchi Bight), the lead-polynya that develops southwest and northeast of Barrow (Barrow Arc), and the Beaufort Slope, and certain (or potential) summer and early autumn feeding areas such as waters near Cape Bathurst, the Yukon Coast, along the southern portion of the Beaufort Sea, the Chukchi Borderland (an area of complex topography in the northern Chukchi Sea), Wrangel Island, and the northern Chukotka coast.

Analysis of sea ice cover

Following analyses of sea ice cover in the eastern Arctic (Stern and Heide-Jørgensen 2003, Heide-Jørgensen and Laidre 2004, Laidre and Heide-Jørgensen 2005), we used sea ice concentrations derived from passive microwave telemetry available in two data sets from the National Snow and Ice Data Center (NSDIC): (1) the Nimbus-7 Scanning Multichannel Microwave Radiometer (SMMR) data set, 1979 to 1987; and (2) the Defense Meteorological Satellite Programs Special Sensor Microwave/Imager data set, 1987 to 2001 (data *available online*).[4] These data sets were calibrated by the

NSIDC, resulting in complete and compatible time series. Sea ice concentration (1% resolution) was derived using the bootstrap algorithm from Comiso (1995), where daily concentrations for the Northern Hemisphere were mapped to a polar stereographic projection (true at 70° N) at 25-km resolution. Sea ice data from the NSIDC were converted from raw binary to ASCII format and imported into a geographic information system (ArcINFO 8.3, ESRI 2002) as raster grids. Within each grid, individual pixels (625-km^2 area) were classified as land or sea ice, with the estimate of average sea ice concentration calculated at the center of each pixel. All regions investigated for sea ice trends were larger than 30 pixels (i.e., $>18\,000$ km^2) and all land pixels were consistently classified from year to year.

Monthly composites of sea ice cover were created as the product of the vertical spatial and temporal average ice concentration for each pixel for all days of the month each year and used to calculate the percentage (fraction) of open water following methods reported in Heide-Jørgensen and Laidre (2004). The months of March, June, September, and November captured maximum ice extent, break-up, maximum ice retreat and ice formation, respectively, providing a "seasonal snapshot" of sea ice trends. The fraction of open water (i.e., the ice-free portion of each habitat, F) was modeled as follows:

$$F = \frac{\sum_{i=1}^{h}\{PC \times [1-(IC/100)]\}}{HA}$$

where i indexes the lowest sea ice concentration in the region to h, the highest sea ice concentration, IC is specific sea ice concentration calculated in full integer units and recorded as a percentage, PC is pixel count for each specific sea ice concentration, and HA is the habitat area in number of pixels.

Analysis of sea ice correlation, covariance, and trends

Autocorrelation in the time series was calculated for all 16 regions in each of four seasons out to 10 years. We used an analysis of covariance (ANCOVA) to examine the influence of region (main effect) and year (covariate) on spatial variation of the fraction of open water. Because the fraction of open water may be correlated among seasons, we performed separate ANCOVAs for March, June, September, and November. Trends in sea ice cover for each region were examined using least squares, as in Comiso (2002) and Parkinson (2000). Trends were expressed as the percentage of change per year over the 24-year record, with a measure of line-fit provided by the coefficient of determination (r^2).

RESULTS

Correlation and covariance

Little year-to-year correlation was present in the detrended time series, with autocorrelation coefficients ranging from −0.01 to 0.3. Spatial correlation between regions during periods of high or receding ice cover (November, March, and June) was negligible (0.1 to 0.2) or often zero. Correlation during the ice minima in September increased to values between 0.55–0.72, with the exception of regions adjacent to one another or within close spatial proximity to the coastline (i.e., the Chukotka coast, Wrangel Island, the southeast Chukchi Bight, Beaufort Slope, and Cape Bathurst polynya), where correlation coefficients were 0.80 to 0.84. This correlation was driven by the substantial amount of open water during this season and correlation coefficients in the more northerly areas (with larger amounts of sea ice in September) were lower.

The fraction of open water varied significantly with region in each month (Table 1), as expected given the seasonal cycle of sea ice in the Arctic. Variation in open water with year was significant ($P < 0.02$) in all months except March, the season of maximum sea ice extent. There were no significant interactions ($P > 0.15$) between region and year in tests for the fraction of open water for any month.

