Benthic amphipod community in the northern Bering Sea: analysis of potential structuring mechanisms

K. O. Coyle, R. C. Highsmith

Institute of Marine Science, School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99775-1080, USA

ABSTRACT: The age class structure of ampeliscid populations is determined largely by competition for space. Population densities of the various ampeliscid species are regulated by a balance between required carbon flux rates to the seafloor, predation rates, competition for space and reproductive potential. The largest taxa require high organic matter input and low predation rates to mature and reproduce. Reductions in organic matter flux favor smaller taxa. Low predation rates favor larger taxa, which can out-compete the smaller taxa for available space. High predation rates favor smaller taxa, which have a higher reproductive rate and are therefore more effective colonizers. The above factors can explain the relative concentrations of *Ampelisca macrocephala*, *Ampelisca birulai* and *Byblis* spp., the most abundant ampeliscids in the northern Bering Sea. Elevated predation losses to gray whales will depress the density of the large-sized *A. macrocephala* populations and increase the density of the smallest species, *A. birulai*. Global warming should elevate ampeliscid food requirements, and may also lead to elevated predation rates, both selecting for smaller species.

KEY WORDS: Ampeliscids · Competition · Predation · Bering Sea

INTRODUCTION

The northern Bering Sea benthic amphipod community, covering an area of about $40\,000$ km^2 in the Chirikov Basin, is one of the most productive benthic communities on record (Highsmith & Coyle 1990). The community is composed primarily of tube-building amphipods of the family Ampeliscidae (Stoker 1981, Grebmeier et al. 1989, Highsmith & Coyle 1991, 1992) and is the primary food source of the California gray whale *Eschrichtius robustus* (Blokhin & Vladimirov 1981, Nerini 1984). One of the largest ampeliscids in the Chirikov Basin is *Ampelisca macrocephala*, which reaches lengths of over 30 mm and is a dominant component of the benthic community, accounting for about 70% of amphipod biomass and production in the ampeliscid bed (Highsmith & Coyle 1992). The high abundance and large size of *A. macrocephala* make it a preferred prey for gray whales. Thus, the gray

whale population is heavily dependent upon ecological conditions favoring high densities of large benthic amphipods.

The ampeliscid community in the Chirikov Basin is composed of 8 species, varying in adult size from about 10 mm to over 30 mm (Coyle & Highsmith 1989). Therefore, the large *Ampelisca macrocephala* species is not necessarily the only amphipod grazer which could fill the niche it currently occupies. A smaller species could presumably dominate, given the proper environmental conditions. Factors affecting amphipod community structure include organic matter flux to the bottom, fecundities, growth rates, inter- and intraspecific competition and predation. The relative influence of each of the above factors on Arctic ampeliscid community structure was evaluated using conventional modeling techniques.

The biology of ampeliscids makes them particularly easy to model. They are essentially sedentary infaunal

organisms. Thus, their population structure can be easily assessed and simulated without the complication of massive emigration or immigration. Ampeliscids are brooders with crawl-away juveniles. Their fecundity and recruitment are, therefore, comparatively easy to measure and simulate over time, in contrast to taxa with planktonic dispersal phases in their life histories. The model presented here is not designed to precisely predict ampeliscid populations, but rather to demonstrate how food supply, reproductive rates, space competition and predation can interact to permit 3 ecologically very similar species to coexist and thrive in the Chirikov Basin ampeliscid bed.

METHODS

The study site is located in the Chirikov Basin, northern Bering Sea, between 64° and 65° N and 168° and 170° W. Environmental data on the Chirikov Basin are available in the literature (Coachman et al. 1975, Grebmeier et al. 1988, 1989, Highsmith & Coyle 1990, Coachman & Hansell 1993).

Sampling was conducted from 1986 through 1988. Four cruises were made to the study site each year during the ice-free period, from late May through early November. Twenty station locations were selected at random and occupied once during each cruise, weather and ice conditions permitting. Five replicate samples were collected at each site with a 0.1 m² 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 analyses. Supplemental ampeliscid samples were collected at 3 stations in the bed, the amphipods were sorted to species, measured to the nearest mm (tip of head to tip of telson), dried at 60°C for 24 h, frozen and returned to the laboratory. In the laboratory the amphipods were thawed, redried at 60°C for 12 h, and dry weight was determined with a Cahn electrobalance. The amphipods were placed in foil, combusted in a muffle furnace at 600°C for 12 h and reweighed following cooling to determine ash weights.

