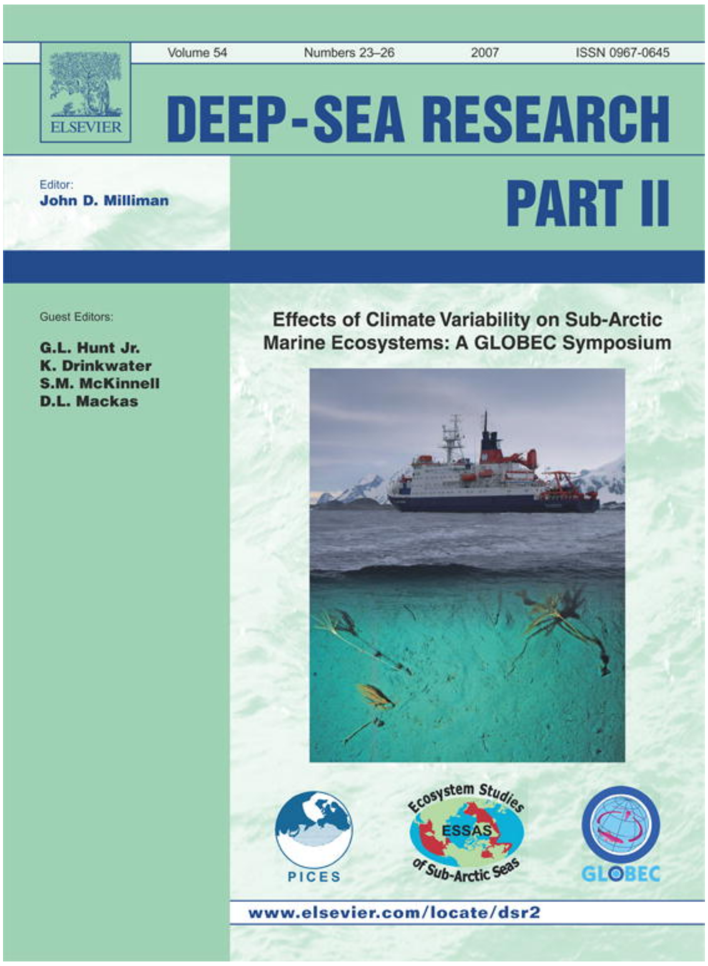

Volume 54 Numbers 23–26 2007 ISSN 0967-0645

DEEP-SEA RESEARCH PART II

Editor:
John D. Milliman

Guest Editors:
G.L. Hunt Jr.
K. Drinkwater
S.M. McKinnell
D.L. Mackas

Effects of Climate Variability on Sub-Arctic Marine Ecosystems: A GLOBEC Symposium

www.elsevier.com/locate/dsr2

Available online at www.sciencedirect.com

ScienceDirect

Deep-Sea Research II 54 (2007) 2919–2933

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

High gray whale relative abundances associated with an oceanographic front in the south-central Chukchi Sea

B.A. Bluhm[a,*], K.O. Coyle[a], B. Konar[a], R. Highsmith[b]

[a]School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 245 O'Neill Building, P.O. Box 757220, Fairbanks, AK 99775, USA
[b]National Institute for Undersea Science and Technology, University of Mississippi, MS 38677, USA

Received in revised form 7 July 2007; accepted 15 August 2007
Available online 5 November 2007

Abstract

We describe gray whale (*Eschrichtius robustus*) distribution in the south-central Chukchi Sea in relation to environmental factors during two 5-day surveys in June and September of 2003. Whale counts per 10-min scan (an index of relative abundance) ranged from 0 to 41 in June and from 0 to 28 in September. CTD data showed an ocean front around 67.8°N with strong horizontal gradients in temperature, salinity, chlorophyll-*a* concentration and water-column stability. Highest whale abundance indices occurred in or near the front in both periods. Preliminary qualitative assessment of biological communities in the study area suggests that infaunal clams, echinoderms, euphausids, chaetognaths and Arctic cod were common, while ampeliscid amphipods, the previously abundant infauna (and likely prey) in the nearby Chirikov Basin feeding area, were not dominant. Euphausids may be a prey for gray whales in this area. We suggest that frontal systems may play an important role in eastern North Pacific gray whale foraging grounds. Further study is needed to fully describe the role of frontal systems in gray whale foraging grounds.

Keywords: Gray whale; Relative abundance; Distribution; Fronts; Prey

1. Introduction

The eastern North Pacific (ENP) gray whale (*Eschrichtius robustus*) population migrates from the wintering grounds in Baja California north to the Bering and Chukchi Seas to exploit the rich northern foraging grounds during the summer (Marquette and Braham, 1982). The distribution of the summer foraging grounds is generally well-documented, ranging from the Siberian Koryak coast to the Chirikov Basin, near-shore sites of Chukotka and to the Alaskan Chukchi coast off Point Franklin and the Chukchi Sea shoals (Berzin, 1984; Moore et al., 2000; summary in Highsmith et al., 2006). Whale use of these grounds is temporally and spatially variable (Moore, 2000; Moore et al., 2003). Variability in the foraging ground use might be resulting from increases in the total gray whale stock over the past 150 years (Rice and Wolman, 1971; Le Boeuf et al., 2000; Witting, 2003), environmental conditions (Moore, 2000), and change of available food sources due to

---

*Corresponding author. Tel.: +1 907 474 6332;
fax: +1 907 474 7204.
E-mail addresses: bluhm@ims.uaf.edu (B.A. Bluhm), coyle@ims.uaf.edu (K.O. Coyle), konar@ims.uaf.edu (B. Konar), ray@olemiss.edu (R. Highsmith).

0967-0645/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.dsr2.2007.08.015

climate variability or top-down processes (Moore et al., 2001; Grebmeier et al., 2006a; Coyle et al., 2007).

During the 1980s, gray whales used the Chirikov Basin in the northern Bering Sea in dense aggregations (Highsmith and Coyle, 1990, 1992; Moore et al., 2000). During this period, ampeliscid amphipods occurred in high density in the Chirikov Basin (Grebmeier et al., 1989; Highsmith and Coyle, 1990) and were considered the major prey item of gray whales in this area (Yablokov and Bogoslovskaya, 1984). Indirect evidence for the abundance and importance of these amphipods as prey was given by Obst and Hunt (1990) who found these amphipods in stomachs of sea birds feeding in gray whale mud plumes. The biomass of these amphipods has since been reduced by as much as 50% relative to the 1980s (Moore et al., 2003; Coyle et al., 2007), and in 2002, gray whale relative abundance in the Chirikov Basin feeding area was as much as 17 times lower than in the 1980s (Moore et al., 2003). Concurrently, relatively high gray whale densities were recorded in the south-central Chukchi Sea near the Convention Line in 2002 (Moore et al., 2003). This area is occupied by the Bering Shelf Anadyr Water and the Alaska Coastal Water with a frontal boundary between them (Belkin et al., 2003; Coachman et al., 1975). In other areas, fronts are known to support elevated biomass of pelagic (Munk et al., 1995) and hyper-benthic communities (Dewicke et al., 2002) as well as bird and mammal aggregations (Hunt and Harrison, 1990; Mendes et al., 2002).

A considerable amount of survey effort was dedicated to gray whales in their Arctic summering grounds during the 1980s and early 1990s, concomitant with plans to develop oil and gas lease sales there (Moore and DeMaster, 1998; Moore, 2000; Moore et al., 2000; Clarke and Moore, 2002). After delisting of the eastern North Pacific gray whale stock (ENP) in 1994, and the decline in interest in oil and gas development in the northern Bering and Chukchi Seas, less effort has been spent surveying this species in the summering areas. Analysis of gray whale habitat selection in Alaskan waters using published ice charts and water transport data showed that gray whales preferred coastal/shoal and shelf/trough habitat and open water/light ice cover (Moore and DeMaster, 1998; Moore, 2000; Moore et al., 2000). Shelf habitat was selected during low-moderate transport through Bering Strait, while coastal and shoal areas were used more in high transport situations (Moore, 2000).

This study surveyed an area in the south-central Chukchi Sea in the summer and fall of 2003, an area previously noted for high gray whale densities. Our primary objective was to describe gray whale distribution in relation to specific environmental factors including salinity, temperature, chlorophyll-*a* concentration and water-column stability. Results are discussed in the context of prey availability and productivity near an oceanographic front.

2. Materials and methods

2.1. Field sampling

The study area was located in the south-central Chukchi Sea (box in Fig. 1) between 67.38°N and 68.35°N and between 167.39°W and 168.98°W. Water depths were between 40 and 60 m. The western and eastern boundaries of the survey area were determined by the international convention line (Fig. 1) and decreasing numbers of whale sightings, respectively. Northern and southern boundaries were determined by the estimated location of an oceanographic front based on preliminary data from the westernmost CTD transect, and by available ship time.

Gray whale counts were conducted during June 24–27 and September 20–24, 2003 to assess a relative index of abundance of whales relative to environmental conditions. Counts were made from a moving ship along a transect grid (black dots in Fig. 2) with a haphazardly chosen starting point. The height of the observation platform was 8 m above sea level. Every 10 min, one of two observers conducted a 180° visual scan from the vessel bridge using Fujinon 7 × 50 binoculars. Observers switched shifts every hour. A third person noted whale numbers, sea state according to the Beaufort scale, and occurrence of fog and glare. Travel speed varied between 6 and 10 knots, depending on other cruise activities. Whale surveys were interrupted by other station activities, dark hours or dense fog. In 42 areas where a whale was observed to first surface, we approached the whale to visually assess whether a mud plume was present behind it.