Trends and variability in sea ice cover in large regions

Trends in open water over the 24-year period were positive, but very weak (+0.01% to +0.12% per year) during the period of maximum sea ice cover in March, with the best fit regression accounting for only 34% of

TABLE 1. Results of ANCOVA, used to test the effect of region and year on the fraction of open water during months of sea ice maxima (March), retreat (June), minima (September), and advance (November) in the Bering, Chukchi, and Beaufort seas.

Source of variation	df	SS	MS	F	P
March					
Region	16	4.079	0.255	50.9	<0.0001
Year	1	0.006	0.006	1.248	0.2646
Region × year	16	0.027	0.002	0.347	0.9917
June					
Region	16	53.496	3.344	238.98	<0.0001
Year	1	0.148	0.148	10.576	0.0012
Region × year	16	0.144	0.009	0.644	0.8474
September					
Region	9	22.84	2.538	90.2	<0.0001
Year	1	0.507	0.507	18.05	<0.0001
Region × year	9	0.261	0.029	1.034	0.4138
November					
Region	16	49.0	3.062	220.07	<0.0001
Year	1	0.082	0.082	5.922	0.0155
Region × year	16	0.307	0.019	1.381	0.1481

Note: Seven regions were ice free in September (df = 9), so could not be included in trend analysis.

the total variation (Table 2). Trends were strongest during the period of minimum sea ice cover in September, particularly in the East Siberian (+1.24% per year, $r^2 = 0.16$), Beaufort (+1.19% per year, $r^2 = 0.16$), and Chukchi (+0.71% per year, $r^2 = 0.17$) regions. Trends in open water were positive for all large regions in June (+0.25% to +0.52% per year) and November (+0.06% to +1.02% per year), but regression could account for only 1% to 11% of the variation (Table 2).

Interannual variability in sea ice cover was the dominant signal in each large-region time series. In the Bering Sea, variability in the fraction of open water ranged from roughly 20% to 60% in March, with exceptionally light-ice years in 1989, 1996, and 2001 (Fig. 3a). In the Chukchi Sea, extreme ranges in interannual variability occurred in all months except March, when ice cover was nearly solid (Fig. 3b). For example, in June, the fraction of open water fluctuated by over 30% in successive years (i.e., <10% in 1983 and 1985, >40% in 1986, ~10% in 1988, and >40% in 1993, 1996—1997, and 2002). In September, the fraction of open water ranged from ~70% to 100%, with nearly ice-free conditions since 1997. The greatest extremes of interannual variability occurred in November (open water <10% to ~85%), with the fraction of open water being <20% in 1981, 1983, and 1985, shifting to >60% in 1991 and 1995–1998, and back to values <20% in 1994 and 2001.

Interannual variability in fraction of open water was especially pronounced in September (from ~30% to 100%), in both the East Siberian (Fig. 3c) and Beaufort Sea (Fig. 3d). Consistent years of light-ice conditions (~75–100% open water) occurred first in the East

TABLE 2. Trends and a measure of linear fit (r^2) in sea ice cover for 16 regions of the western Arctic.

Large and small regions	Total area (km^2)	March Trend (% per yr)	March Fit (r^2)	June Trend (% per yr)	June Fit (r^2)	September Trend (% per yr)	September Fit (r^2)	November Trend (% per yr)	November Fit (r^2)
Bering Sea	874 375	+0.12	0.01	0	0	NI	NI	+0.06	0.01
Nunivak Island	15 625	+0.17	0.01	NI	NI	NI	NI	−0.83	0.15
St. Matthew Island	18 750	+0.48	0.02	NI	NI	NI	NI	NI	NI
Chirikov Basin	81 875	+0.004	0.000	+0.03	0.002	NI	NI	−0.08	0.002
Anadyr Gulf	30 625	−0.08	0.01	+0.09	0.004	NI	NI	+0.17	0.01
Chukchi Sea	340 000	+0.02	0.10	+0.52	0.10	+0.71	0.16	+1.02	0.11
SE Chukchi Bight	29 375	+0.07	0.09	+0.54	0.03	NI	NI	+0.65	0.04
Barrow Arc	56 875	+0.05	0.09	+0.35	0.05	+0.81	0.13	+1.06	0.16
East Siberian Sea	546 250	+0.04	0.34	+0.25	0.05	+1.24	0.16	+0.11	0.07
Chukotka Coast	51 250	+0.02	0.01	+0.89	0.14	+0.33	0.01	+0.15	0.004
Wrangel Island	35 625	+0.02	0.11	+0.35	0.24	+1.39	0.14	+0.53	0.09
Beaufort Sea	462 500	+0.01	0.01	+0.41	0.07	+1.19	0.16	+0.24	0.11
Beaufort Slope	207 500	+0.003	0.001	+0.40	0.15	NI	NI	+0.22	0.11
Cape Bathurst	28 750	+0.02	0.02	+0.38	0.01	−0.12	0.004	+0.40	0.11
Yukon Coast	61 250	+0.02	0.03	+0.65	0.05	+0.56	0.07	+0.19	0.09
Chukchi Borderland	67 500	−0.02	0.03	+0.03	0.02	+0.59	0.23	+0.01	0.003

