ELSEVIER

Amphipod prey of gray whales in the northern Bering Sea: Comparison of biomass and distribution between the 1980s and 2002–2003

Kenneth O. Coyle[a],[*], Bodil Bluhm[a], Brenda Konar[a],
Arny Blanchard[a], Raymond C. Highsmith[b]

[a]*School of Fisheries and Ocean Science, Institute of Marine Science, University of Alaska, Fairbanks, AK 99775-7220, USA*
[b]*National Institute for Undersea Science and Technology, University of Mississippi, MS 38677-7685, USA*

Abstract

The ampeliscid amphipod community in the Chirikov Basin of the northern Bering Sea was a focus of study during the 1980s because they were a major food for the Eastern North Pacific (ENP) population of gray whales *Eschrichtius robustus*. Information from the 1980s benthic investigations, published accounts of ENP gray whale population trends and the occurrence in 1999–2000 of an unusual number of gray whale mortalities prompted concern that the whale population may have exceeded the carrying capacity of its food base. Therefore, during two cruises per year between June and September, 2002 and 2003, we resampled the 20 stations occupied during the 1980s, to determine if there had been any significant changes in ampeliscid abundance and biomass. During 2002–2003, average ampeliscid dry weight biomass was about $28 \pm 10\,\mathrm{g\,m^{-2}}$ (95% confidence interval), a decline of nearly 50% from maximum values in the 1980s. Amphipod length measurements indicated that the declines were due mainly to the absence of the larger animals (20–30 mm length). Two hypotheses were considered regarding the amphipod declines: gray whale predation and climate. Ampeliscid production ($105\,\mathrm{kcal\,m^{-2}\,yr^{-1}}$) and gray whale energy requirements ($1.6 \times 10^8\,\mathrm{kcal\,individual^{-1}\,yr^{-1}}$) indicated that as little as 3–6% of the current estimate of the ENP gray whale population could remove 10–20% of the annual ampeliscid production from the study site in 2002–2003, a finding consistent with the hypothesis that top-down control by foraging whales was the primary cause of the observed declines. A 10-yr time series of temperature near the bottom in the Bering Strait and northward transport did not reveal a consistent trend between 1990 and 2001, suggesting that climate influences were not the major cause of the observed declines. Arctic ampeliscids have slow growth rates and long generation times; therefore the ampeliscid community may require decades to recover to densities observed in the 1980s. Predicted warming trends in the northern Bering Sea could impact ampeliscid recovery by lowering primary production or altering the community composition of the benthos.
© 2007 Elsevier Ltd. All rights reserved.

Keywords: Amphipods; Benthos; USA; Alaska; Bering Sea

---

*Corresponding author. Tel.: +1 907 474 7705; fax: +1 907 474 7204.

E-mail addresses: coyle@ims.uaf.edu (K.O. Coyle), bluhm@ims.uaf.edu (B. Bluhm), bkonar@guru.uaf.edu (B. Konar), arnyb@ims.uaf.edu (A. Blanchard), ray@olemiss.edu (R.C. Highsmith).

1. Introduction

The northern Bering Sea amphipod community in the Chirikov Basin is composed primarily of tube-dwelling amphipods of the family Ampeliscidae (Stoker, 1981; Grebmeier et al., 1989; Highsmith and Coyle, 1991, 1992). Measurements in the 1980s indicated that the Chirikov Basin ampeliscids comprised one of the most productive amphipod communities on record (Highsmith and Coyle, 1990), with maximum values on the order of 170–230 $kcal\,m^{-2}\,yr^{-1}$ and a mean dry weight biomass of 30–40 $g\,m^{-2}$. The Chirikov Basin amphipod bed was a focus of research in the 1980s, because the region was a major foraging ground of the Eastern North Pacific (ENP) population of the gray whale *Eschrichtius robustus* (Kim and Oliver, 1989; Moore, 2000; Moore et al., 2003), and dietary analysis indicated that ampeliscids were the primary prey item (Bogoslovskaya et al., 1981; Nerini, 1984). Historically, about 87% of the ENP gray whale population spent some time foraging in this area while in transit, and about 17% spent approximately 6 months of the year (May–October) in the Chirikov Basin to obtain most of their annual energetic requirements (Berzin, 1984; Thomas and Martin, 1986).

Although the gray whale population had been growing at a rate of 3.29% yr^{-1} since 1980 (Perryman et al., 1998; Rugh et al., 1999), a more than threefold increase in gray whale mortality occurred in the late 1990s and a decline in calf production of about 80% was observed (Le Boeuf et al., 2000; Moore et al., 2001). Abundance estimates have fallen from 29,758 whales in 1997/1998 to 18,178 ($\pm$10% coefficient of variation) in 2001/2002 (Rugh et al., 2005), a decline of about 30%. The reasons for the gray whale population declines are uncertain; however, food limitation is one potential cause. Recent evidence indicates that gray whales may be approaching the carrying capacity of their habitat (Moore et al., 2001; Rugh et al., 2005) and the gray whale population may have been high enough to impose top-down control on the amphipod community in the Chirikov Basin as early as the 1980s (Highsmith and Coyle, 1992). In addition, climate-related changes in the Bering Sea ecosystem (Napp and Hunt, 2001; Hunt and Stabeno, 2002; Schumacher et al., 2003) suggest that gray whale food resources may be impacted by global climate change. To determine if gray whale food sources had declined in the Chirikov Basin, in 2002–2003 we resampled stations from the earlier amphipod study in the 1980s, to permit comparisons of amphipod abundance, biomass, and productive capacity in the two periods. Here we present the most recent estimates of ampeliscid abundance and biomass in the Chirikov Basin, and compare the results with those of earlier studies.

1.1. Site description

The Chirikov Basin covers about 40,000 km^2 in the northern Bering Sea between St. Lawrence Island and the Bering Strait (Fig. 1). The bottom is flat and sandy (Grebmeier et al., 1989) with an average bottom depth of about 40 m. Low ^{210}Pb-ex concentrations (9.3–16.7 $mBq\,g^{-1}$) suggest a very low sedimentation rate (Grebmeier, 1993). The region is characterized by three major water masses, the Alaska Coastal Water (ACW), the Anadyr Water (AW), and the Bering Self Water (BSW). The Chirikov Basin, where the amphipod bed occurs (Fig. 1), is occupied by AW and BSW water masses (Coachman et al., 1975). The AW originates at the Bering Sea shelf break and is the source of nutrients driving the high primary production over the amphipod bed (Walsh et al., 1989). Because ampeliscids are sedentary tube dwellers that feed primarily on phyto-detritus (Highsmith and Coyle, 1991), they require a high flux of phytoplankton to the bottom to maintain their dense populations and high productivity.