Respiration rate measurements were made on ampeliscids at sea to determine their carbon demand. Experimental amphipods were collected as outlined above, transferred to sea water taken from just above the bottom, and placed in an incubator adjusted to ambient bottom-water temperatures (0 to 2°C). Bottom sediments from the grab samples were rinsed through the 1 mm screen, allowed to settle and used in the incubation chambers. The incubation chambers consisted of 2.6 cm diameter plastic tubes 30 to 50 cm long. The chambers were pushed into the sediment to between 11 and 19 cm depth and pulled out, thus extract-

ing a core. The remainder of the tube volume was filled with bottom water, the chamber was capped at both ends with rubber stoppers and placed in the incubator for several hours until the silt settled from the water. Water volume in the chambers (250 to 450 ml) was adjusted relative to the size of the experimental amphipods such that oxygen concentration decreased by about 10% during the incubations.

After settling, 1 to 3 ampeliscids were added to each chamber, except for 2 chambers which served as controls. The chambers were placed in the incubator for an additional 2 to 4 h, until the amphipods had burrowed into the sand and settled down. The water was then pipetted from each tube and bottom water was added. Oxygen samples were collected from the bottom water to serve as initial values. The tubes were corked shut such that no bubbles remained in the chambers, and they were placed in the incubator for an additional 9 to 12 h. Two samples for oxygen determination were then drawn from each chamber, and the amphipods were removed from the chambers, dried and weighed as described above. Oxygen determinations were done using a standard micro-Winkler technique (mean precision of n determinations = $\pm 0.003/n^{0.5}$ mg-at. l^{-1}; Strickland & Parsons 1972).

Ampeliscids in the formalin preserved samples were sorted to species, measured as described above and enumerated. Eggs were washed from the brood pouch of females and counted. An INGRES data base system was used for analyses and modeling was done using fortran with IMSL subroutines and MATLAB computational and imaging software. The amphipod model in MATLAB programming language is available from the authors on request.

The *Byblis* species in the northern Bering Sea are very similar and cannot be reliably distinguished when under about 8 mm length (Coyle & Highsmith 1989). Therefore all *Byblis* under 8 mm were pooled under *Byblis* spp., which included *B. gaimardi*, *B. breviramus*, *B. pearcyi*, *B. frigidis* and *B. robustus*, comprising approximately 58%, 6%, 17%, 19% and <1% of the identifiable individuals respectively. Since juveniles could not be identified, these taxa were pooled for simulation and data presentation. Approximately 1.4% of the *Byblis* spp. were above 22 mm length. These specimens were primarily *B. frigidis*. Since *B. frigidis* could not be modeled separately, *Byblis* over 22 mm length were excluded from the model. *Ampelisca macrocephala* and *Ampelisca erythrorhabdota* cannot be distinguished when under about 8 mm length. Therefore, all *A. macrocephala* and *A. erythrorhabdota* under 8 mm length were pooled as *A. macrocephala*. Identifiable *A. erythrorhabdota* comprised about 16% of the 2 taxa pooled. The *A. macrocephala* age class 1 in the data tables includes an unknown number of *A. erythrorhabdota*.

RESULTS

The ash free dry weight (AFDW) of *Ampelisca macrocephala*, *Ampelisca birulai* and *Byblis* spp. was regressed on body lengths, yielding the regression coefficients in Table 1A. The regression lines for *A. macrocephala* and *Byblis* spp. were essentially identical; the line for *A. birulai* was slightly above that of *A. macrocephala* and *Byblis* spp. (Fig. 1A). The above relationships have certain implications, when viewed in the context of the feeding biology and behavior of the animals.

Ampeliscids are tube-dwelling suspension feeders. They obtain their food by positioning themselves ventral side up at the mouth of the tube and creating a posterior to anterior feeding current. The amphipods feed primarily on diatoms in the water column but can also resuspend organic matter from the sediment surface with their second antennae (Highsmith & Coyle 1991). Because of their sedentary, suspension-feeding life style, the ampeliscids depend upon environmental conditions to bring food to them, rather than foraging in the environment. Essentially, the amount of food available to the animal at any given time is the flux of organic matter to the bottom within reach of the second antennae. Linear regression analysis indicates that the length of the second antennae relative to body length (A/B ratio; Table 1B) is fairly constant for a given taxon, with the exception of adult terminal-molt males which do not feed. Therefore, as an amphipod grows in length (L), its food requirements will increase by a factor of about $L^{2.6}$ to $L^{2.9}$, depending on the taxon, but the effective foraging area only increases by $L^{2.0}$. With growth, the organic carbon flux rate to the bottom required by an amphipod increases by some approximately constant factor with respect to length.