Notes: Trend is given as a percentage of change in open water per year (% per yr). NI indicates no or minimal ice in that season. The different regions are depicted with different colors in Fig. 2 as follows: Bering Sea (red), Chukchi Sea (blue), East Siberian Sea (gold), and Beaufort Sea (green).

Siberian Sea (1989–1993), then in the Beaufort Sea (1997–1999). This shift between the two regions in September was preceded by greater interannual variability in June sea ice cover in the Beaufort (Fig. 3d) than in the East Siberian (Fig. 3c) region. Variability in the Beaufort–June fraction of open water was pronounced after 1990, although the overall trend was toward increasing open water (+0.41% per year, $r^2 = 0.07$; Table 2). The fraction of open water was <10% in both large regions in March and November, with the aforementioned best-fit line for the East Siberian–March data set (Table 2).

Trends and variability in sea ice cover in small regions

Trends in open water were positive in the 12 small regions in all seasons, with the exception of four cases: the Nunivak Island polynya in November (−0.83% per year, $r^2 = 0.15$) the Anadyr Gulf and Chukchi Borderland in March and the Cape Bathurst area in September (Table 2). The strongest and most consistent open-water trends occurred in five small regions in June, September, and November. In June, the northern Chukotka coast, Wrangel Island, and the Beaufort slope all showed open-water trends ranging from +0.35% to +0.89% per year, with $r^2 = 0.14–0.24$ (Table 2, Fig. 4). In September, open water increased in the Barrow Arc (+0.81% per year, $r^2 = 0.13$), Wrangel Island (+1.39% per year, $r^2 = 0.14$), and the Chukchi Borderland (+0.59% per year, $r^2 = 0.23$) regions. These results follow the aforementioned trends in increasing open water in the large regions of the Beaufort, East Siberian, and Chukchi seas.

Sea ice cover did not change appreciably in the four small regions associated with wintertime refugia in the northern Bering Sea in March. Similarly, ice cover in

small regions along the spring migration route (i.e., southeast Chukchi Bight and Barrow Arc) did not change substantially in March or June, the period when whales move through the area. In November, open water increased in the Barrow Arc region (+1.06% per year, $r^2 = 0.16$), corresponding with the aforementioned positive trends in the large Chukchi and Beaufort sea regions (Table 2).