Conductivity, temperature, depth (CTD) and chlorophyll fluorescence vertical profiles were taken with a Seabird model 911 Plus CTD (see Fig. 4 for CTD locations). For chlorophyll-*a* analysis, water samples collected with Niskin bottles from a CTD rosette were filtered onto GF/F filters and frozen. For chlorophyll-*a* determination, filters were

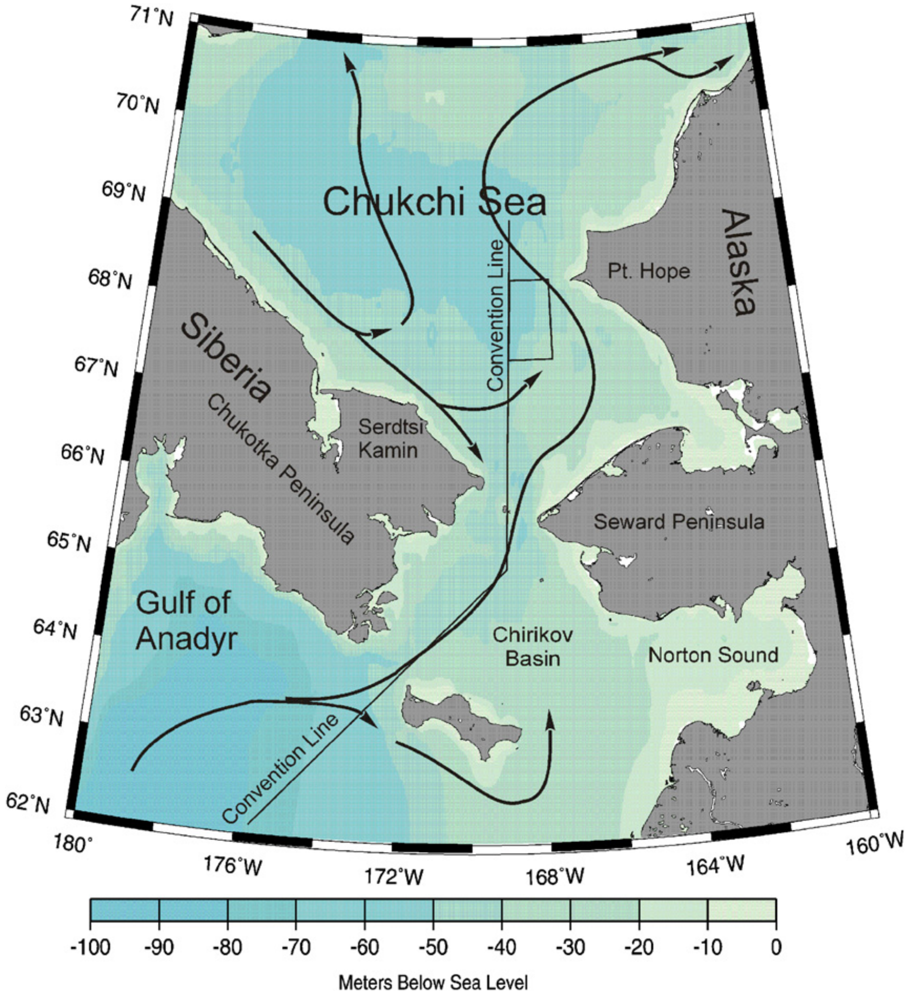

Fig. 1. Map of the northern Bering and Chukchi Seas. The box marks the survey area; the arrows show the prevailing current regime.

extracted with 7 ml of 90% (v:v) acetone for 24 h in the dark at −18 °C (Karl et al., 1990). Chlorophyll-*a* concentration was determined with a Turner TD-700 fluorometer (Arar and Collins, 1992). To obtain preliminary data on the potential prey spectrum available to gray whales, we conducted a qualitative assessment of pelagic and benthic communities at select stations. The presence of potential zooplankton and micronekton prey was determined qualitatively at six stations (Fig. 2) using a 1-m^2 multiple opening and closing net (MOCNESS; Wiebe et al., 1976) with 500-μm mesh nets during the September cruise. Benthic infauna was collected at seven stations along survey transect 1 with three replicate 0.1-m^2 van Veen grab samples per station in June (Fig. 2); infauna samples were sieved over 1-mm mesh. The sieved samples were preserved in buffered 4% (final concentration) formaldehyde seawater solution and blotted total wet weight was determined in the home laboratory. Relative taxonomic composition of the epifauna community was assessed using an Otter trawl with 1-cm mesh size in the cod end at five locations (Fig. 2). The trawl was deployed for 10 min on the bottom at 2–2.5 knots and the catch was sorted on deck upon retrieval. Voucher specimens were preserved in buffered 4% (final concentration) formaldehyde seawater solution for later taxonomic identification.

2.2. Data analysis

For visualization of the quantitatively measured physical and biological variables, contour plots were generated with a minimum curvature gridding algorithm using ©Surfer software. For this purpose, the CTD and whale count data were loaded into an Access database for storage and analysis. Pycnocline depth was computed for each station and cruise by locating the depth where $d\sigma_t/dZ$ was maximum (σ_t = sigma-t; Z = depth in m). Mean

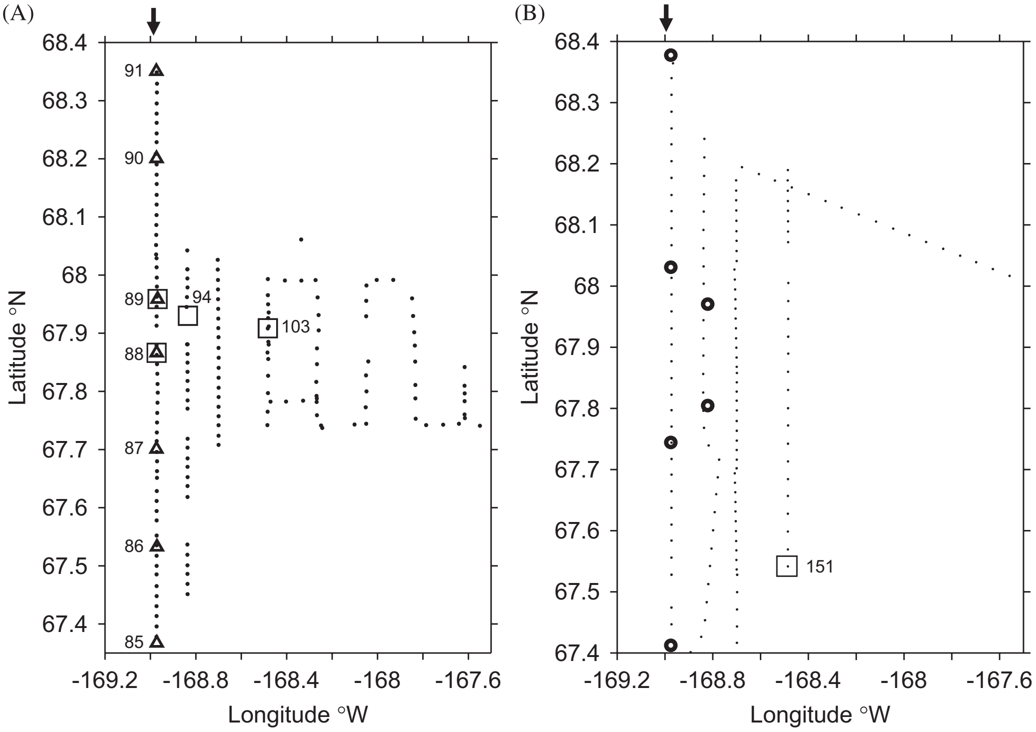

Fig. 2. Survey locations for gray whale counts (black dots) and for qualitative benthic and pelagic sampling in the south-central Chukchi Sea during (A) June 24–28, 2003 and (B) September 20–24, 2003. The arrows mark transect number 1 (referred to in Figs. 3, 5 and 6). Triangles: benthic grab sampling locations; squares: benthic trawling locations; circles: MOCNESS sampling locations; numbers next to symbols represent station numbers referenced in Fig. 3.

salinity and temperature above and below the pycnocline was calculated. In addition, the stability parameter, the energy required to redistribute the water-column mass by complete vertical mixing ($\mathrm{J\,m^{-3}}$), was computed (Simpson et al., 1977; Fielder et al., 1998). Whale counts overlaid on the oceanographic data in Figs. 4 and 7 were bin-averaged by two observations to reduce distracting overlap of the symbols in the figures. Fluorescence was converted to chlorophyll (chl) using linear regression of fluorescence with chl (June cruise: $\mathrm{chl} = 0.15 + 2.41 \times \mathrm{fluorescence}$, $r^2 = 0.77$; September cruise: $\mathrm{chl} = 3.0 + 2.4 \times \mathrm{fluorescence}$; $r^2 = 0.50$).

To identify potential correlations of physical and biological variables, we conducted a factor analysis using ©Systat software (version 11) with Equimax rotation mode in which the number of variables that load highly on a factor and the number of factors needed to explain a variable are minimized. For this purpose, gradients in temperature and salinity above and below the pycnocline were calculated between station pairs and normalized for the distance between stations. Variables used in the factor analysis are listed in Table 1. Since CTD stations did not exactly match whale survey stations, whale counts at the two whale survey stations closest to any one CTD station were averaged. Secondly, we used a backward stepwise general linear model (Systat software) to identify which variables (Table 1) best estimated the whale abundance index. Both analyses were conducted for the summer and fall surveys individually.