Organic flux requirements were estimated from respiration rate measurements ($n = 27$) on *Ampelisca macrocephala*. There was no apparent relationship between the AFDW of the experimental animals and respiration rate (Fig. 1B). The mean oxygen consumption rate, $0.20\ \mu l\ mg^{-1}$ AFDW h^{-1} (SD = 0.10), was converted to the annual carbon requirement ($0.94\ g\ C\ g^{-1}$ AFDW yr^{-1}) and multiplied by the AFDW per individual in each age class, computed from the regression coefficients for body length and AFDW (Table 1A) and

Table 1. *Ampelisca macrocephala*, *Byblis* spp., *A. birulai*. (A) Regression coefficients relating total body length (L) to ash free dry weight (AFDW), where AFDW $= aL^b$ (B) Linear regression coefficients relating length of the second antenna to total body length (A/B ratio). (C) Carbon flux to the benthos required for ampeliscids in each size category to grow to the next, assuming the area occupied is equivalent to the area of a circle with a radius of 0.52 (*A. birulai*), 0.50 (*Byblis* spp.) and 0.35 (*A. macrocephala*) body lengths

(A) AFDW vs length

	A. macrocephala	Byblis spp.	A. birulai
r^2	0.99	0.98	0.98
a	0.0047	0.0058	0.0146
b	2.95	2.89	2.62

(B) Second antenna length vs body length

	A. macrocephala	Byblis spp.	A. birulai
r^2	0.96	0.93	0.95
Slope (A/B)	0.35	0.50	0.52
Intercept	0.80	1.66	−0.46

(C) Carbon flux

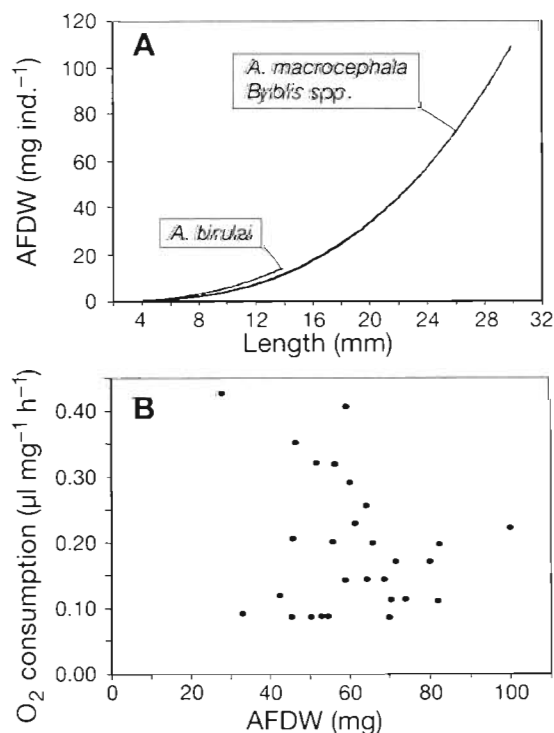| Body length (mm)	Flux (g m^{-2} yr^{-1})		
	A. birulai	Byblis spp.	A. macrocephala
4–8	49	34	64
8–12	67	54	104
12–16	83	73	144
16–20	–	92	182
20–24	–	110	221
24–28	–	–	260
28–32	–	–	298

Fig. 1. (A) Regression of length vs ash free dry weight of *Ampelisca macrocephala*, *A. birulai* and *Byblis* spp. from the Chirikov Basin. Regression coefficients in Table 1A. (B) Oxygen consumption rate by *A. macrocephala* of different ash free dry weights

the median length of each age class. The average effective foraging area of an individual in a given age class was estimated by:

$$A = \pi (R L_m)^2$$

where A is the area, R is the A/B ratio for a given taxon (Table 1B) and L_m is the median body length of the age class. The annual carbon requirement for each age class was divided by the foraging area, yielding estimates of the annual carbon flux (converted to g m^{-2}) required for ampeliscids in each size category to grow to the next size category in 1 yr (Table 1C). Because the A/B ratio ranged from 0.52 to 0.35 depending upon the species (Table 1B), fluxes for each of the 3 taxa are given. *A. birulai* requires the lowest carbon flux because it does not exceed 14 mm length and has the highest A/B ratio. *A. macrocephala* requires the highest carbon flux due to its greater size (reaching 32 mm length) and lower A/B ratio. Carbon flux requirements for *Byblis gaimardi*, which matures at about 18 to 20 mm, are intermediate between the above 2 extremes. Although there is a rather broad carbon flux range over which one or another of the ampeliscid species inhabiting the Chirikov Basin could persist, decreases in organic input should impact the larger species before the smaller ones.