2. Methods

2.1. Amphipod sampling

Baseline data to assess changes in amphipod populations were collected between late May and early November 1986–1988 (Table 1), as reported in earlier publications (Highsmith and Coyle, 1990, 1991, 1992). During 2002 and 2003, two cruises were made to the study site between late June and the end of September of each year. Twenty stations were sampled in the Chirikov Basin between 63°N and 65°N and 168°W and 170°W (Fig. 1(B), black dots). Sampling locations and methodology were identical to those in the earlier study. Five replicate benthic samples were taken at each station with a 0.1 m^2 van Veen grab. The samples were sieved through a 1-mm screen and all animals retained on the screen were preserved in 10% buffered formalin for later sorting and analysis.
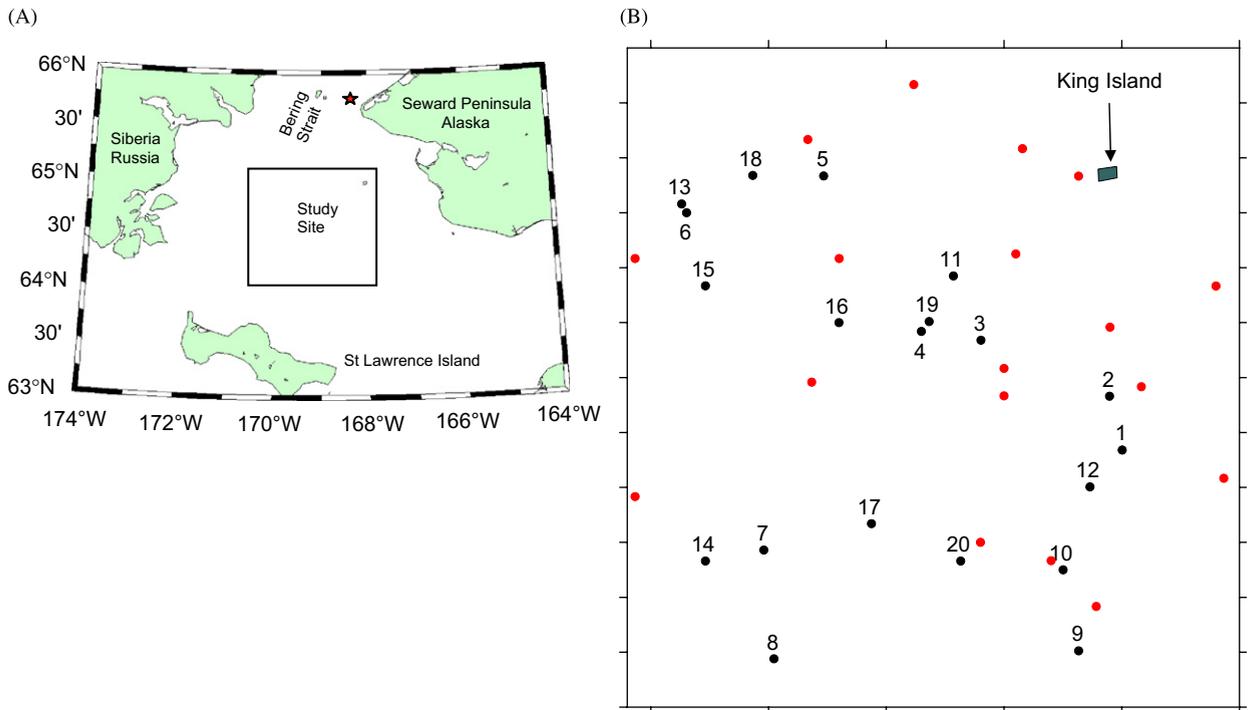
(A)

(B)

Fig. 1. (A) Location of the ampeliscid study site in the Chirikov Basin of the northern Bering Sea (red star is the location of Mooring A2 in Bering Strait). (B) Station locations for 1986–1988 and 2002–2003 (black dots and numbers) and for 1973–1974 (red dots).

Table 1
Cruise dates for sample periods 1 (1986–1988) and 2 (2002–2003)

Period 1			Period 2	
1986	1987	1988	2002	2003
May 28–Jun 4	Jun 14–18	Jun 5–11	Jul 1–10	Jun 20–27
Jul 27–31	Jul 16–19*	Jul 18–24*	Sep 6–14	Sep 15–24
Sep 10–13	Aug 21–25*	Aug 26–28*	–	–
Sep 27–Oct 9	Oct 31–Nov 4	Oct 14–17	–	–

Asterisk indicates cruise where CTD data only were available.

Additional samples were collected at selected sites for dry-weight determinations. Amphipods from dry-weight samples were sorted to species. The head length was measured using a digitizing board and converted to total body length (to the nearest mm from the tip of the head to the tip of the telson) using a head length–body length regression. The specimens were then dried at 60 °C for 24 h, frozen, and returned to the lab for analysis. The frozen samples were thawed, redried at 60 °C for an additional 24 h, and dry weight was measured with a Cahn Electrobalance. A subsample of material from the formalin preserved samples was measured and weighed to determine length–wet weight re-lationships. The relationship between amphipod length and ash free dry weight (AFDW) was computed from data taken in the 1980s (Highsmith and Coyle, 1991, 1992). A MatLab curve fitting algorithm was used to relate wet weight, dry weight, and AFDW to animal length. The resulting regression coefficients were used to convert the length and abundance data to biomass. Caloric content was estimated using caloric-AFDW ratios determined in an earlier study (Highsmith and Coyle, 1992). Amphipods in the formalin-preserved samples were sorted to species and enumerated. The head length was measured and converted to body length as outlined above.

The *Byblis* species in the northern Bering Sea are very similar and cannot be reliably distinguished when under about 8 mm length (Coyle and Highsmith, 1989). Therefore, all *Byblis* for these analyses were pooled as *Byblis* spp. The species present included *B. gaimardii*, *B. breviramus*, *B. pearcyi*, *B. frigidis*, and *B. robustus*. *Ampelisca macrocephala* and *Ampelisca erythrorhabdota* cannot be distinguished when under 8 mm length. *A. macrocephala*, *A. erythrorhabdota*, and *Ampelisca eschrichti* were pooled as *Ampelisca* spp. for the analyses in this paper. *Ampelisca birulai* were reported separately based on their different body shape.