3. Results

3.1. *Whale counts*

A total of 174 and 159 ten-minute whale surveys were conducted in June 2003 and September 2003, respectively, resulting in a total of 1546 whales counted in the summer and 1038 whales in the fall. Weather conditions during the surveys ranged from Beaufort 0–3, with no to dense fog and with no to moderate glare. Beaufort 1–2, no-fog and no-glare were the dominant conditions. Whale counts from all conditions except dense fog were used for analysis.

Gray whale numbers per 10-min count ranged from 0 to 41 in June and from 0 to 28 in September. In the summer, the highest whale abundance index

Table 1
Rotated loading matrix for factor analysis for June and September 2003 cruises

Variable	June 2003				September 2003			
	Factor 1	Factor 2	Factor 3	Factor 4	Factor 1	Factor 2	Factor 3	Factor 4
Mean whale counts (per 10 min survey)	0.176	−0.070	−0.113	**0.927**	0.069	0.199	**0.904**	0.057
Mean T below P (°C)	**0.912**	−0.161	−0.157	−0.130	**0.909**	−0.021	−0.045	0.012
Mean S below P	**0.927**	−0.030	0.118	0.140	0.320	**−0.603**	−0.079	0.406
Mean T above P (°C)	0.178	0.029	**−0.884**	0.103	**0.897**	−0.169	0.078	0.112
Mean S above P	**0.882**	−0.040	0.065	0.160	**−0.870**	−0.021	0.190	0.153
Stability parameter ($J\,m^{-3}$)	**−0.720**	0.119	−0.384	0.244	0.153	0.031	−0.036	**−0.890**
Mean F above P (V)	0.250	0.081	**0.781**	0.133	0.286	−0.018	0.442	**0.777**
Mean F below P (V)	**0.689**	−0.155	0.244	−0.019	**−0.826**	0.158	0.223	−0.249
Gradient mean T below P (°C)	−0.243	**0.567**	0.343	**0.559**	0.311	**0.661**	0.096	−0.013
Gradient mean T above P (°C)	0.032	**0.887**	0.043	−0.147	−0.234	**0.862**	−0.082	0.163
Gradient mean S below P	−0.180	**0.923**	0.026	0.178	−0.215	**0.872**	0.047	−0.205
Gradient mean S above P	−0.023	**0.638**	−0.045	**0.638**	0.121	**0.595**	**−0.618**	−0.110
Water depth (m)	−0.409	−0.186	**−0.502**	0.303	0.271	0.046	**−0.826**	−0.181

Loadings above 0.5 are marked in bold print. F: fluorescence, P: pycnocline, T: temperature, S: salinity.

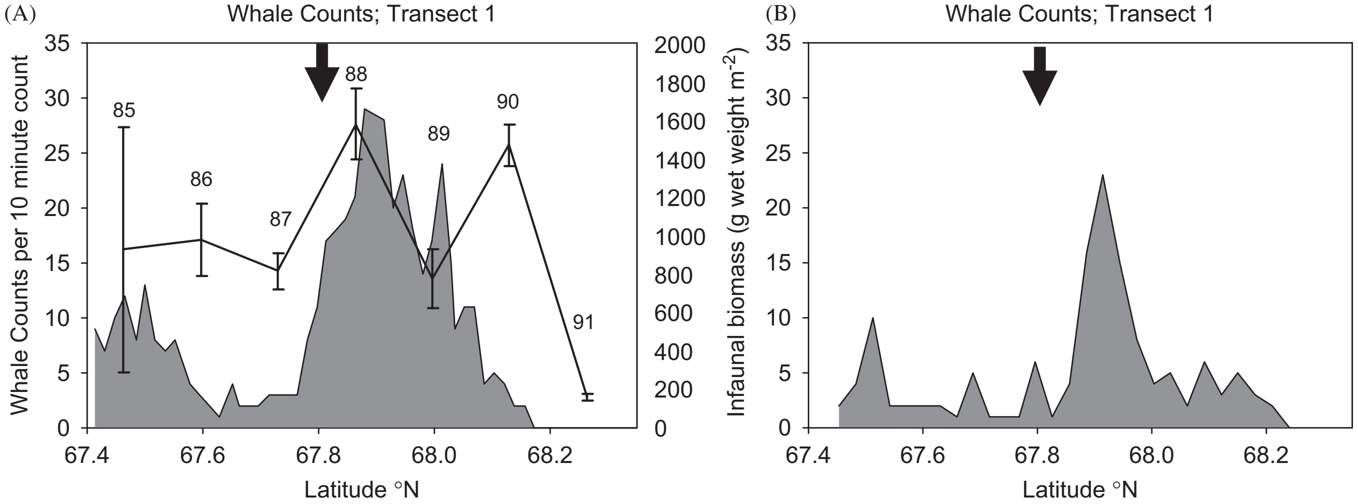

Fig. 3. Distribution of gray whale counts (shaded area) along transect 1 (marked by arrows in Fig. 2) during surveys conducted (A) June 24–28, 2003 and (B) September 20–24, 2003. Overlaid is the total infaunal benthic biomass (thin black line, ±S.D.) along this transect in June 2003. Numbers on the plot indicate station locations as shown in Fig. 2. Arrows indicate the location of the front based on the oceanographic data depicted in Figs. 4–7.

was observed north of 67.8°N and west of 168°W (Figs. 3A, 4A and 5). At this time, the counts were low in the southern and eastern parts of the survey area and in the northern part of transect 1 (Fig. 4). In the fall, whale densities were highest between 67.8°N and 68°N (Figs. 3B, 4B and 6). At this time, whale counts were lowest, often zero, in the northern and southern parts of the survey area.

Mud plumes were found in 20 out of 42 (48%) approaches to areas where a whale first surfaced. In 5 of the 42 cases, seabirds (shearwaters and kittiwakes) were present in the area of the surfacing whale; 3 were associated with mud plumes while two were not.

3.2. Oceanographic conditions

In the summer survey, the distribution of temperature, salinity and chlorophyll-*a* concentration was characterized by strong horizontal gradients

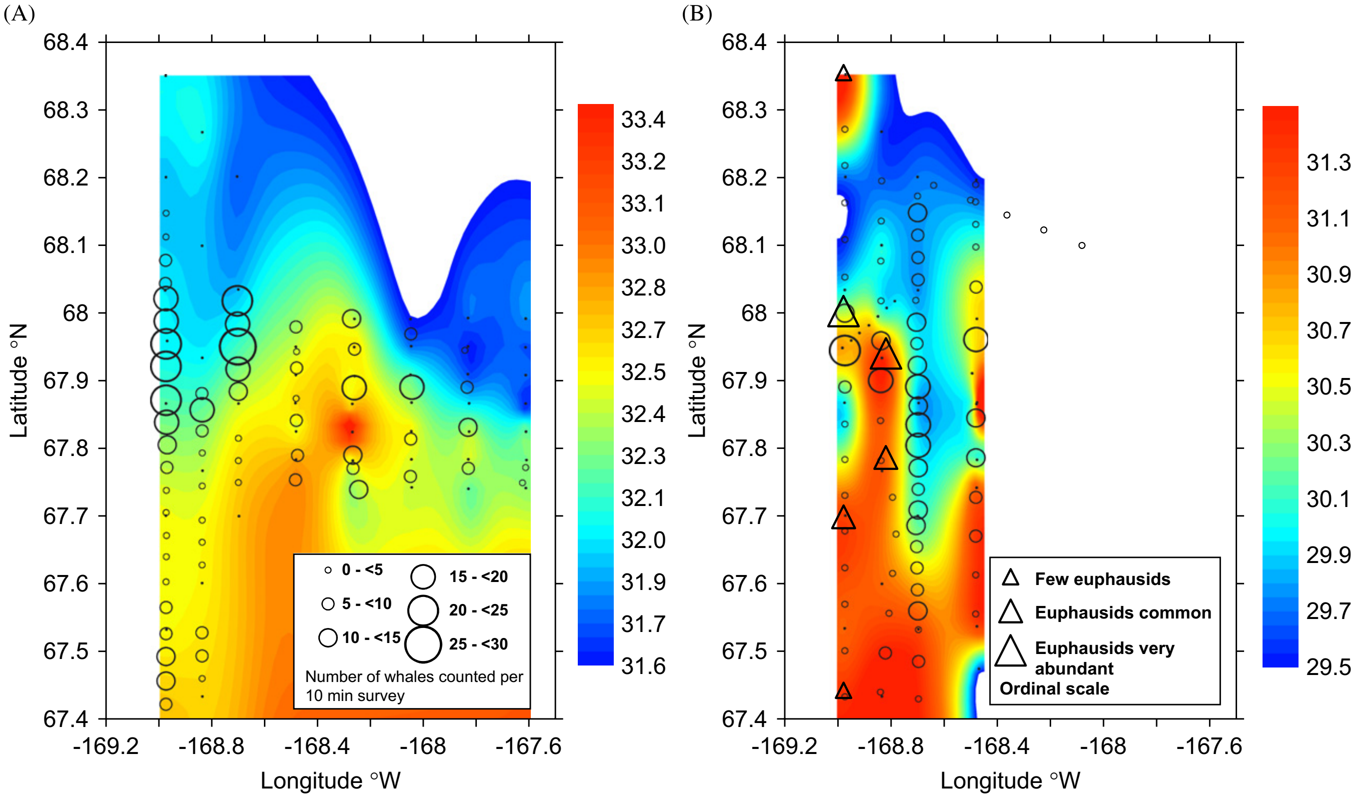

Fig. 4. Gray whale counts overlaid on mean salinity above the pycnocline in the study area during (A) June 24–28, 2003 and (B) September 20–24, 2003. Black dots indicate CTD locations; different scales were necessary in the two figures to illustrate the strong gradients appropriately. The size of the circles in (A) is scaled to the number of whales counted in a 10 min survey. Euphausid occurrence in (B) is given on an ordinal scale only.

across the center of the survey area, around 67.8°N, where the bottom depth increased from about 50 to 60 m (Fig. 4A, example of survey transect 1 in Fig. 5). Water with low levels of chlorophyll-*a* and salinity (31.9–32.2), but high temperature (maximum 6.4 °C) occupied the upper 25 m of the northern side of the front (Fig. 5). The bottom water north of 67.8°N was colder and higher in chlorophyll-*a* and salinity relative to the upper 25 m. Chlorophyll-*a* was high in the summer throughout the water column south of 67.8°N with a near-surface peak just south of the strong gradient in *T*, *S* and chlorophyll-*a*. High chlorophyll-*a* concentrations also were measured in a band below the surface waters on the north side of the front.