DISCUSSION

Given recent reports of widespread Arctic sea ice retreats, thinning, and extreme areal loss of sea ice coincident with our study period (e.g., Parkinson 2000, Comiso 2002, Comiso and Parkinson 2004), we anticipated strong trends toward increased open water in all regions occupied by BCB bowhead whales. Instead, our results were dominated by strong interannual variability and weak, but consistent, annual increases in open water. Except for an increase in sea ice near Nunivak Island in November, there were no dramatic changes in sea ice cover in wintertime refugia in the northern Bering Sea, nor was there a shift to more open water along the primary springtime migration corridor in the Chukchi Sea. The most striking result of our analysis was the extreme interannual variability in sea ice cover, particularly in the large Bering (March), Chukchi (September and November), and East Siberian/Beaufort (September) regions. This variability, emphasized by low year-to-year correlation within regions, is reported by native inhabitants of the western Arctic as the most alarming feature of climate change and is the most intrusive to their subsistence activities (e.g., Krupnik and Jolly 2002, George et al. 2003).
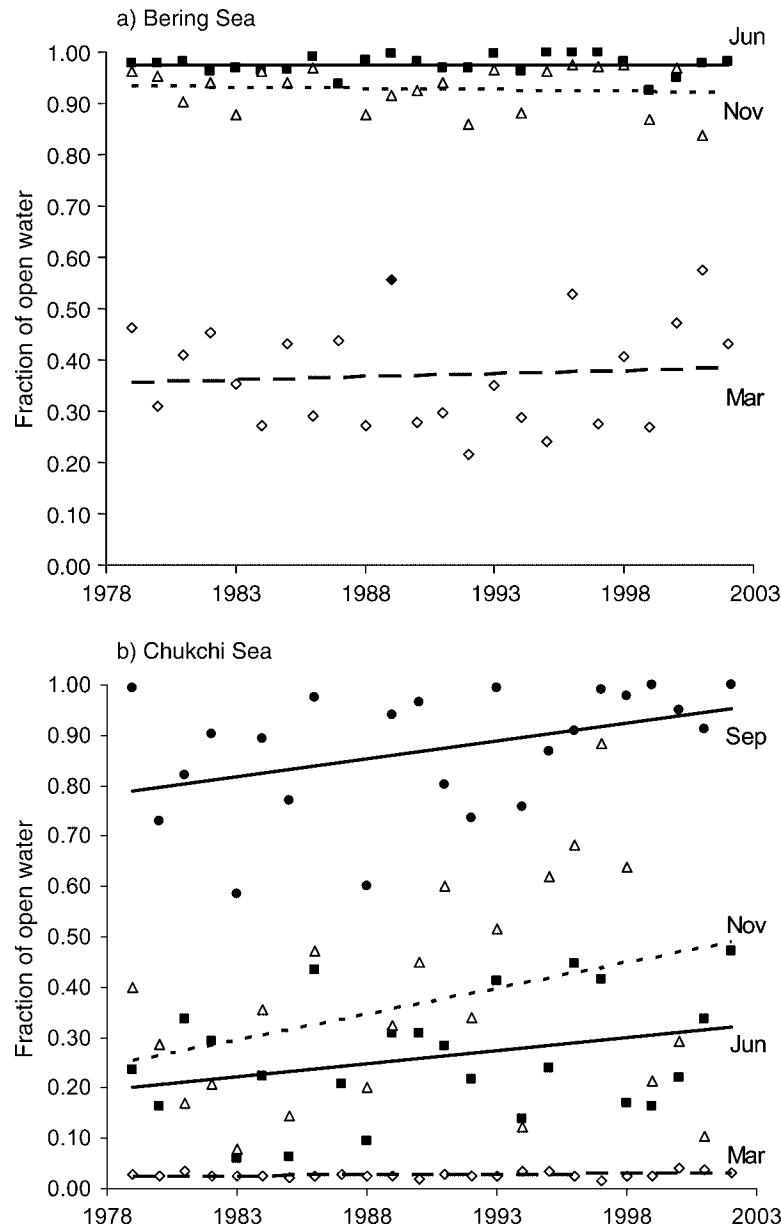
FIG. 3. Fraction of open water in the four large regions: (a) Bering Sea, (b) Chukchi Sea, (c) East Siberian Sea, and (d) Beaufort Sea in March (open diamonds), June (solid squares), September (solid circles), and November (open triangles), 1979–2002. Note that the Bering Sea region is ice-free in September.