2.2. Physical oceanographic data

Conductivity–temperature–depth (CTD) profiles were taken at each station using a Seabird model 911 Plus CTD. The depth of the pycnocline was computed for each station and cruise by locating the depth where $d\sigma t/dZ$ was maximum ($\sigma t = \text{sigma } t$; $Z = \text{depth m}$). The mean water-column temperature and salinity above and below the pycnocline were computed. In addition, the stratification parameter, the energy required to redistribute the water-column mass by complete vertical mixing ($J\,m^{-3}$), was computed (Fielder et al., 1998; Simpson et al., 1977). For analysis of chlorophyll-*a* and phaeopigments, water samples collected with Niskin bottles from a CTD rosette were filtered on GF/F filters and frozen. Pigments were extracted with 7 ml of 90% (v:v) acetone for 24 h in the dark at $-18\,^\circ C$ (Karl et al., 1990). Chlorophyll-*a* concentration was then determined with a Turner TD-700 fluorometer (Arar and Collins, 1992).

Supplemental temperature data was obtained from a long-term mooring in the Bering Strait (Fig. 1(A), see Woodgate et al., 2005). The temperature sensors were positioned 5–10 m off the bottom at a depth of about 45 m. Temperature records included data at 30- to 60-s intervals. The record started in September 1990 and ended in June 2002, with a gap between September 1996 and July 1997. The temperature records were converted to daily averages and the calendar date was attached to each average before writing the data to a database. The temperature data for each complete year were converted to Kelvin from centigrade units and integrated from March 1 to the end of February of the following year to look for any consistent trends in the temperature regime in the bottom water.

2.3. Statistical treatment

Since sampling and methodology were identical between the 1980s and 2002–2003 collections, direct comparisons can be made between periods. Station locations were selected randomly before the initial study as outlined in Highsmith and Coyle (1992). Samples from Period 1 included material from eight cruises (Table 1). The mean abundance, biomass, and caloric content of the major taxa were computed for each station by period. A one way analysis of variance was used to look for differences in mean values between periods. Consistent trends between periods also were documented using a nonparametric sign test. The mean biomass by length and period was computed for the major taxa to document significant changes in the size distribution of animals between periods.

Supplemental data on ampeliscid wet weight biomass from 1973 to 1974 were also available (Stoker, 1981). Stations were selected to include only those within the study site (Fig. 1(B), red dots). Because ampeliscid distribution in the study area is highly spatially correlated, and the station distribution in the early 1970s was different from that in the later studies, formal statistical tests are not appropriate. We therefore limit comparison with the earlier data set to observations of the trend in mean values.

3. Results

3.1. Length weight relationships

The curve fitting routine generated exponential relationships between amphipod length and wet weight, dry weight, and AFDW. The R^2 values were all above 0.9 (Table 2), indicating that the length measurements can serve as a reliable quantitative predictor of biomass.

3.2. Ampeliscid abundance and biomass

Ampelisca spp. dominated ampeliscid abundance and biomass during both periods (Table 3). Mean biomass of *Ampelisca* spp. was significantly lower during Period 2, as revealed by both analysis of variance and a sign test comparing changes in biomass by station; these results indicate that a significant decline in *Ampelisca* spp. biomass occurred during the intervening years between Periods

1 and 2. A similar trend was observed for the dry weight and AFDW biomass of *Byblis* spp. and *A. birulai* (Table 3), although differences in mean dry-weight biomass of *Byblis* spp. were not significantly different between Periods 1 and 2 ($P < 0.05$). In contrast to biomass, the abundance of *Ampelisca* spp. and *Byblis* spp. showed no significant change between the two periods (Table 3).

The declines in biomass occurred primarily in the southern half of the study region (Fig. 2). Compar-ison of mean AFDW biomass by length category and period indicated that losses in biomass were due primarily to lower contributions by the larger animals (Figs. 3 and 4). Comparison of wet weight biomass from the early 1970s, the 1980s and 2002–2003 indicated a decline in *Ampelisca* biomass between the three periods (Table 4). Declines in biomass of *Byblis* spp. and *A. birulai* between the early 1970s and 1980s were not observed. *Ampelisca* spp. made up at least 80% of the ampeliscid biomass during all periods, *Byblis* made up 11–14% of the biomass, but *A. birulai* showed substantial declines from about 6–9% during the 1970s and 1980s to about 2% of the total biomass during 2002–2003 (Table 4). The cause of the decline in relative biomass of *A. birulai* is not known.

3.3. Oceanographic data

Mean temperatures above and below the pycno-cline were higher by about 1.5–3 °C during the 2002–2003 sampling period relative to the 1980s (Table 5). Although mean salinity below the pycnocline was higher in 2002–2003, the differences were marginal. Water-column stability was on average higher in 2002–2003 relative to the 1980s. Mean integrated chlorophyll was by about 1.5 times higher during the 2002–2003 cruises. A more complete temperature record for the interval be-tween Periods 1 and 2 was obtained from Mooring

Table 2

Regression coefficients for ampeliscid weight data from the Chirikov Basin

Taxa	a	b	R^2
Length (mm) versus dry weight (mg)			
Ampelisca macrocephala	1.62	0.16	0.94
Byblis spp.	1.28	0.17	0.96
Ampelisca birulai	0.38	0.30	0.93
Length (mm) versus ash free dry weight (mg)			
Ampelisca macrocephala	1.21	0.16	0.95
Byblis spp.	0.64	0.20	0.96
Ampelisca birulai	0.23	0.32	0.95
Length (mm) versus wet weight (mg)			
Ampelisca macrocephala	7.14	0.13	0.93
Byblis spp.	4.75	0.17	0.96
Ampelisca birulai	1.01	0.31	0.91

The coefficients correspond to the exponential function weight $= a \exp(b \times \text{length})$.

Table 3

Mean abundance, biomass and caloric content of major ampeliscid species in the Chirikov Basin during the 1980s (Period 1) and in 2002–2003 (Period 2)

Data type	Period 1	Period 2	P value	Sign test
Ampelisca spp.				
Abundance (No. m^{-2})	2144	1154	0.127	0.2630
Dry weight (g m^{-2})	41	22	0.018	0.0008
AF dry weight (g m^{-2})	33	18	0.017	0.0008
Caloric content (kcal m^{-2})	173.6	101.1	0.017	0.0008
Byblis spp.				
Abundance (No. m^{-2})	737	532	0.420	0.052
Dry weight (g m^{-2})	6.6	3.4	0.074	0.015
AF dry weight (g m^{-2})	5.4	2.5	0.035	0.004
Caloric content (kcal m^{-2})	27.3	14.1	0.074	0.015
Ampelisca birulai				
Abundance (No. m^{-2})	648	101	0.0004	0.0007
Dry weight (g m^{-2})	2.48	0.44	0.0005	0.0007
AF dry weight (g m^{-2})	1.80	0.32	0.0006	0.0007
Caloric content (kcal m^{-2})	9.9	1.8	0.0005	0.0007

P value is for an ANOVA comparing mean values between periods. Sign test lists the P value for sign tests between periods.