In the fall survey, there was also a strong horizontal gradient in mean salinity above the pycnocline with a more complex distribution of less saline water in the northern part of the study area (Fig. 4B). Water with temperatures around 6.4 °C and salinities as low as 28.9 occupied the upper 20–25 m north of about 68°N (Fig. 6). Chlorophyll-*a* concentrations were generally low on the south side of the front, with small peaks at 20–30 m water depth. Generally, gradients were less pronounced in this survey.

In both periods, the stability parameter was lower in the southern part of the study area than in the northern part with steep gradients between 67.8–68.0°N and 67.5–67.7°N in June and September, respectively (Fig. 7). Overall, water-column stability was considerably higher in September than in June.

3.3. Whale– oceanography correlations

The factor analysis for the June cruise identified four factors with eigenvalues > 1. After rotation, factors 1–4 explained 29.6%, 19.1%, 15.6% and 14.4%, respectively, of the total variance (total: 78.7%). Based on the factor loading matrix (Table 1), factor 1 represented correlations between four major hydrographical variables and mean fluorescence below the pycnocline; factor 2 was determined by gradients in temperature and salinity; factor 3 showed an inverse correlation between

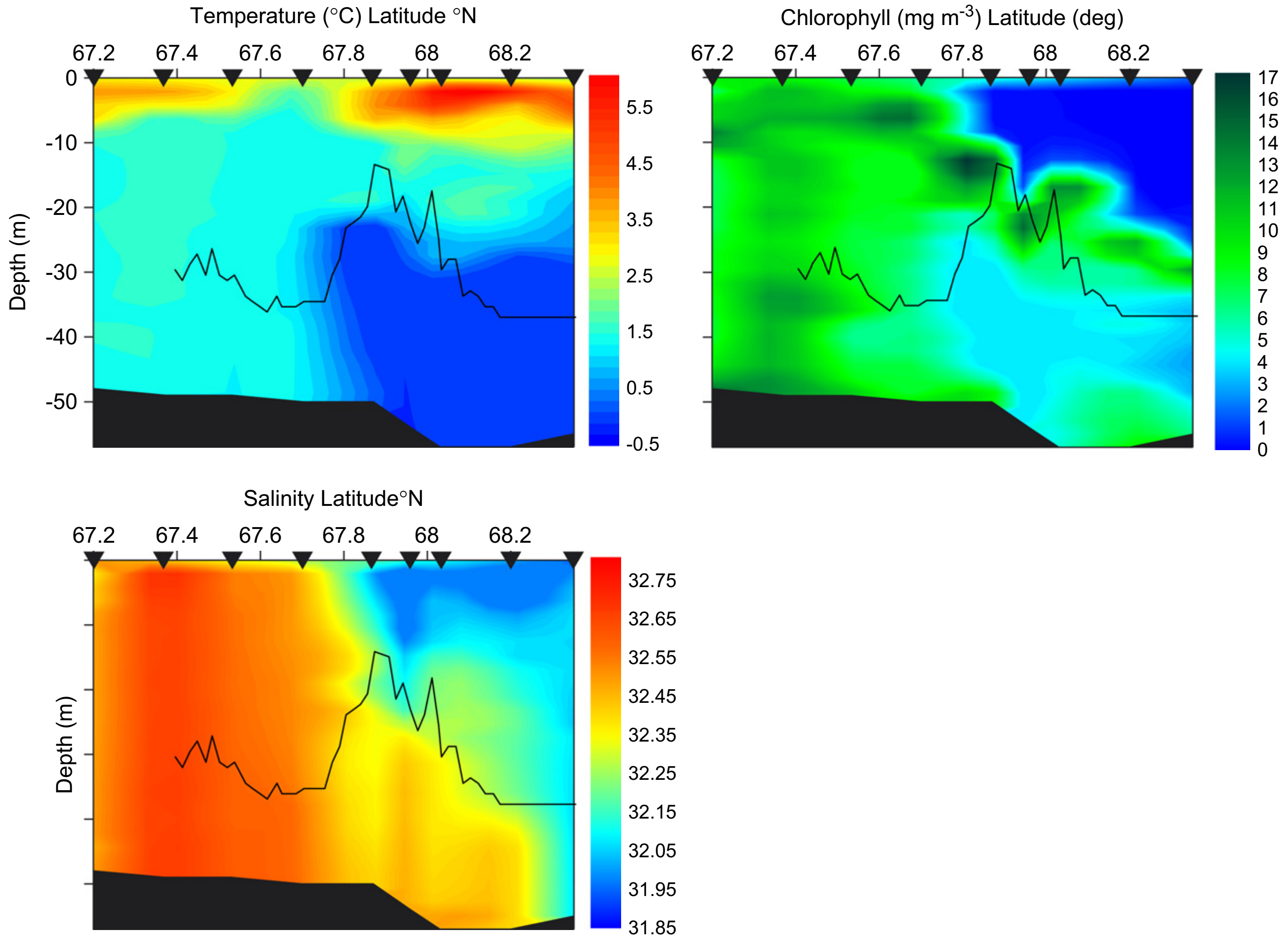

Fig. 5. Distribution of temperature, salinity and chlorophyll concentrations in June 2003 along survey transect 1 marked in Fig. 2. Overlaid are gray whale counts (thin, black line) along the same transect (for actual count values see Fig. 3). Black triangles along the *x*-axes indicate CTD locations. Strong vertical gradients in all three sets of measurements occurred at approximately 67.8°N.

mean temperature above the pycnocline and water depth on the one hand, and mean fluorescence above the pycnocline on the other hand; and factor 4 was determined by correlations between the mean whale counts and the gradients of temperature below the pycnocline and salinity above the pycnocline. Of all the variables used in the factor analysis (Table 1), the general linear model determined five variables that best described the equation for the whale abundance index (mean salinity above pycnocline, gradient of mean temperature below pycnocline, gradient of mean salinity below pycnocline, gradient of mean salinity above pycnocline and water depth; Table 2); these explained 65.9% of the variability in the whale counts. For all variables and the overall equation, $p<0.001$, except for the gradient in the mean temperature below the pycnocline where $p=0.003$.

The factor analysis for the September cruise also identified four factors with eigenvalues >1, of which factor 1–4 explained 27.5%, 21.2%, 16.9% and 13.7% of the total variance, respectively, for a sum of 79.3%. According to the factor loading matrix (Table 1), factor 1 represented correlations between three major hydrographical variables and mean fluorescence below the pycnocline; factor 2 again was determined by gradients in temperature and salinity but also mean salinity below the pynocline; factor 3 was determined by an inverse correlations between the mean whale counts and the gradient of salinity below the pycnocline along with water depth; factor 4 was driven by an inverse correlation between the stability parameter and mean fluorescence above the pycnocline. The general linear model applied to the September data identified three variables that best described the equation for