Trends and variability in sea ice cover in overwintering and migration habitats

Although the winter range of BCB bowheads can extend south to the marginal ice zone in the northern Bering Sea (Moore and Reeves 1993), whales are most commonly seen in coastal waters and polynyas associated with St. Lawrence Island and the southern Chukotka coast. These waters comprise a dynamic overwintering habitat, with reports of mating activity, possible feeding, and active exchange of individuals between coastal waters of the island and the peninsula (Bogoslovskaya et al. 1982, Bogoslovskaya 2003). Sea ice cover did not change appreciably in these winter refugia, nor did our analysis detect a reduction in sea ice in the large Bering Sea region. Our analysis was restricted to the northern third of the Bering Sea basin, thus, reported trends in sea ice reduction over the entire Bering Sea (e.g., Overland et al. 2003) are likely driven by areas farther south, outside of bowhead wintering habitat.
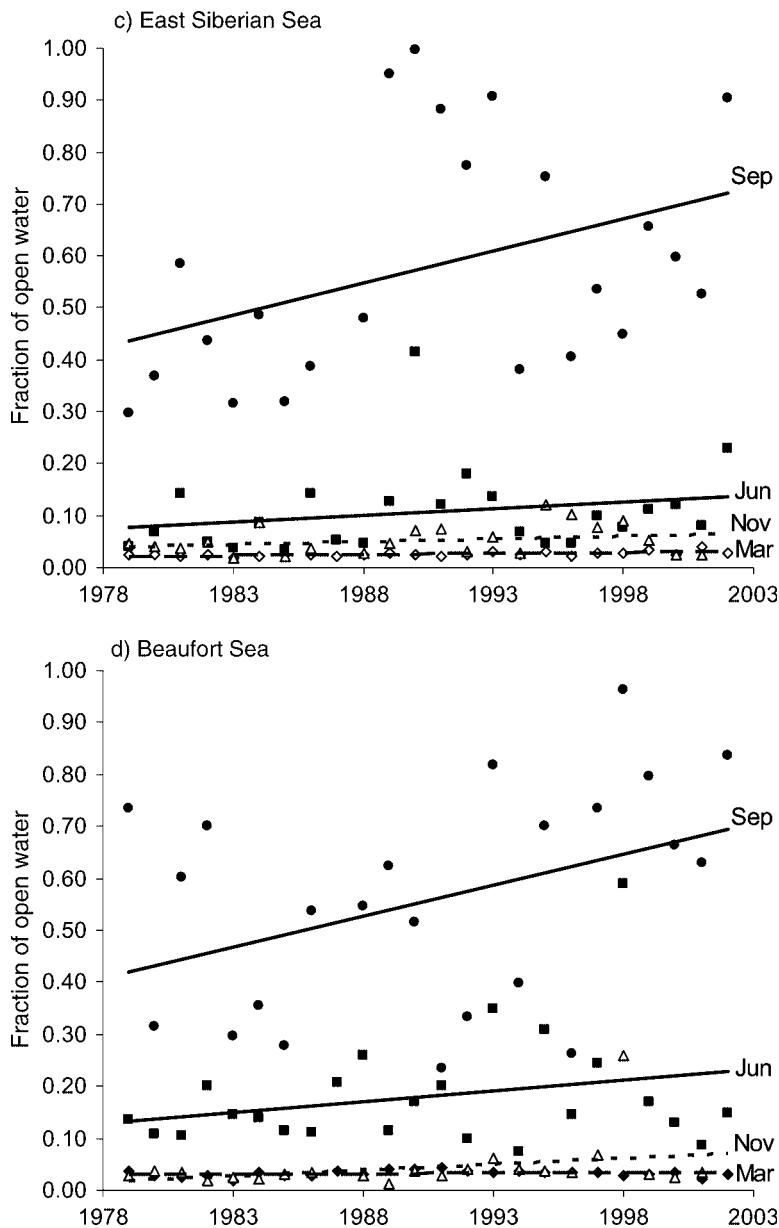
FIGURE 3.   Continued.

Sea ice cover did not change along the primary springtime BCB bowhead migration corridor or within the Cape Bathurst polynya in March or June. However, there were detectable increases in open water along the Chukotka coast, the Beaufort slope, and near Wrangel Island in June. Twenty-five years ago, persistent sea ice along the northern Chukotka coast was thought to block the bowhead spring migration and force whales to "follow the open-water lead" past Barrow (Braham et al. 1980). However, this ice blockage now appears to be obsolete (Comiso 2002). This early-summer opening of regional habitats where whales have been observed feeding (Moore et al. 1989, 1995) may provide migrating

BCB bowheads access to areas they could not occupy two decades ago when sea ice cover was more extensive.