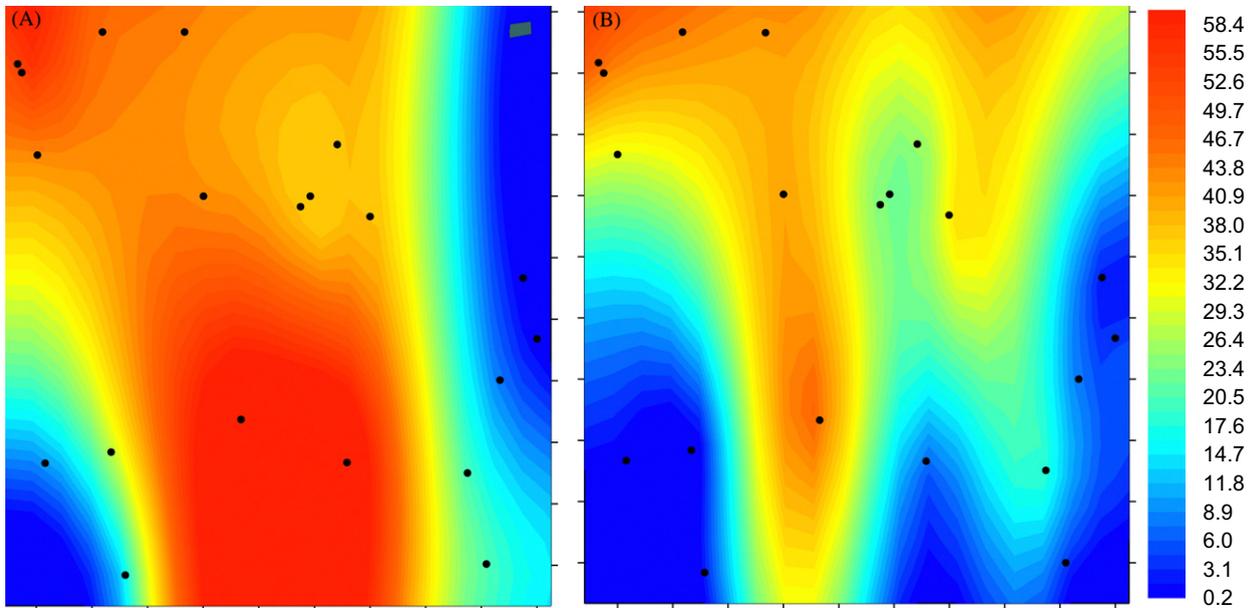**_Ampelisca_ spp.; Ash Free Dry Weight (g m^{-2})**

Fig. 2. Distribution of mean ash-free dry weight (g m^{-2}) of _Ampelisca_ spp. in the Chirikov Basin of the northern Bering Sea. (A) Period 1 (1986–1988). (B) Period 2 (2002–2003); black dots indicate station locations.
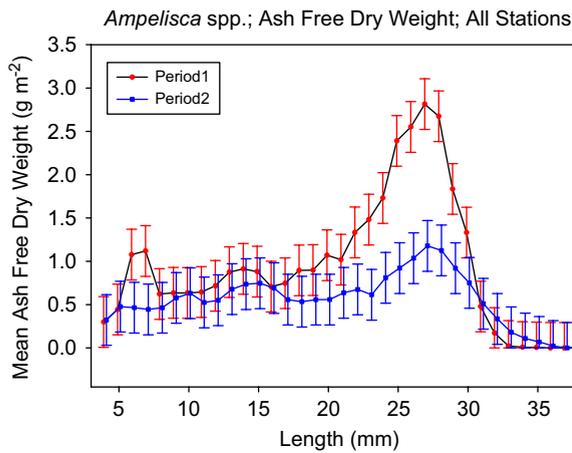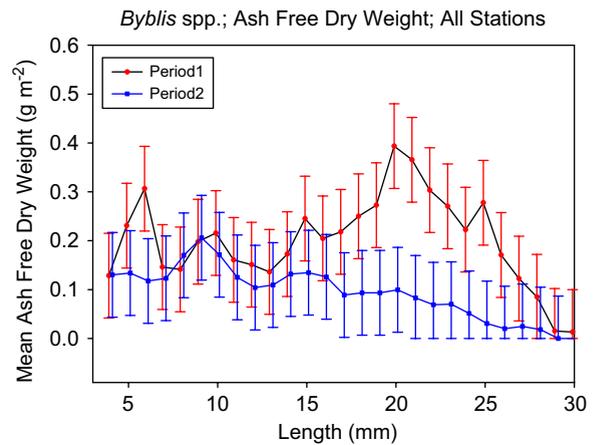

Fig. 3. Length distribution of _Ampelisca_ spp. specimens making up the mean ash-free dry weight for all stations in the Chirikov Basin of the northern Bering Sea in 1986–1988 (Period 1) and 2002–2003 (Period 2). Error bars are 95% confidence intervals.

Fig. 4. Length distribution of _Byblis_ specimens making up the mean ash-free dry weight for all stations in the Chirikov Basin of the northern Bering Sea in 1986–1988 (Period 1) and 2002–2003 (Period 2). Error bars are 95% confidence intervals.

A2 (Fig. 1) in Bering Strait (Fig. 5). The integrated annual temperature–time series was computed for each complete year. Temperatures occasionally exceeded 7 °C in late summer but most values throughout the year were below 0 °C. The integrated temperature values ranged between 9.88 and 9.93 × 10^4 K d (Fig. 5).

4. Discussion

Our results indicate a decline in ampeliscid biomass beginning as early as the early 1970s. In addition, amphipod biomass declines on the order of 40–60% occurred at three stations in the Chirikov Basin throughout the 1990s (Moore

Table 4

Wet weight biomass (g m^{-2}) of major ampeliscid taxa in the Chirikov Basin during the last 30 years: Period 1 = 1973–1974; Period 2 = 1986–1988; Period 3 = 2002–2003

Species	Period 1		Period 2		Period 3	
	Wet weight	Percent	Wet weight	Percent	Wet weight	Percent
Ampelisca spp.	146.7	83	103.2	80	62.4	87
Byblis spp.	20.4	12	18.6	14	7.9	11
Ampelisca birulai	8.9	5	7.5	6	1.3	2

Table 5

Mean physical oceanographic measurements in the Chirikov Basin by period

Data type	Period 1	Period 2	*P* value
UpperMeanTemp	2.64	4.74	0
LowerMeanTemp	1.25	2.70	0
UpperMeanSal	31.948	32.030	0.218
LowerMeanSal	32.202	32.341	0.001
Stability	15.66	19.72	0.056
Chlorophyll	122.2	269.6	0