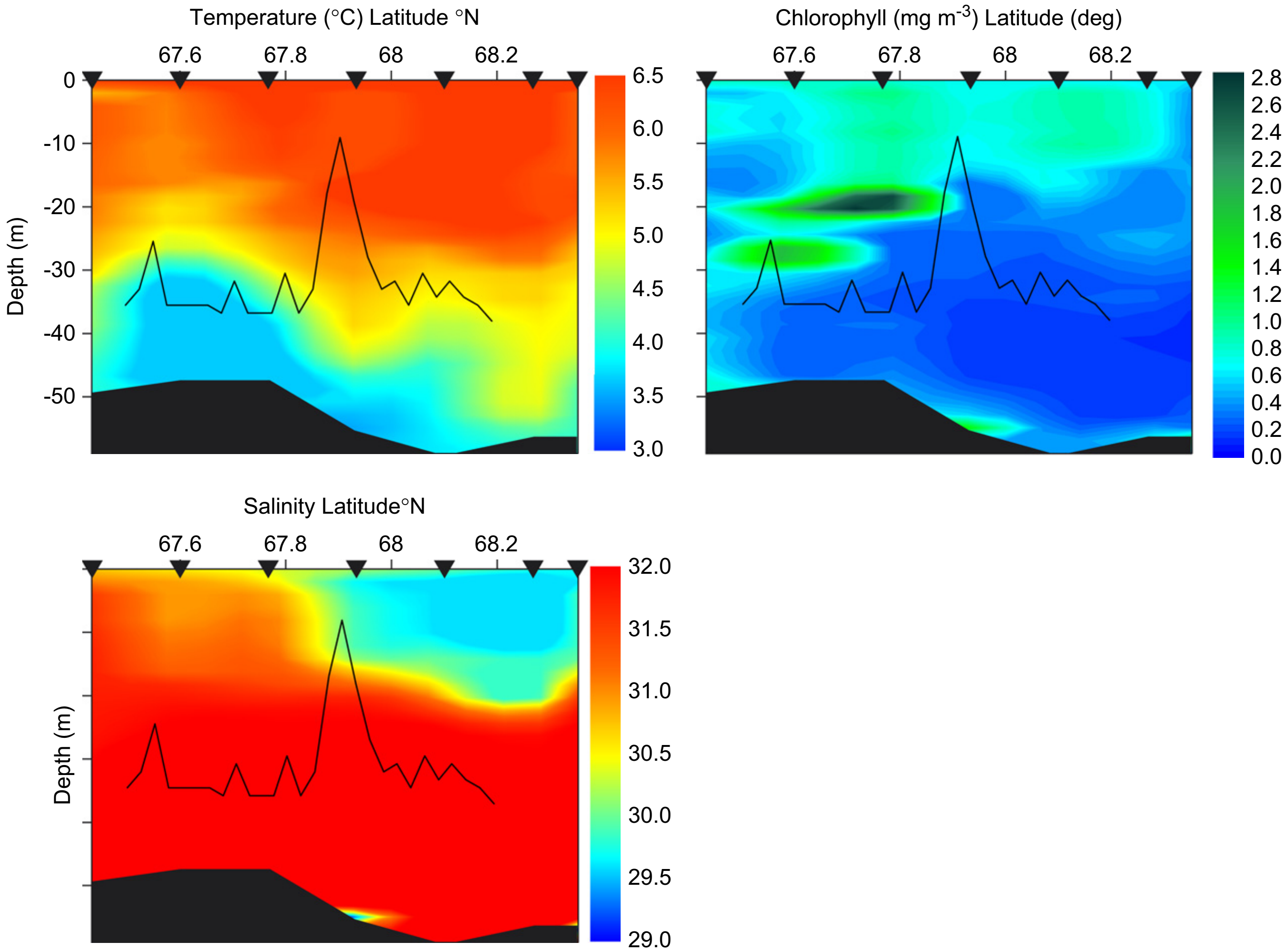

Fig. 6. Distribution of temperature, salinity and chlorophyll concentrations in September 2003 along survey transect 1 marked in Fig. 2. Overlaid are gray whale counts along the same transect (for actual count values see Fig. 3). Black triangles along the x-axes indicate CTD locations. Due to the different range of values measured in this season relative to June 2003, different scaling than in Fig. 5 was necessary to illustrate the gradients appropriately.

the whale abundance index: mean salinity below pycnocline ($p = 0.009$), mean fluorescence below pycnocline ($p = 0.014$), and water depth ($p < 0.001$); $p = 0.001$ for the overall equation (Table 2).

3.4. Qualitative pelagic and benthic sampling

Qualitative evaluation of zooplankton MOCNESS hauls showed that, overall, euphausids, *Thysanoessa raschii*, chaetognaths, and copepods were the dominant taxa in September 2003. Other groups present included cnidarians, pteropods, amphipods and mysids. Euphausids along with chaetognaths were largest in size and relatively most abundant in the frontal area where whale counts were highest in June and high in September (Fig. 4). Euphausids contributed less to the faunal composition outside the front, where whale counts were low, and occurred at intermediate levels near the south side of the front. Benthic infaunal biomass at seven stations on transect 1 ranged from 200 (S.D. 20) g wet weight m^{-2} to 1623 (S.D. 186) g wet weight m^{-2}; mean biomass was 1000 (S.D. 505) g wet weight m^{-2}. Benthic biomass was highest where whale counts were highest in June (stn. 88, Fig. 3). However, benthic biomass was also relatively high at a station where whale counts were low during the survey periods (stn. 90, Fig. 3). Visual assessment of infaunal biomass from grab samples suggested that clams were dominant at all stations. Amphipods, mostly *Pontoporeia femorata,* were present at all stations, but infrequent north of

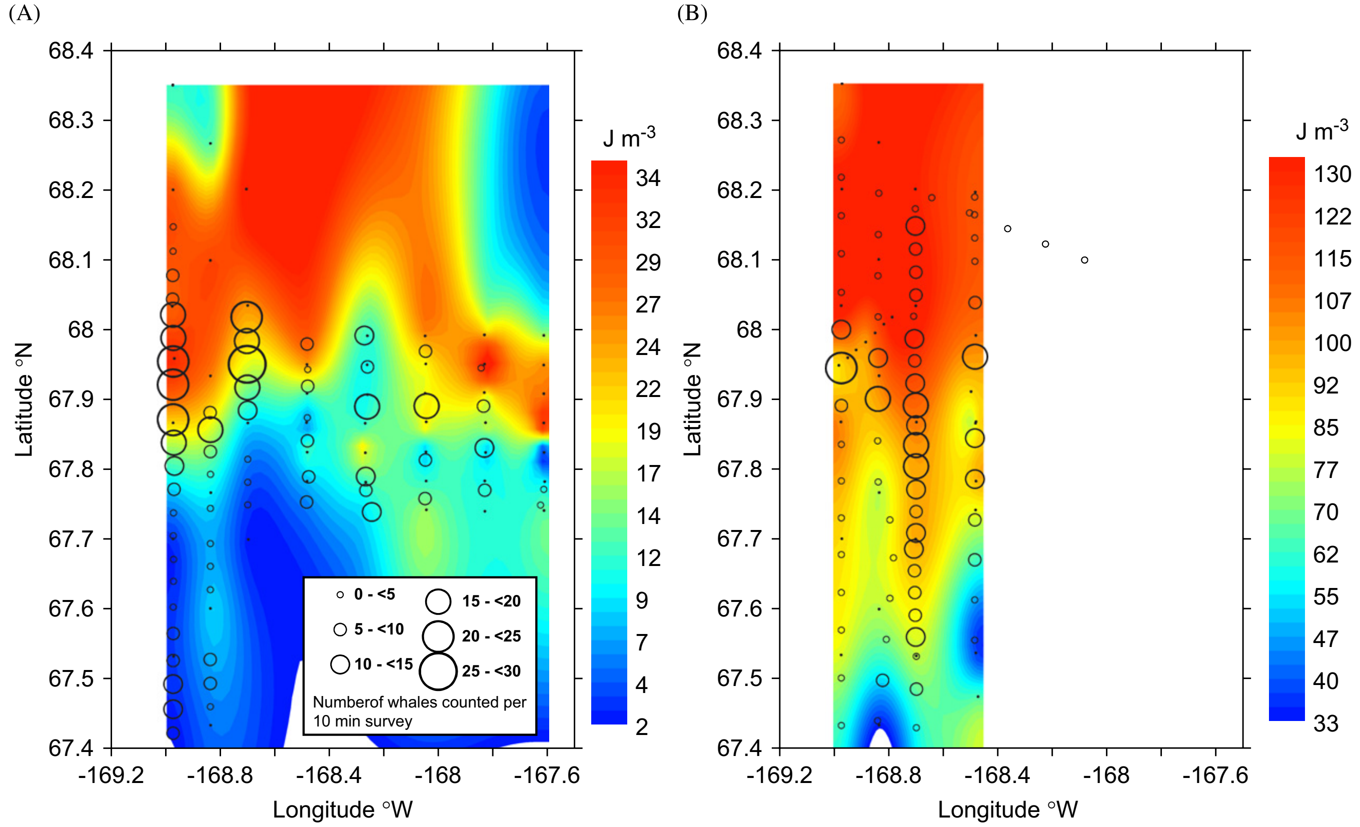

Fig. 7. Gray whale counts overlaid on the stability parameter (J m^{-3}) in the south-central Chukchi Sea during (A) June 24–28, 2003 and (B) September 20–24, 2003. Black dots indicate CTD locations; different scales were necessary in the two figures to illustrate the strong gradients appropriately.

Table 2
Results from stepwise backward general linear model to estimate a relative index of whale abundance in the south-eastern Chukchi Sea front in June and September 2003

June 2003				September 2003			
Effect	Coefficient	S.E.	*p*-Value	Effect	Coefficient	S.E.	*p*-Value
Constant	−49.644	12.861	0.000	Constant	79.740	14.048	0.000
Mean *S* above P	3.689	0.901	0.000	Mean *S* below P	−3.348	1.108	0.009
Gradient mean *T* below P	318.362	99.903	0.003	Mean *F* below P	−3.316	1.188	0.014
Gradient mean *S* below P	−1575.573	393.289	0.000	Water depth	−1.450	0.276	0.000
Gradient mean *S* above P	964.456	221.869	0.000				
Water depth	1.033	0.241	0.000				

F: fluorescence, P: pycnocline, *T*: temperature, *S*: salinity.