Trends and variability in sea ice cover in foraging habitats

We report consistent reductions in sea ice cover in regions important to bowheads for feeding in late summer and autumn. In September, open water increased across the large regions of the East Siberian, Chukchi, and Beaufort seas, as well as waters near the Barrow Arc, near Wrangel Island, and the Chukchi Borderland. This trend may extend the period for primary and secondary production in late-summer stratified water. Reports of bowheads feeding in ice-free
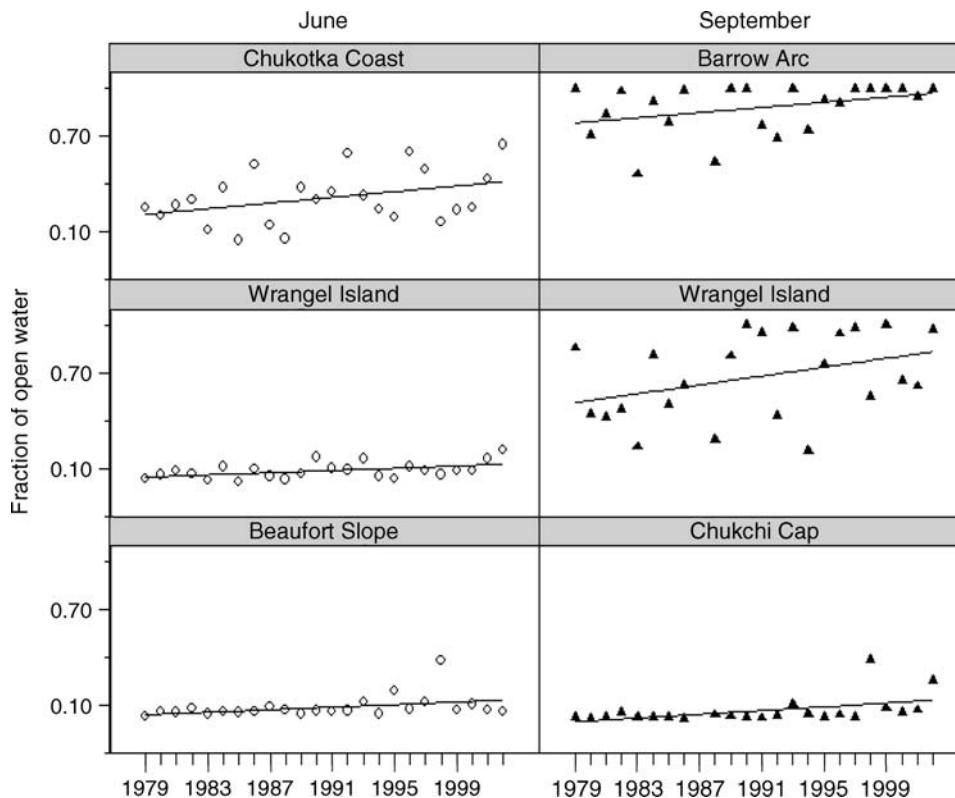
FIG. 4. Trends in the fraction of open water in five small regions occupied by bowhead whales in June and September, 1979–2002. The November trend in the Barrow Arc region is similar to September; all trends (b) and line-fits (r^2) are given in Table 2.

waters northeast of Barrow from August through October were more frequent in the 1990s (e.g., Treacy 2002) than between the late 1970s and mid-1980s (Ljungblad et al. 1986). This altered occupancy of the northeastern portion of the Barrow Arc has contributed to an increased autumn harvest at Barrow since the mid-1990s (e.g., Bodenhorn 2003), with most landed whales having stomachs full of euphausiids that have been advected to the western Beaufort Sea from the northern Bering Sea (Lowry et al. 2004). Advection of prey may be a key mechanism associated with the (potential) bowhead occupancy of the Chukchi Borderland, as modeled scenarios of Bering Strait inflow show concentrations of Bering Sea water over the Chukchi Plateau (Maslowski et al. 2000).

Conceptual model

While data do not yet exist to allow us to quantitatively predict how changes in sea ice will affect the population dynamics of BCB bowhead whales, the importance of sea ice to the Arctic ecosystem suggest that the changes we report here will have a significant impact on the ecology of this species. We constructed a conceptual model of the influence of sea ice cover on bowhead prey composition and availability, based on two underlying pathways that affect zooplankton (Fig. 5). Bowhead whales feed on zooplankton produced

locally within a foraging area (i.e., *Calanus* spp.) and on zooplankton advected to foraging areas from elsewhere (*Calanus* spp. and *Thysanosessa* spp.) (Lowry et al. 2004). Sea ice can influence both: (1) the production path through impacts on predictable solar forcing (i.e., the seasonal light cycle) and water stratification, and/or (2) the advective path through impacts on the dynamics of water flow (i.e., currents and upwelling), driven by highly variable atmospheric (wind) forcing. There are some empirical measures of the effects of sea ice on production, while the influence of sea ice on prey advection must be inferred from empirical measures of current flow and physical models.