UpperMeanTemp = mean temperature above the pycnocline (°C); LowerMeanTemp = mean temperature below the pycnocline (°C); UpperMeanSal = mean salinity above the pycnocline; LowerMeanSal = mean salinity below the pycnocline; Stability = mean stability parameter. Chlorophyll = integrated chlorophyll *a* (mg m^{-2}). Period 1 = 1986–1988; Period 2 = 2002–2003.
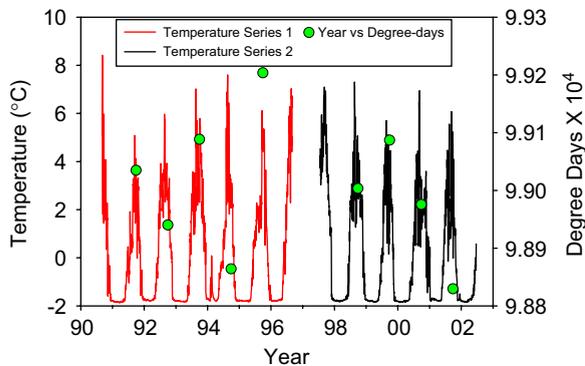

Fig. 5. Temperature time series and annual integrated temperature (green dots) from mooring A2 in Bering Strait (Fig. 1).

et al., 2003). Assuming a wet-weight carbon conversion of 6.8% for ampeliscids (Grebmeier, 1987), the biomass reported for the late 1990s (Moore et al., 2003) would convert to about 88 g wet weight m^{-2}, slightly higher than our Period 3 estimate of 72 g m^{-2} for total ampeliscids in our study site (Table 4). We do not have detailed measurements of the biomass of other taxa within our study site and are therefore unable to assess changes in the total infaunal biomass over this period. However, we examined the appendix tables in Grebmeier (1987) to determine the proportion of ampeliscids within her ampeliscid cluster group in her stations within our study area. Ampeliscids comprised about 55% of the total biomass in the cluster group; other taxa included primarily bivalves. Ampeliscids at stations from the early 1970s (Stoker, 1981) within our study site comprised about 26% of the total wet weight biomass. The remaining taxa included primarily echinoderms (25%), bivalves (30%), gastropods (4%), polychaetes (7%), other amphipods (2%), and decapods (2%). Samples from this and earlier studies were unable to assess the deep-dwelling infaunal bivalves (Grebmeier, 1987; Stoker, 1981). As we do not have biomass estimates of non-ampeliscid fauna from our study site, it is not known if the marked declines in ampeliscid biomass observed between the 1970s and 2003 were accompanied by similar declines in the other taxa. While the reason for the decline in ampeliscid biomass is uncertain, two possible causes are indicated: top-down control by the gray whale populations and climate-related changes in the Chirikov Basin. The following discussion outlines the evidence for both possibilities.

4.1. Top-down control

In earlier studies, amphipod production and biomass in the Chirikov Basin were compared to estimates of energy demand by gray whales foraging in the area (Highsmith and Coyle, 1992). Based on the whale population in the 1980s (Breiwick et al., 1988), the residence time of foraging whales (Thomas and Martin, 1986), and the energy requirements of the whales (Rice and Wolman, 1971; Sumich, 1983; Thomas and Martin, 1986), it was estimated that whales were removing about 8–18% of the annual ampeliscid production. At the

rate that whale populations were increasing in the 1980s, 3.29% $\pm 0.44\%$ standard error (Buckland et al., 1993), Highsmith and Coyle (1992) predicted that gray whale populations would reach about 31,000 animals by 2000. Actual populations peaked in 1997/1998 at about 28,000 animals (Rugh et al., 2005).

While the gray whale population was increasing in the 1990s, ampeliscid biomass was apparently in sharp decline. Between 1986 and 1988 ampeliscid biomass and production had declined by about 20%, from a high of 51 g dry weight $m^{-2} yr^{-1}$ in 1986 to 35.4 g dry weight $m^{-2} yr^{-1}$ in 1988, for an 8-month production cycle (Highsmith and Coyle, 1992). Given the same production biomass ratio of about 0.9 for an 8-month production cycle, production by 2002–2003 had declined to about 25 g m^{-2}, about a 50% decline from the highest value in 1986. However, the above production rate for 2002–2003 is probably an overestimate because amphipod growth rates in these cold environments are approximately linear but biomass accumulation rates are exponential (Highsmith and Coyle, 1991). Most secondary production by populations with the above age-class structure resides in the older larger animals. In *A. macrocephala* for example, roughly 75% of the production occurred in animals larger than 12 mm during the 1980s (Highsmith and Coyle, 1991), because most of the biomass occurred in the larger animals (Fig. 3). Declines in the proportion of the larger animals in the ampeliscid population from the 1980s to 2002–2003 indicate that actual production was probably under 25 g m^{-2} in the late 1990s and the first several years of the twenty-first century.

Although we know of no surveys of whale populations in the Chirikov Basin between the 1980s and 2002, a rough estimate of the number of whales supportable by ampeliscid populations in the region in 2002–2003 can be made from estimates of production and whale energy demands. Since the area of our study site (about 91 km $\times$ 98 km) is about $8.9 \times 10^9 m^2$, and the estimated annual production for 2002–2003 was 105 kcal m^{-2} (assuming an 8 month production season, a measured production to biomass ratio of 0.9, and a measured dry weight–caloric conversion of 4000–4247 cal g^{-1}; Highsmith and Coyle, 1992), the total annual production was roughly 9.4×10^{11} kcal for the study area. The average annual energy demand per gray whale is about 1.6×10^8 kcal (Highsmith and Coyle, 1992). The above estimates indicate that, in

2002–2003, between 5500 and 6000 whales could remove all of the estimated ampeliscid production from the study area in a single season and about 500–1000 whales could remove 10–20% of the annual ampeliscid production. Given the current gray whale population estimate of about 18,000 animals (Rugh et al., 2005), just 3–6% of the total gray whale population feeding in the area for one entire production season would be sufficient to remove 10–20% of the annual ampeliscid production from the study site.

Due to their low temperature habitats, high-latitude amphipods have longer generation times relative to more temperate species (Sainte-Marie, 1991; Poltermann, 2000; Bluhm et al., 2001). Generation times of up to 6 years are indicated by length frequency information on the largest species, *A. macrocephala* (Coyle and Highsmith, 1994). The highest fecundity measure for *A. macrocephala* during the 1980s was 58 eggs (Coyle and Highsmith, 1994). Actual fecundity was undoubtedly lower because the brood pouch of many females was infested with egg-consuming nicothoid copepods. Thus, due to their low reproductive potential, Arctic ampeliscids are not capable of rapid recovery from major population declines. Slow recovery and/or colonization also would be true for other high latitude invertebrates, which are generally characterized by slow growth, high longevity (Brey, 1991; Bluhm et al., 1998; Bluhm and Brey, 2001), and relatively slow colonization (Gutt, 2001).