Another major consequence of large size in ampeliscids is an increase in the generation time. The effect of generation time on reproductive potential can be illustrated using the instantaneous rate of natural increase:

$$\sum l_x m_x e^{-rx} = 1$$

where l_x is the proportion of individuals that survive to reproductive age x, m_x is the number of female offspring produced by an individual female while her age is between x and $x+1$, r is the instantaneous rate of natural increase and x is the age of the reproducing female (Pielou 1974). Since, for comparison, the survival of all taxa is assumed to be 1, and the majority of individuals breed once during their life, the above equation reduces to:

$$m_x e^{-rx} = 1$$

Reproductive potential was computed by substituting $f/2$ for m_x, where f is the number of eggs per female (assuming an equal sex ratio) and solving the above equation for r:

$$r = -\ln(2/f)/x$$

where r is redefined as the reproductive potential, the instantaneous rate of increase assuming $l_x = 1$ for

all taxa. The equation for population growth is:

$$N = N_0 e^{rt}$$

where N is the population at time t and N_0 is the population at time $t = 0$ (Pielou 1974). The above ampeliscid species mature somewhere between 2 and 5 yr of age, depending on their size. The fecundity estimates of ampeliscids vary considerably, since eggs are easily lost from the brood pouch during collection. The highest number of eggs recorded in *Ampelisca macrocephala* was 58, but fecundity across the population may have been lower, because about 4 % of the *A. macrocephala* and *A. erythrorhabdota* adult females were infested with nicothoid (Choniostomatidae) copepods, which consume crustacean eggs (Heron & Damker 1986). *A. erythrorhabdota* had about 18 to 20 eggs female^{-1}, when brood pouches appeared to be full. Model prediction (see below) indicated that *A. birulai*, *A. macrocephala* and *Byblis* spp. can coexist with fecundities of approximately 17–18, 37 and 35 eggs female^{-1} respectively. The brood time, a minimum of 5 mo (Highsmith & Coyle 1991), was added to the age at maturity, yielding generation times of approximately 3, 4, 5 and 6 yr for *A. birulai*, *A. erythrorhabdota*, *Byblis* spp. and *A. macrocephala* respectively.

The above data were used to compute a reproductive potential for the above taxa, and the ratio of *Ampelisca macrocephala* abundance to that of the other taxa was plotted against time (Fig. 2). For ease of comparison, *A. macrocephala* abundance was set at twice that of the other species, although *A. macrocephala*, *A. birulai* and *Byblis* spp. actually made up
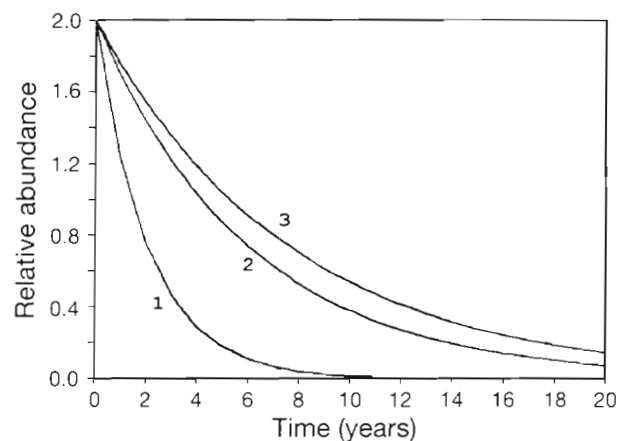

Fig. 2. Changes in the relative abundance of *Ampelisca macrocephala* with respect to *A. birulai* (1), *A. erythrorhabdota* (2) and *Byblis gaimardi* (3), assuming *A. macrocephala* density is twice that of the other taxa at time 0 and equal mortality for all taxa

57, 19 and 24 % of the population respectively (Highsmith & Coyle 1992). All of the resulting curves have negative exponential slopes (Fig. 2). Thus, despite the greater fecundity of the larger species, with equal mortalities the smaller species would quickly supplant the larger ones because of shorter generation times. Therefore, the larger ampeliscids, which are actually dominant, must not only live in a highly productive environment, they must also have a lower mortality rate than smaller ampeliscids.