68°N. Ampeliscidae occurred in low numbers at stations north of the front. Based on counts, the epibenthic megafauna composition from trawl hauls was dominated by echinoderms, specifically *Myriotrochus rinkii*, *Leptasterias polaris* and *Ophiura sarsi* at the three stations where whale counts were high (stns. 88, 89 and 94; Figs. 4 and 8). Crustaceans, mostly *Chionoecetes opilio* and several shrimp species as well as fish (Arctic cod, sculpins and flatfishes) were dominant at the two trawl stations where gray whale counts were low (stns. 103, 151).

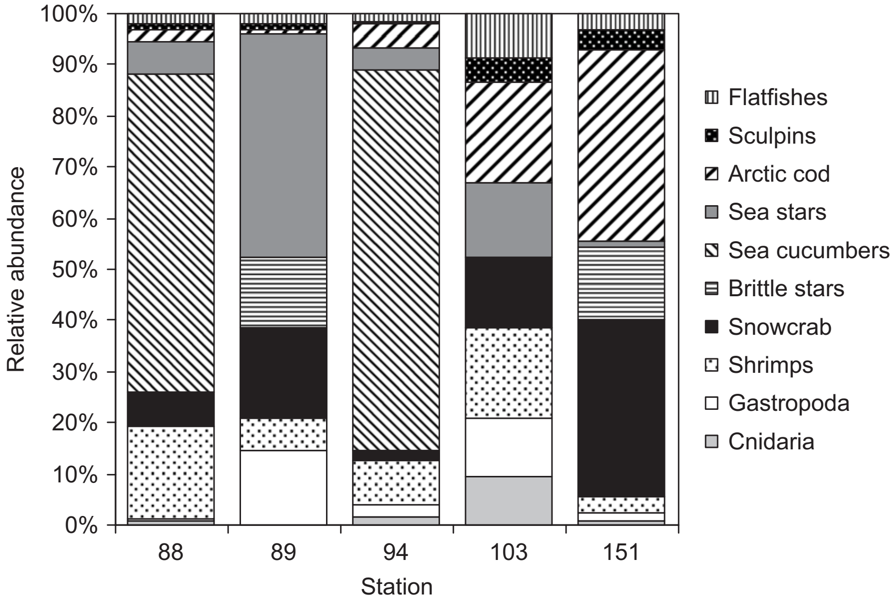

Fig. 8. Faunal composition of trawl hauls taken in the south-central Chukchi Sea in 2003. Station locations are shown in Fig. 2.

4. Discussion

4.1. Gray whales in the south-central Chukchi Sea

Hundreds of gray whales were observed in the south-central Chukchi Sea in the summer and fall of 2003. Gray whales have been reported in this area and adjacent waters to the west of the convention line for over 30 years. In 1973 and 1980, ship-board observers counted 588 and 1021 gray whales, respectively, in 4-day periods between 67°40′N–68°15′N and 169°40′W–172°00′W (Berzin, 1984). Repeated surveys between 1982 and 1991 in the months of July to November yielded high gray whale counts in July and October in an area that overlapped with our study area in south-central Chukchi Sea (Moore, 2000; Clarke and Moore, 2002). No reported survey effort occurred in this area between 1992 and 2001, but in an aerial survey in July 2002, Moore et al. (2003) again reported high gray whale densities. Our survey supports the conclusion from these previous studies that the south-central Chukchi Sea has been and continues to be a significant site for gray whales during the summer and fall.

Whether the use of the south-central Chukchi Sea by gray whales has changed over time or is linked to the concurrent decline of whale sightings in the Chirikov Basin (Moore et al., 2003) is unclear and cannot be answered by our study. However, comparable sighting numbers in the area by Berzin (1984) for 1973 and 1980 with a similar survey effort as in this study could be indicative of consistent use over the last decades. Both consistent and variable use of gray whale feeding sites has been documented from southern feeding areas. In a recent summary of 26 years of gray whale studies off Vancouver Island, Darling et al. (1998) showed that gray whales used certain feeding sites on an annual basis while other sites were used with >10-year intervals between use. Habitat selection for feeding, e.g. water column versus sea floor, within areas was also variable (Dunham and Duffus, 2001, 2002). This variability in feeding site selection and use may be occurring in the northern feeding sites, including the site we investigated. The significant recovery of the gray whale population after the intense period of commercial harvest may be based on this ability to exploit a variety of food resources and habitat types. The gray whale population was estimated at around 15,000–20,000 before intense harvest in the mid-1900s reduced the population to 4000 or less (Rice and Wolman, 1971; Henderson, 1984). It then rebounded to around 26,000 whales in 1997–1998 (Rugh et al., 1999) but has experienced high mortalities and low calving rates since 1999 (Le Boeuf et al., 2000; Moore et al., 2001; Perryman et al., 2002). Most ENP gray whale studies were conducted when population numbers were comparatively low (e.g. Jones et al., 1984), perhaps resulting in a limited understanding of feeding patterns of these whales in the northern foraging grounds. Among the foraging grounds, most effort reported to date in the English language literature has focused on the Chirikov Basin. The south-central Chukchi Sea, in contrast, has received little attention in terms of its characteristics as a gray whale feeding site. However, general ecological information is available for this area and our findings will be discussed in the light of these ecological studies.

4.2. Food availability

The intense use of the study area by gray whales is likely linked to high prey density in this area. Prey density in a gray whale feeding site appears to be more important than the taxonomic composition of the available prey (Darling et al., 1998; Moore et al., 2003). During their summer feeding period, gray whales require energy hot spots to build up reserves to sustain their metabolism and for the females to feed their calves throughout the winter months (Moore et al., 2003). Along with the central Chirikov Basin, the south-central Chukchi Sea (including our study site) has been described as such an energy-rich site and our preliminary observations on faunistic patterns confirm this finding. Specifically, the south-central Chukchi Sea under the nutrient-rich Bering Shelf Water had the highest algal and faunal biomass on the combined Bering Sea Shelf and the southern Chukchi Sea in the 1980s and beyond (Walsh et al., 1989; Grebmeier et al., 2006b). Depth-integrated chlorophyll-*a* was as high as 500–1000 mg m^{-2} and oxygen uptake rates of the sediment reached peak values up to 40 mmol O_2 m^{-2} day^{-1} (Grebmeier and McRoy, 1989; Grebmeier et al., 2006b). This uptake is the result of tight benthic–pelagic coupling driven by high sedimentation rates allowing a high biomass of benthic fauna to build up, with macro-infaunal biomass reaching 30–40 g C m^{-2} (Grebmeier et al., 2006b). In 1976, high epibenthos abundance and biomass were also recorded in this area (53,285 individuals km^{-2}, 2330 kg wet weight km^{-2}), although even higher values were measured near Point Hope and towards Kotzebue Sound, respectively (Feder et al., 2005). Recent studies have documented declines of benthic infaunal biomass in the northern Bering Sea over the last decades (Moore et al., 2003; Grebmeier et al., 2006a; Coyle et al., 2007), but such temporal trends have to our knowledge not yet been published for the Chukchi Sea.

The potential benthic prey composition available in the study area is somewhat different from the ampeliscid amphipod-dominated community utilized by gray whales in the nearby Chirikov Basin foraging area (this study; Bogoslovskaya et al., 1981; Highsmith and Coyle, 1992; Moore et al., 2003; Grebmeier et al., 2006b; Coyle et al., 2007). The infaunal community in the south-central Chukchi Sea is dominated by several filter-feeding clam species, in addition to polychaetes and non-ampeliscid amphipods (this study; Stoker, 1981; Grebmeier et al., 2006b; Feder et al., 2007: cluster group III), all of which have been recorded to occur in gray whale stomachs (Nerini, 1984). In the 1980s, ampeliscids contributed only 9% to the infaunal biomass in this area; grabs taken during this study showed that ampeliscids were rare at several stations. In the 1970s, epifaunal biomass in the south-central Chukchi Sea was dominated by the brittle star *O. sarsi* and the sea star *L. polaris* as well as the crab *C. opilio*, the snail *Neptunea heros* and the sea star *Asterias amurensis* (Feder et al., 2005). The first four species plus the sea cucumber *M. rinki*, the snail *Natica clausa* and anemones were dominant in this region during our 2003 survey. Of these epifaunal organisms, *Chionoecetes* and *Neptunea* have been reported from gray whale stomach contents (Nerini, 1984).

Although gray whales may prefer benthic amphipods as prey in the Chirikov Basin and off Chukotka (Bogoslovskaya et al., 1981; Nerini, 1984), their prey spectrum overall is extensive and reflects opportunistic foraging (Nerini, 1984; Darling et al., 1998). Off Vancouver Island, gray whale prey included herring eggs and larvae, crab larvae, mysids, amphipods and ghost shrimp in addition to benthic taxa (Darling et al., 1998; Dunham and Duffus, 2002). Our results and other recent studies from around Kodiak Island, where gray whales appear to be feeding on cumaceans (Moore et al., 2007), suggest this flexibility in prey choice may have been underappreciated at the northern feeding sites. Habitats used off Vancouver Island comprised the water column, the ocean surface and the sea floor, which included sandy or muddy sediments, eel grass beds, and kelp beds. In the present study, about half of the areas where whales first surfaced had mud plumes, an indication of benthic or near-bottom feeding. The other half did not produce a mud plume, which may be an indication of pelagic feeding, non-feeding dives or a consequence of us having missed the first surfacing after the dive. Pelagic feeding has so far been reported less frequently from the northern feeding areas than from Vancouver Island (Darling et al., 1998). We suggest euphausids and Arctic cod, which were collected in our MOCNESS tows and demersal trawls, respectively, may serve as alternative food sources to benthic prey. Based on these catches, we propose that one or both taxa also made up the strong acoustic signal we saw in opportunistic acoustic recordings done within the frontal area. Based on seabird diet studies, Piatt and Springer (2003) suggest euphausids to be abundant in the northern Bering Sea, from where they get advected, along with other zooplankton, into the central southern Chukchi Sea. Adult euphausids are poorly sampled by plankton nets and their distribution in the southern Chukchi is poorly known (Piatt and Springer, 2003). Euphausids are especially energy-rich prey (Percy and Fife, 1980) utilized by other cetaceans in the Arctic (Lowry et al., 2004).