Finally, ampeliscid juveniles are unlikely to disperse widely from their natal location. Submersible observations by Coyle and Highsmith indicate that individuals outside their burrows are highly susceptible to predation by lysianassid amphipods, which swarm over ampeliscids driven from their burrows by sediment disturbance. The evidence suggests that juvenile survival is highly dependent on their ability to quickly settle into an unoccupied location and excavate a new burrow after leaving the brood pouch. Thus, ampeliscid life history tends to produce dense patches of high biomass rather than widely dispersed populations of low biomass. Ampeliscids are therefore likely to be vulnerable to the filter-feeding gray whales, even if the mean ampeliscid biomass for the Chirikov Basin is low, because remaining populations are likely to be concentrated in dense patches. Note that the highest number of gray whale sightings in July–August 2002 occurred on the northwest edge of the sample grid (Moore et al., 2003), where amphipod biomass in

our study site was highest. Gray whales feed where prey densities are high and their presence can indicate areas of unusually high secondary production (Moore et al., 2003).

In summary, estimates of gray whale populations and energy demand, declining ampeliscid biomass and production, and the clumped distribution of ampeliscid populations are all consistent with top-down control of ampeliscid populations by gray whale predation. Ampeliscids are also consumed by a variety of benthic invertebrates and fishes. In addition to lysianassid amphipods, we have observed crabs feeding on ampeliscids, and myoxocephalid fish from our trawl samples contained ampeliscids in their gut. Because ampeliscid populations sustain intense predation from a variety of sources, their abundance and biomass are also probably influenced by predators other than gray whales. Nevertheless, gray whales are probably the more efficient ampeliscid predator because they are homeotherms, and therefore not subject to the physiological constraints of their poikilotherm competitors in these very cold arctic environments. In addition, gray whales are highly motile and can move on after exhausting a local food stock. They therefore can quickly exploit different invertebrate populations in different locations to maximize their energy intake. Indeed, the 2002 census indicates a decline of 3–17 fold in the number of whales feeding in the Chirikov Basin between the 1980s and 2002 (Moore et al., 2003). Because of their ability to focus on preferred prey populations over large areas, changes in the whale population may result in substantial impacts on the abundance and biomass of the preferred prey.

4.2. Climate influences

Much of the high production in the ampeliscid community during the 1980s was maintained by a high flux of organic carbon to the seabed. Sediment trap measurements in the 1980s indicated that total POC flux in the Chirkov Basin varied from 253 to $654\,mg\,C\,m^{-2}\,d^{-1}$ (Fukuchi et al., 1993). A low C/N ratio of organic material in the sediment traps (4.9–7.4) indicated that fresh organic matter was falling to the benthic community. The mean carbon flux ($501\,mg\,C\,m^{-2}\,d^{-1}$) was similar to the estimated organic carbon utilization at the seafloor ($464\,mg\,C\,m^{-2}\,d^{-1}$; Grebmeier and McRoy, 1989), suggesting a tight coupling between the carbon flux to the sea floor and amphipod production. Such

tight pelagic benthic coupling is typical of several regions in the northern Bering and southern Chukchi seas (Grebmeier, 1993; Grebmeier and Cooper, 1995; Grebmeier and Dunton, 2000).

The carbon flux to the Chirikov Basin ampeliscid community was driven by high primary production, which was estimated at $250–300\,g\,C\,m^{-2}$ for the summer months (Walsh et al., 1989) or about $2\,g\,C\,m^{-2}\,d^{-1}$. Given an amphipod production of about $30–40\,g$ dry $wt\,m^{-2}\,yr^{-1}$ in the 1980s (Highsmith and Coyle, 1990), or about $70\,mg\,C\,m^{-2}\,d^{-1}$, assuming a 6 month production season and a growth efficiency of about 15%, the amphipods were apparently consuming nearly all of the available carbon flux over the densest regions of the ampeliscid bed. The above evidence indicates that any change in the ecosystem resulting in consistent declines in primary production would quickly result in declines in ampeliscid production. In addition, because the amphipods are sedentary tube dwellers, the larger animals will require a greater carbon flux to maintain their larger tissue mass (Coyle and Highsmith, 1994). Loss of the larger animals is therefore consistent with declines in organic flux to the sea floor which would result from lower overall primary production. Reduced transport through the Bering Strait might result in lower transport of nutrients northward onto the Bering shelf and lower annual production over the amphipod bed (Grebmeier and Dunton, 2000). In addition, based on declines in $\delta^{13}C$ values between 1947 and 1997, Schell (2000) postulated that declines in primary production of 30–40% may have occurred between 1966 and 1997, although Schell's interpretation of the stable isotope data has been challenged (McRoy et al., 2002, 2004). Thus, the observed declines in amphipod biomass and production are consistent with declines in primary production related to a climate scenario.

Nevertheless, an equally compelling argument can be made that global warming will produce elevated primary production in the Chirikov Basin, thus enhancing amphipod production. Nutrients are carried into the basin by the Anadyr Current, which is driven by sea-level differences between the Arctic Ocean and Bering Sea (Coachman et al., 1975). Mixing of Anadyr and Bering Shelf water over the amphipod bed results in a consistent nutrient supply and high primary production throughout summer (Springer and McRoy, 1993). An earlier retreat of sea ice in spring associated with climate warming may result in an earlier phytoplankton bloom and

prolonged production seasons due to the removal of the ice barrier to light penetration into the water column during spring. A longer production season might result in a greater integrated flux of carbon to the amphipod community, thus greater amphipod production. As long-term current meter data in the Bering Strait show no consistent trend toward greater or lesser northward transport (Woodgate et al., 2005), there is no evidence of reduced nutrient transport northward into the Chirikov Basin and hence lower primary production between 1991 and 2002.

The oceanographic data reported in this study indicate higher mean chlorophyll during the 2002–2003 sampling period relative to the 1980s, which contradicts the hypothesis that lower primary production is impacting ampeliscid production. The higher chlorophyll may have been due to higher water-column stability promoting overall higher production during the 2002–2003 sampling period. The above observations, however, are insufficient to document changes in annual carbon flux to the benthos. Production during summer is undoubtedly episodic, so our measurements are highly influenced by the time of sampling during any particular season. Documentation of actual changes in annual production over the ampeliscid bed would require seasonally integrated measurements over the whole production season for each period under comparison, and such measurements are not available. While our oceanographic data do not rule out a climate–primary production scenario to explain the lower amphipod production and biomass observed during Period 2 relative to Period 1, they are insufficient to reject or verify the hypothesis.