Variability in sea ice cover has cascading effects on pelagic productivity. For example, primary production in the Cape Bathurst polynya, an important feeding area for bowhead whales in summer (Harwood and Smith 2002), exhibited large variation in the timing and intensity of the phytoplankton bloom with varying sea ice regimes (Arrigo and van Dijken 2004). Production blooms were generally most intense following late-summer stratification, with a peak bloom associated with anomalous warming and early stratification (in 1998). Similarly, variability in the timing of phytoplankton blooms related to sea ice retreat has been hypothesized as a mechanism that regulates top-down vs. bottom-up ecosystem function in the southeast
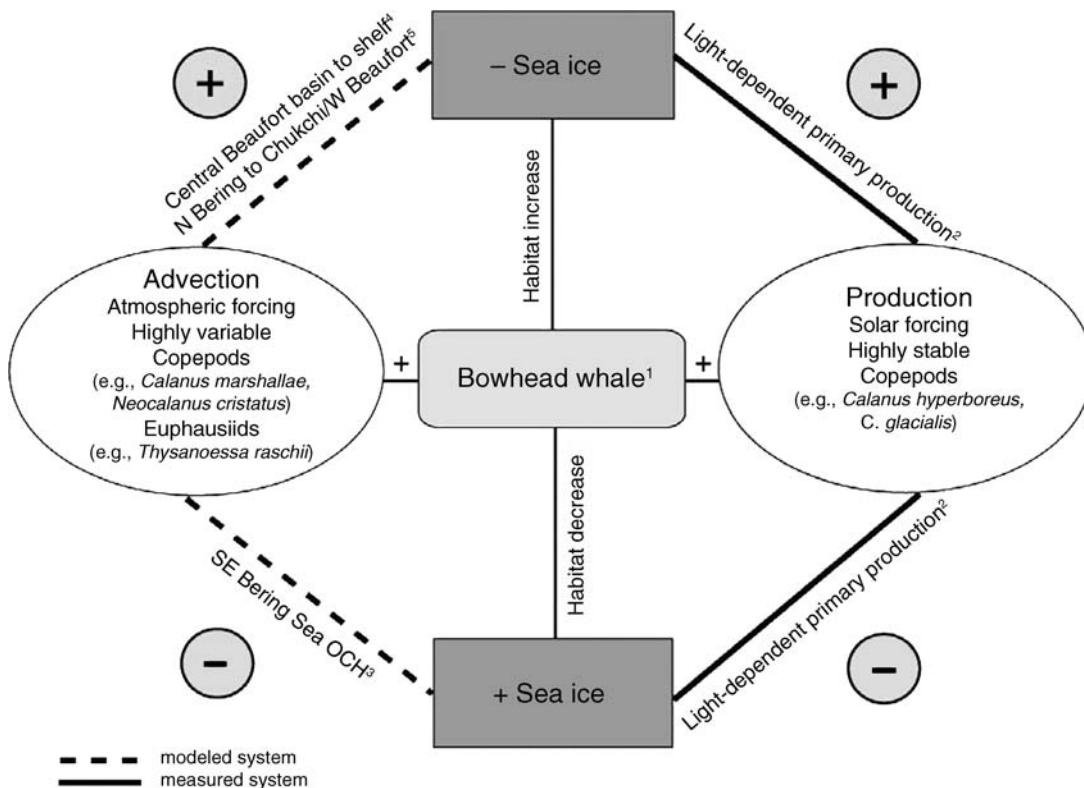
FIG. 5. A conceptual model of sea ice effects on production and advection pathways that influence BCB bowhead whale prey availability. Superscripts denote the following: (1) recruitment between 1978 and 2001 at +3.4% per year and highest-ever calf count in 2001 (George et al. 2004); (2) timing of sea ice retreat and water column stratification impacts primary production (Hunt et al. 2002, Arrigo and van Dijken 2004), but mismatch in timing of these events may lead to secondary production decoupling (Hansen et al. 2003); (3) timing of sea ice retreat in the southeast Bering Sea can influence zooplankton abundance and availability for advection (oscillating control hypothesis [OCH]; Hunt et al. 2002); (4) prey advection can involve simple upwelling (Carmack and Chapman 2003); and/or (5) longer range transport (Woodgate and Aagaard 2005).

Bering Sea (Hunt et al. 2002; oscillating control hypothesis, or OCH), with early ice departure related to increased pelagic zooplankton stocks that (potentially) can be advected to the northern Bering Sea and through Bering Strait (Woodgate and Aagaard 2005).