4.3. *Frontal systems*

Gray whales in this study were concentrated at a frontal system that was identified by strong gradients in temperature, salinity, chlorophyll-*a* concentration and water-column stability. The front in our study area has been identified as a recurrent long-term feature documented by physical measurements (Coachman et al., 1975) and through satellite surface seawater temperature records (1985–1996; Belkin et al., 2003). In this area, the highly productive Anadyr Water, flowing through Bering Strait into the Chukchi Sea, meets the fresher and less productive Alaska Coastal Water (this study; Weingartner, 2005). During our June survey, we encountered a phytoplankton bloom in the Bering Shelf/Anadyr Water (see also Weingartner (2005) for June 2001–2005 data), with part of the chlorophyll apparently submerging under the Coastal Current Water on the northern side of the front and presumably partially settling out. Little algal biomass was left by late September, as indicated by the low chlorophyll-*a* values.

Fronts are narrow bands of horizontal gradients in physical, chemical and biological properties that separate broader areas of different vertical structure (Belkin et al., 2003). Oceanic, tidal, estuarine and other fronts can support enriched biomass of biologic communities on several trophic levels, from phytoplankton to marine birds and cetaceans (Iverson et al., 1979; Schneider, 1982; Hunt and Harrison, 1990; Franks, 1992; Mendes et al., 2002). Although clearly incomplete, our faunal assessment also points towards high faunal densities of clams, epibenthic megafauna, pelagic crustaceans (especially euphausids) and Arctic cod along the front during the survey periods. Other benthic biomass data from this area are indicative of long-term correlations between high primary and secondary production and the inflow of nutrient-rich Anadyr water (Grebmeier et al., 1988; Walsh et al., 1989; Piatt and Springer, 2003 and references therein; Feder et al., 2005, 2007; Grebmeier et al., 2006b; Fig. 4), although high biomass values were not limited to the front itself. At other frontal systems, e.g. in the North Sea, larval and juvenile Atlantic cod densities were elevated in a recurrent narrow band in a front with enhanced primary production and algal biomass (Munk et al., 1995). Similarly, zooplankton and larval sprat densities peaked in a tidal front along the 20–30 m depth contour separating two water masses in the Danish North Sea, and fish larvae grew better in the frontal zone than outside it (Munk, 1993). Hyperbenthic crustacean accumulated in the Frisian Front in the North Sea (Dewicke et al., 2002); enrichment in this front peaked in August, but was not present in the spring. Many more studies report on similar findings.

Mechanisms of high biomass accumulations in the Chukchi frontal area and vicinity are different for pelagic (phyto- and zooplankton) and benthic organisms. The strong gradients in water mass properties rather than individual physical–chemical variables themselves were associated with the dense gray whale aggregations. For primary producers in general, these frontal gradients provide a sufficiently stratified but mixed water column for rapid phytoplankton growth at the front, while phytoplankton are limited by nutrients on the stratified side of the front and by light on its mixed side (Floodgate et al., 1981). Alternatively, suspended matter including phyto- and zooplankton and detritus may be advected into a front due to convergence at fronts; microbial degradation may then enhance new production in the front, which would result in enhanced sedimentation to the benthos (Floodgate et al., 1981). Euphausids and other zooplankton we encountered at the Chukchi Sea front may accumulate here, perhaps seasonally, as a result of physical processes described and modeled for euphausids and other zooplankton at fronts (Simard et al., 1986; Franks, 1992). Previous studies (Feder et al., 2005; Grebmeier et al., 2006b and references therein) showed that the high biomass of long-lived less mobile benthic infauna and epibenthic megafauna occurred over a larger area than where we sampled them, as a consequence of high algal biomass in the Bering Shelf Anadyr water and high sedimentation rates in the south-central Chukchi Sea, resulting in tight pelagic–benthic coupling (Grebmeier et al., 2006b). It remains unresolved if benthic biomass was especially enhanced immediately underneath or near the front. Fine-scale resolution of both pelagic and benthic biomass across the front is needed to resolve biomass enhancement and patchiness at the front. With regard to whale aggregations, the frontal area may be particularly attractive for gray whales to feed at because of an apparently constant supply of various types of prey throughout the whole summer to fall feeding period of gray whales: in addition to the apparently long-term rich benthic biomass on the Anadyr water side, pelagic (and potentially benthic) biomass may be enriched as a consequence of frontal processes.

4.4. Concluding remarks

Gray whales occurred in high relative abundances in association with a recurrent oceanic front in the south-central Chukchi Sea. The observed front, characterized by steep gradients in temperature, salinity and chlorophyll-*a* concentration, enhanced biological production and biomass, potentially on several trophic levels, and may be an important gray whale foraging area. Previous and this study's benthic sampling suggests that ampeliscid amphipods, previously abundant in a nearby gray whale feeding area (Chirikov Basin in the northern Bering Sea), were not dominant in the Chukchi frontal region, but high densities of other benthic and pelagic fauna, including euphausids, were present. The preliminary data from this study suggest that food sources other than benthic amphipods may be more commonly preyed upon in Arctic gray whale summering areas than previously appreciated. In addition, fronts may play an important role in structuring gray whale feeding sites. Further study should include the adjacent area west of the convention line as well as concurrent quantitative assessments of the pelagic and benthic fauna and oceanographic conditions.

Acknowledgments

Vessel operations were supported by the captain and crew of the R/V Alpha-Helix. Dave Aldridge, Elisabeth Creelman, Nicole Koehler, and Mette Nielson, University of Alaska Fairbanks, are acknowledged for supporting the whale survey efforts. Max Hoberg, University of Alaska Fairbanks, helped with trawl voucher identification. The manuscript benefited from instructive discussion with Dr. Meike Scheidat, Science and Technology Center at Buesum, Germany, and with Dr. Rolf Gradinger, University of Alaska Fairbanks. We greatly appreciate the very helpful comments by Sue Moore and an anonymous reviewer on previous drafts of the manuscript. Fish were collected under University of Alaska Fairbanks Institutional Animal Care and Use Committee permit number #03–05. This research was part of a project funded by the National Science Foundation, Office of Polar Programs, award no. OPP 0101773.

This paper was first presented in the GLOBEC-ESSAS Symposium on ''Effects of climate variability on sub-arctic marine ecosystems'', hosted by PICES in Victoria, BC, May 2005.

References

Arar, E.J., Collins, G.B., 1992. In vitro determination of chlorophyll *a* and phaeophytin *a* in marine and freshwater by fluorescence. EPA Methods 445.0.

Belkin, I.M., Cornillon, P., Ullman, D., 2003. Ocean fronts around Alaska from satellite SST data. In: Proceedings of the American Metereological Society's 7th Conference on the Polar Metereology and Oceanography, Hyannis, MA, Paper 12.7, 15pp.

Berzin, A.A., 1984. Soviet studies of the distribution and numbers of the gray whale in the Bering and Chukchi Seas, from 1968–1982. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), The Gray Whale *Eschrichtius robustus*. Academic Press Inc., Orlando, FL, pp. 409–419.

Bogoslovskaya, L.S., Votrogov, L.M., Semenova, T.N., 1981. Feeding habits of the gray whale off Chukotka. Reports of the International Whaling Commission 31, 507–510.

Clarke, J.T., Moore, S.E., 2002. A note on observations of gray whales in the southern Chukchi and northern Bering Seas, August–November, 1980–89. Journal of Cetacean Research and Management 4, 283–288.

Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: The Regional Oceanography. University of Washington Press, Seattle.

Coyle, K.O., Bluhm, B., Konar, B., Blanchard, A., Highsmith, R.C., 2007. Amphipod Prey of Gray Whales in the Northern Bering Sea: Comparison of biomass and distribution between the 1980's and 2002–2003. Deep-Sea Research II, this issue [doi:10.1016/j.dsr2.2007.08.026].

Darling, J.D., Keogh, K.E., Steeves, T.E., 1998. Gray whale (*Eschrichtius robustus*) habitat utilization and prey species off Vancouver Island, B.C. Marine Mammal Science 14, 692–720.

Dewicke, A., Rottiers, V., Mees, J., Vincx, M., 2002. Evidence for an enriched hyperbenthic fauna in the Frisian front (North Sea). Journal of Sea Research 47, 121–139.

Dunham, J.S., Duffus, D.A., 2001. Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada. Marine Ecology Progress Series 223, 299–310.

Dunham, J.S., Duffus, D.A., 2002. Diet of gray whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia, Canada. Canadian Marine Mammal Science 18, 419–427.

Feder, H.M., Jewett, S.C., Blanchard, A., 2005. Southeastern Chukchi Sea (Alaska) epibenthos. Polar Biology 28, 402–421.

Feder, H.M., Jewett, S.C., Blanchard, A.L., 2007. Southeastern Chukchi Sea (Alaska) macrobenthos. Polar Biology 30, 261–275.