The thermal regime experienced by the amphipods is probably better characterized by the continuous temperature record in Bering Strait than by measurements taken only during our cruises. The water masses over our study area in the central Chirikov Basin consist of a mixture of Bering Shelf and AW (Coachman et al., 1975; Coachman, 1993; Springer and McRoy, 1993). The Bering Shelf water mass moves northward through the Bering Strait, primarily on the east side of the strait (Coachman et al., 1975). The mean flow is northward at 0.8 Sv, driven by a 0.5 m difference in sea-level height between the Bering Sea and Arctic Ocean (Coachman, 1993). Given the location of the mooring and the prevailing currents, temperatures measured at the mooring are the best data available for assessing long-term temperatures in the benthic amphipod

habitat upstream in the Chirikov Basin. While spikes of over $7\,^{\circ}$C were occasionally observed, a consistent warming trend was not obvious and temperatures were subzero for most of the year. The annual integrated temperatures (Fig. 5) characterize the thermal regime in the bottom water for any given year. All integrated values were between 9.88 and 9.93×10^4 degree-days. This range of integrated temperature falls between 9.87×10^4 degree-days (the value if temperatures were constant at $-1.8\,^{\circ}$C for 1 year) and 9.94×10^4 degree-days (the value if temperatures were constant at $0\,^{\circ}$C for 1 year). This temperature record provides the strongest evidence that the thermal habitat in the amphipod bed was not changing in any consistent manner between the late 1980s and 2002–2003.

Nevertheless, gradual increases in atmospheric temperature, decreases in the area influenced by permafrost on the land masses near the Bering Sea coast, the retreat of Alaskan glaciers, and declines in the thickness and extent of Bering Sea and Arctic Ocean sea-ice cover (Chapman and Walsh, 1993; Osterkamp, 1994; Wadhams, 1995, 2000) all indicate a consistent warming trend in the Alaskan arctic. For example, average April air temperatures over Alaska, the southern Beaufort Sea, and the Canadian archipelago for 1989–1998 were $3\,^{\circ}$C warmer than those for 1980–1988 (Stabeno and Overland, 2001). Although conditions were colder in winter of 1998–1999, warmer conditions with earlier ice retreat were again observed in 2001–2002 (Clement et al., 2004). Data on spring ice conditions indicate that early ice retreat may not lead to higher production or an earlier onset of production (Clement et al., 2004). However, warming conditions may cause physiological impacts on the amphipod species comprising the ampeliscid community, or impact the ampeliscids by allowing the intrusion of competitors and predators that were previously excluded from the region by the low temperatures. Warming conditions on the southeastern Bering Sea shelf, for example, were correlated with increases in fin-fish consumers of infaunal invertebrates (Livingston et al., 1999).

4.3. Conclusions

The declines we observed in amphipod biomass and production in the northern Bering Sea were coincident with increasing gray whale populations and were probably the result of top-down control

by gray whales on the amphipod populations. Long-term mooring data in the Bering Strait revealed no consistent trend in temperature or northward flow suggestive of climate-related changes in the nutrient supply or water mass properties. While climate change may affect primary production, leading to higher or lower carbon fluxes to the sea bed and thus changing production in the benthic amphipod community, there is no compelling evidence that such changes actually occurred between the late 1980s and 2002–2003 in the Chirikov Basin amphipod community. In addition, the available data indicate very low sedimentation rates on the northern Bering Sea shelf (on the order of 0.01–$0.03\,\mathrm{mm\,yr^{-1}}$; Grebmeier, 1993). In the absence of any dramatic geophysical events such as strong earthquakes or turbidity flows, there is no reason to suspect that a change in sediment grain size affected the amphipod beds between the late 1980s and 2002–2003. Modeling studies indicate that recovery of the ampeliscid populations may require decades because of their slow growth rates and long generation times (Coyle and Highsmith, 1994). Although the data available to date do not indicate a strong climate impact on the ampeliscid community, long-term warming trends could slow or stall the recovery of ampeliscid populations by altering the benthic community structure and/or particulate carbon flux to the ampeliscid community.

Acknowledgments

References

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

Berzin, A.A., 1984. Soviet studies of the distribution and numbers of the gray whale in the Bering and Chukchi seas, from 1968 to 1982. In: Jones, M.L., Swartz, S.L., Leatherwood, S. (Eds.), The Gray Whale *Eschritchius robustus*. Academic Press, New York, pp. 409–450.

Bluhm, B.A., Brey, T., 2001. Age determination of the Antarctic shrimp *Notocrangon antarcticus*, using the autofluorescent pigment lipofuscin. Marine Biology 138, 247–257.

Bluhm, B.A., Piepenburg, D., von Juterzenka, K., 1998. Distribution, standing stock, growth, mortality and production of *Strongylocentrotus pallidus* (Echinodermata: Echinoidea) in the northern Barents Sea. Polar Biology 20, 325–334.

Bluhm, B.A., Brey, T., Klages, M., 2001. The autofluorescent age pigment lipofuscin: key to age, growth and productivity of the Antarctic amphipod *Waldeckia obesa* (Chevreux, 1905). Journal of Experimental Marine Biology and Ecology 258, 215–235.

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

Breiwick, J.M., Rugh, D.J., Withrow, D.E., Dahlheim, M.E., Buckland, S.T., 1988. Preliminary population estimate of gray whales during the 1987/1988 southward migration. International Whaling Commission Scientific Committee, San Diego, Doc. SC/40/PS12.

Brey, T., 1991. Population dynamics of *Sterechinus antarcticus* (Echinodermata: Echinoidea) on the Weddell Sea shelf and slope, Antarctica. Antarctic Science 3, 251–256.

Buckland, S.T., Breiwick, J.M., Cattahach, K.L., Laake, J.L., 1993. Estimated population size of the California gray whale. Marine Mammal Science 9 (3), 235–249.

Chapman, W.L., Walsh, J.E., 1993. Recent variation of sea ice and air temperatures in high latitudes. Bulletin of the American Meteorological Society 74, 33–47.

Clement, J.L., Cooper, L.W., Grebmeier, J.M., 2004. Late winter water column and sea ice conditions in the northern Bering Sea. Journal of Geophysical Research (C Oceans) 109 (C3), C03022.

Coachman, L.K., 1993. On the flow fields in the Chirikov Basin. Continental Shelf Research 13 (5/6), 481–508.

Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: The Regional Oceanography. University of Washington Press, Seattle, 172pp.

Coyle, K.O., Highsmith, R.C., 1989. Arctic ampeliscid amphipods: three new species. Journal of Crustacean Biology 9, 157–175.

Coyle, K.O., Highsmith, R.C., 1994. Benthic amphipod community in the northern Bering Sea: analysis of potential structuring mechanisms. Marine Ecology Progress Series 107, 233–244.

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.

Fukuchi, M., Sasaki, H., Hattori, H., Matsuda, O., Tanimura, A., Handa, N., McRoy, C.P., 1993. Temporal variability of particulate flux in the northern Bering Sea. Continental Shelf Research 13, 693–704.

Grebmeier, J.M., 1987. The ecology of benthic carbon cycling in the northern Bering and Chukchi seas. Ph.D. Dissertation, University of Alaska, 189pp.

Grebmeier, J.M., 1993. Studies of pelagic–benthic coupling extended onto the Soviet continental shelf in the northern Bering and Chukchi seas. Continental Shelf Research 13, 653–668.

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., Cooper, L.W., 1995. Influence of the St. Lawrence island polynya on the Bering Sea benthos. Journal of Geophysical Research 100, 4439–4460.

Grebmeier, J.M., Dunton, K.H., 2000. Benthic processes in the northern Bering/Chukchi seas: status and global change. In: Huntington, H.P. (Ed.), Impacts of Changes in the Sea Ice and Other Environmental Parameters in the Arctic. Report of the Marine Mammal Commission Workshop, Girdwood, Alaska, 15–17 February 2000. Marine Mammal Commission, Bethesda, MD, pp. 61–71.

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.

Gutt, J., 2001. On the direct impact of ice on marine benthic communities, a review. Polar Biology 24, 553–564.

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., 1991. Amphipod life histories: community structure, impact of temperature on decoupled growth and maturation rates, productivity, and P:B ratios. American Zoologist 31, 861–873.

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

Hunt Jr., G.L., Stabeno, P.J., 2002. Climate change and the control of energy flow in the southeastern Bering Sea. Progress in Oceanography 55, 5–22.

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/protocols.html⟩, Hawaii.

Kim, S.L., Oliver, J.S., 1989. Swarming benthic crustaceans in the Bering and Chukchi seas and their relation to geographic patterns in gray whale feeding. Canadian Journal of Zoology 67, 1531–1542.

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

Livingston, P.A., Low, L.L., Marasco, R.J., 1999. Eastern Bering sea trends. In: Sherman, K., Tang, Q. (Eds.), Large Marine Ecosystems of the Pacific Rim: Assessment, Sustainability and Management. Blackwell Science Inc., Malden, MA, pp. 140–162.

McRoy, C.P., Springer, A., Nakanishi, S., Mizobata, K., Saitoh, S., 2002. Climate control of new production on the shelf of the southeastern Bering Sea. EOS Transactions of the American Geophysical Union, OS32Q-08 (abstract).

McRoy, C. P., Gradinger, R., Springer, A., Bluhm, B., Iverson, S., Budge, S., 2004. Stable carbon isotopes reveal food web shift. EOS Transactions of the American Geophysical Union, 85(17), Joint Assembly Suppl., Abstract B34A-05.

Moore, S.E., 2000. Variability of cetacean distribution and habitat selection in the Alaskan Arctic, autumn 1982–1991. Arctic 55, 448–460.

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.

Napp, J.M., Hunt Jr., G.L., 2001. Anomalous conditions in the south-eastern Bering Sea, 1997: linkages among climate, weather, ocean, and biology. Fisheries Oceanography 10, 61–68.

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, New York, pp. 423–450.

Osterkamp, T.E., 1994. Evidence for warming and thawing of discontinuous permafrost in Alaska. EOS, Transactions of the American Geophysical Union 75, 85.

Perryman, W.L., Donahue, M.A., Reilly, S.B., Perkins, P.C., 1998. Annual calf production for the California Stock of gray whales 1994–1997. Working paper SC/49/AS13, Report of the International Whaling Commission, 26pp.

Poltermann, M., 2000. Growth, production and productivity of the Arctic sympagic amphipod *Gammarus wilkitzkii*. Marine Ecology Progress Series 193, 109–116.

Rice, D.W., Wolman, A.A., 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). American Society of Mammalogists, Special Publication 3, 1–142.

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, 96.

Rugh, D.J., Hobbs, R.C., Lerczak, J.A., Breiwick, J.M., 2005. Estimates of abundance of the eastern north Pacific stock of gray whales 1997 to 2002. Journal of Cetacean Research and Management 7 (1), 1–12.

Sainte-Marie, B., 1991. A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of the life history traits with latitude, depth, salinity and superfamily. Hydrobiologia 223, 189–227.

Schell, D.M., 2000. Declining carrying capacity in the Bering Sea: isotopic evidence from whale baleen. Limnology and Oceanography 45, 459–462.

Schumacher, J.D., Bond, N.A., Brodeur, R.D., Livingston, P.A., Napp, J.M., Stabeno, P.J., 2003. Climate change in the southeastern Bering Sea and some consequences for biota. In: Hempel, G., Sherman, K. (Eds.), Large Marine Ecosystems of the World. Elsevier, Amsterdam, pp. 17–40.

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.

Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern Bering Sea—III. Patterns of Primary Production. Continental Shelf Research 13 (5/6), 575–599.

Stabeno, P.J., Overland, J.E., 2001. Bering Sea shifts toward an earlier spring transition. EOS Transactions of the American Geophysical Union 82 (29), 317–321.

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

Sumich, J.L., 1983. Swimming velocity, breathing patterns, and estimated costs of locomotion in the migrating gray whale, *Eschrichtius robustus*. Canadian Journal of Zoology 61, 647–652.

Thomas, D.H., Martin, L.R., 1986. Feeding ecology of gray whales (*Eschrichtius robustus*) in the Chirikov Basin, summer 1982. US Department of Commerce, NOAA, OCSEAP Final Report 43(1986), pp. 377–460.

Wadhams, P., 1995. Arctic sea ice extent and thickness. Philosophical Transactions of the Royal Society, London, A 352, 301–319.

Wadhams, P., 2000. Further evidence of ice thinning in the Arctic Ocean. Geophysical Research Letters 27 (24), 3973–3975.

Walsh, J.J., McRoy, C.P., Coachman, K.L., 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., Deleersnuder, E., Henriksen, K., Lund, B.A., Anderson, P., Muller-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.

Woodgate, R.A., Aagaard, K., Weingartner, T., 2005. Monthly temperature, salinity and transport variability of the Bering strait through flow. Geophysical Research Letters 32 (4), L04601.