Increased primary production will augment the bowhead prey base *only* if it remains well coupled with zooplankton life cycles (Hansen et al. 2002). While BCB bowhead whales do not appear to be food limited at present, if primary production becomes decoupled with the vertical migration of zooplankton (e.g., Niehof 2000), or the increasing fetch of open water enhances storm-driven mixing and retards stratification required for peak production in the Arctic (e.g., Yang et al. 2004), any gain in bowhead prey base could be short lived. Indeed, some ecosystem models suggest that reductions of ice cover over the deep Canada Basin may ultimately result in less energy transfer to higher trophic levels (Walsh et al. 2004). Spatial and temporal thresholds for such cascades require regional investigation. Ultimately, any decoupling of the system that reduces secondary production will have negative effects on upper trophic levels, including bowhead whales.

Although the influence of sea ice on advection of bowhead prey is speculative, data from long-term moorings and physical models provide a framework to construct possible scenarios (Fig. 5). Empirical measures demonstrate a strong seasonal northward transport of seawater and nutrients from the northern Bering Sea through Bering Strait (Woodgate and Aagaard 2005). However, interannual variability of this advective flow is quite high and, like production, must be timed with zooplankton prey availability to provide food for bowheads. For example, if the timing of sea ice retreat in the southeast Bering Sea affects zooplankton abundance (Hunt et al. 2002), fewer zooplankton may be available for transport through the strait in years of late ice retreat. In the Beaufort Sea, a second advective pathway may simply upwell and push copepods from the deep Canadian Basin (Ashjian et al. 2003) onto the continental shelf (Carmack and Chapman 2003), in which case, timing may not be as critical. In brief, shelf–basin exchange in polar regions is strongly moderated by the location of the ice edge relative to the underlying bathymetry. A numerical model suggests that upwelling-favorable winds generate very little exchange when the

ice edge remains shoreward of the shelf break, but that abrupt and forceful upwelling occurs when the ice edge retreats seaward of the shelf break (Carmack and Chapman 2003). Sea ice has retreated well beyond the Alaskan Beaufort Sea shelf break in the recent years (e.g., Comiso and Parkinson 2004), providing the exact mechanism to advect arctic copepods onto the shelf, where bowheads have been observed feeding in late summer and autumn (Lowry et al. 2004).

This conceptual model suggests that, overall, reductions in sea ice cover should increase BCB bowhead whale prey availability, via both production and advection pathways (Fig. 5). What is lost in such a static representation is the *dynamics* of the system, as revealed by the extreme interannual variability evident in our analyses of sea ice cover at scales relevant to bowhead whales. That is, between 1979 and 2002, BCB bowhead whales experienced annual oscillations between "positive" and "negative" sea ice cover at spatial and temporal scales that may impact prey availability in known feeding habitats (e.g., Cape Bathurst, the Yukon Coast, the Barrow Arc, and the Chukotka Coast). This is a far different picture of conditions faced by the whales than scenarios provided by basin-scale depictions of extreme ice retreats, thinning, and wind-driven movements (e.g., Comiso 2002, Rigor and Wallace 2004. Yu et al. 2004). Clearly, additional empirical data are needed, especially measures of prey abundance and variability in situ at regional scales, to better understand the forces that organize these complex ecosystems in space and time (Levin et al. 1997, Green et al. 2005).

CONCLUSIONS

Here we report trends and variability in sea ice cover linked to regions seasonally occupied by BCB bowhead whales, but not necessarily at the temporal and spatial scales critical to the whales. Bowhead whales can hummock or break though sea ice and routinely migrate through open-water leads and cracks that can occur at a scales much smaller than examined here (e.g., Ellison et al. 1987, George et al. 1989). The spatial resolution of sea ice data (625 km^2) is limited by satellite resolution, and often with remote sensing studies, the spatial scale must be sacrificed for high temporal resolution. It is important to note that sea ice thinning (Yu et al. 2004), not examined or detected through an analysis of ice concentration, may play an important role in habitat change.

The pan-Arctic effects of sea ice expansion or retreat on cetacean populations will vary with the temporal and spatial scale of ecological modification, and will be mediated by regional differences in trophic cascades and the behavioral resiliency of each species. Summaries of pan-Arctic climate change suggest that, thus far, interannual and seasonal variability trumps strong trends in most physical parameters when measured at regional scales (e.g., Overland et al. 2003, Johannessen et al. 2004, Whitfield et al. 2004). In all cases, spatial and

temporal sampling scale affects the reported pattern. Our examination of the 24-year sea ice cover time series offers a comparatively precise look into the conditions seasonally experienced by BCB bowhead whales in areas known to be important to the population. We recommend future investigations of climate parameters adopt this species-focused approach to identify change at spatial and temporal scales relevant to animal movements and foraging ecology.

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