Fielder, P.C., Reilly, S.B., Hewitt, R.P., Demer, D., Philbrick, V.A., Smith, S., Armstrong, W., Croll, D.A., Tershy, B.R., Mate, B.R., 1998. Blue whale habitat and prey in the California Channel Islands. Deep-Sea Research II 45, 1781–1801.

Floodgate, G.D., Fogg, G.E., Jones, D.A., Lochte, K., Turley, C.M., 1981. Microbiological and zooplankton activity at a front in Liverpool Bay. Nature 290, 133–136.

Franks, P.J.S., 1992. Sink or swim: accumulation of biomass at fronts. Marine Ecology Progress Series 82, 1–12.

Grebmeier, J.M., McRoy, C.P., 1989. Pelagic–benthic coupling on the shelf of the Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. Marine Ecology Progress Series 53, 79–91.

Grebmeier, J.M., McRoy, C.P., Feder, H.M., 1988. Pelagic–benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. Marine Ecology Progress Series 48, 57–67.

Grebmeier, J.M., Feder, H.M., McRoy, C.P., 1989. Pelagic–benthic coupling on the shelf of the Bering and Chukchi Seas. II. Benthic community structure. Marine Ecology Progress Series 51, 253–268.

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006a. A major ecosystem shift in the northern Bering Sea. Science 311, 1461–1464.

Grebmeier, J.M., Cooper, L.W., Feder, H.M., Sirenko, B.I., 2006b. Pelagic–benthic coupling and ecosystem dynamics in the Pacific-influenced Amerasian Arctic. Progress in Oceanography.

Henderson, D.A., 1984. Nineteenth century gray whaling: grounds, catches and kills, practices and depletion of the whale population. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), The Gray Whale *Eschrichtius robustus*. Academic Press Inc., Orlando, FL, pp. 159–186.

Highsmith, R.C., Coyle, K.O., 1990. High productivity of northern Bering Sea benthic amphipods. Nature 344, 862–864.

Highsmith, R.C., Coyle, K.O., 1992. Productivity of arctic amphipods relative to gray whale energy requirements. Marine Ecology Progress Series 83, 141–151.

Highsmith, R.C., Coyle, K.O., Bluhm, B.A., Konar, B., 2006. Gray whales in the Bering and Chukchi Seas. In: Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M., Brownell, Jr., R.L. (Eds.), Whales, Whaling and Ocean Ecosystems. UC Press, St. Cruz, CA.

Hunt Jr., G.L., Harrison, N.M., 1990. Foraging habitat and prey taken by least auklets at King Island, Alaska. Marine Ecology Progress Series 65, 141–150.

Iverson, R.L., Whitledge, T.E., Goering, J.J., 1979. Fine-structure of chlorophyll and nitrate in the southeastern Bering Sea shelf break front. Nature, London 281, 664–666.

Jones, M.L., Swartz, S.L., Leatherwood, S., 1984. The Gray Whale, *Eschrichtius robustus*. Academic Press Inc., Orlando, FL.

Karl, D.M., Winn, C.D., Hebel, D.V.W., Letelier, R., 1990. JGOFS Hawaii Ocean Time-Series Program Field and Laboratory Protocols. 〈http://hahana.soest.hawaii/edu/hot/protocols/html〉, Hawaii.

Le Boeuf, B.J., Perez-Cortes, M.H., Urban, R., Mate, B.R., Ollervides, F.U., 2000. High gray whales mortality and low recruitment in 1999: potential causes and implications. Journal of Cetacean Research and Management 2, 85–99.

Lowry, L.F., Sheffield, G., George, J.C., 2004. Bowhead whale feeding in the Alaskan Beaufort Sea, based on stomach contents analyses. Journal of Cetacean Research and Management 6, 215–223.

Marquette, W.M., Braham, H.W., 1982. Gray whale distribution and catch by Alaskan Eskimos: a replacement for the bowhead whale? Arctic 35, 386–394.

Mendes, S., Turrell, W., Lütkebohle, T., Thompson, P., 2002. Influence of the tidal cycle and a tidal intrusion front on the spatio-temporal distribution of coastal bottlenose dolphins. Marine Ecology Progress Series 239, 221–229.

Moore, S.E., 2000. Variability of cetacean distribution and habitat selection in the Alaskan Arctic, autumn 1982–1991. Arctic 53, 448–460.

Moore, S.E., DeMaster, D.P., 1998. Cetacean habitats in the Alaskan Arctic. Journal of Northwest Atlantic Fisheries Science 22, 55–69.

Moore, S.E., DeMaster, D.P., Dayton, P.K., 2000. Cetacean habitat selection in the Alaskan Arctic during summer and autumn. Arctic 53, 432–447.

Moore, S.E., Urban, J.R., Perryman, W.L., Gulland, F., Perez-Cortez, H.M., Wade, P.R., Rojas-Bracho, L., Rowles, T., 2001. Are gray whales hitting "K" hard? Marine Mammal Science 17, 954–958.

Moore, S.E., Grebmeier, J.M., Davies, J.R., 2003. Gray whale distribution relative to habitat in the northern Bering Sea: current conditions and retrospective summary. Canadian Journal of Zoology 81, 734–742.

Moore, S.E., Wynne, K.M., Clement Kinney, J., Grebmeier, J.M., 2007. Gray whale occurrence and forage southeast of Kodiak Island, Alaska. Marine Mammal Science 23, 419–428.

Munk, P., 1993. Differential growth of larval sprat *Sprattus sprattus* across a tidal front in the eastern North Sea. Marine Ecology Progress Series 99, 17–27.

Munk, P., Larsson, P.O., Danielsen, D., Moksness, E., 1995. Larval and small juvenile cod *Gadus morhua* concentrated in the highly productive areas of a shelf break front. Marine Ecology Progress Series 125, 21–30.

Nerini, M., 1984. A review of gray whale feeding ecology. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), The Gray Whale, *Eschrichtius robustus*. Academic Press Inc., Orlando, FL, pp. 423–450.

Obst, B.S., Hunt Jr., G.L., 1990. Marine birds feeding at gray whale mud plumes in the Bering Sea. The Auk 107, 678–688.

Percy, J.A., Fife, F.J., 1980. The proximate composition and caloric content of arctic marine invertebrates from Frobisher Bay. Canadian Data Report on Fisheries and Aquatic Sciences 214, iv + 35.

Perryman, W.L., Donahue, M.A., Perkins, P.C., Reilly, S.B., 2002. Gray whale calf production 1994–2000: are observed fluctuations related to changes in seasonal ice cover? Marine Mammal Science 18, 121–144.

Piatt, J.F., Springer, A.M., 2003. Advection, pelagic food webs and the biogeography of seabirds in Beringia. Marine Ornithology 31, 141–154.

Rice, D., Wolman, A., 1971. The Life History and Ecology of the Gray Whale (*Eschrichtius robustus*). The American Society of Mammalogists, Special Publication No. 3.

Rugh, D.J., Muto, M.M., Moore, S.E., DeMaster, D.P., 1999. Status Review of the Eastern North Pacific Stock of Gray Whales. NOAA Technical Memorandum NMFS-AFSC-103.

Schneider, D., 1982. Fronts and seabird aggregations in the southeastern Bering Sea. Marine Ecology Progress Series 10, 101–103.

Simard, Y., de Ladurantaye, R., Therriault, J., 1986. Aggregation of euphausiids along a coastal shelf in an upwelling environment. Marine Ecology Progress Series 32, 203–215.

Simpson, J.H., Hughes, D.G., Morris, N.C.G., 1977. The relation of seasonal stratification to tidal mixing on the continental shelf. Deep-Sea Research 24 (Suppl.), 327–340.

Stoker, S.W., 1981. Benthic intertebrate macrofauna of the eastern Bering/Chukchi continental shelf. In: Hood, D.W., Calder, J.A. (Eds.), The Eastern Bering Sea Shelf: Oceanography and Resources. NOAA, University of Washington Press, Seattle, WA, pp. 1069–1090.

Walsh, J.J., McRoy, C.P., Coachman, L.K., Goering, J.J., Nihoul, J.J., Whitledge, T.E., Blackburn, T.H., Parker, P.L., Wirick, C.D., Shuert, P.G., Grebmeier, J.M., Springer, A.M., Tripp, R.D., Hansell, D.A., Djenidi, S., Deleersnijder, E., Henriksen, K., Lund, B.A., Andersen, P., Mueller-Karger, F.E., Dean, K., 1989. Carbon and nitrogen cycling within the Bering/Chukchi Seas: source regions for organic matter affecting AOU demands of the Arctic Ocean. Progress in Oceanography 22, 277–359.

Weingartner, T.J., 2005. Regional Web Pages with Ocean Color Images. 〈http://halibut.ims.uaf.edu:800/~mschmidt/ak_chukchi_sea_summary.html〉.

Wiebe, P.H., Burt, K.H., Boyd, S.H., Morton, A.W., 1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. Journal of Marine Research 34, 313–325.

Witting, L., 2003. Reconstructing the population dynamics of eastern Pacific gray whales over the past 150 to 400 years. Journal of Cetacean Research and Management 5, 45–54.

Yablokov, A.V., Bogoslovskaya, L.S., 1984. A review of Russian research on the biology and commercial whaling of the gray whale. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), The Gray Whale *Eschrichtius robustus*. Academic Press Inc., Orlando, FL, pp. 465–485.