One advantage of larger size is the ability to defend limiting resources against smaller competitors. Competitive interactions influencing cohort survival and population structure have been demonstrated in the tube-dwelling amphipods *Corophium volutator* and *C. arenarium*, where individuals have been observed to force smaller animals from their tubes (Jensen & Kristensen 1990). Elevated juvenile mortality of *Monoporeia affinis* in the presence of adults may be due to increased competition for food or predation by adults on juveniles (Hill 1992), and the lack of overlap between similar ampeliscid species in Long Island Sound (USA) is thought to be caused by competition for a limiting resource (Sanders 1956).

A resource which may be limiting in the Chirikov Basin is space. The amount of space available to these amphipods per square meter can be estimated from the size-frequency distribution of the populations of ampeliscid species at each station. Assuming that the maximum possible territory occupied by an individual of each taxon is a circle equal in radius to the second antenna length (Table 1B), the average surface area occupied by ampeliscids at 6 stations where ampeliscids were most abundant, during 6 cruises over a 3 yr period, was estimated (Table 2). The results indicate that intense competition for space was probably occurring at Stns 5 and 6 during cruise HX082 and at Stn 5 during HX091, where nearly all the available space was occupied. Competition for space was probably much lower at other stations, where as little as 38 % of the available space was occupied. If space competition is defined as the probability of a larger individual displacing a smaller individual, then the larger taxa will have the greatest competitive advantage at locations where the greatest proportion of the space is occupied. As the proportion of occupied space declines, the probability that larger individuals will displace smaller individuals drops, decreasing the competitive advantage of larger size. Displaced individuals are readily attacked by predatory lysianassid amphipods, *Chionoecetes opilio*, and other predators (observations from a submersible; Klaus et al. 1990). Thus, the proportion of available space may be a measure of intra- and interspecific size-related mortality rates.

Table 2. Mean area (m²) required by ampeliscids per m² of surface area at 6 stations during 6 cruises, assuming each animal occupies an area equivalent to that of a circle having a radius of 1 antenna length. Standard deviation in parentheses. A mean of 1 indicates all space is occupied. Values greater than 1 indicate crowding and reduced feeding area per amphipod

Stn	Cruise					
	HX082	HX091	HX099	HX107	HX113	HX119
3	0.64	0.52	0.46	0.51	0.58	0.53
	(0.10)	(0.14)	(0.06)	(0.14)	(0.11)	(0.07)
4	0.49	0.51	0.54	0.43	0.65	0.82
	(0.13)	(0.14)	(0.11)	(0.05)	(0.09)	(0.17)
5	1.02	1.02	0.73	0.57	0.61	0.38
	(0.29)	(0.13)	(0.13)	(0.18)	(0.11)	(0.12)
6	1.00	0.66	0.84	0.67	0.79	0.63
	(0.15)	(0.15)	(0.05)	(0.11)	(0.13)	(0.11)
9	0.50	0.59	0.37	0.37	0.47	0.72
	(0.10)	(0.13)	(0.09)	(0.06)	(0.10)	(0.07)
10	0.73	0.55	0.54	0.40	0.68	0.54
	(0.08)	(0.08)	(0.08)	(0.09)	(0.04)	(0.16)

Assuming the major source of size-related mortality (loss from the population) is displacement of smaller individuals by larger ones, a model was constructed to simulate population densities of *Ampelisca macrocephala* for each age class. The size-related mortality experienced by individuals of a given age class was simulated by computing the average space occupied by larger individuals (from older age classes) and by other individuals of the same age class. The probability that an individual will find suitable space was assumed to be equal to the proportion of the area remaining; the radius used to compute area was equal to the length of the individual multiplied by a factor (labeled proximity coefficient) which could be modified to adjust model predictions to realistic values. Reproductive and growth rates were based on measurements made from field collections (37 eggs female^{-1}, growth rates were 4 mm yr^{-1} from 5 mm hatchling size to 32 mm; Highsmith & Coyle 1991). Most ampeliscids produce 1 brood, but a small percentage of female *A. macrocephala* may produce a second brood (Kanneworff 1965), which was simulated in the model by assuming that 25 % of the surviving females produce a second brood. Food was assumed not to be limiting.

The model was run with initial densities of each age class below 10 ind. m^{-2} and allowed to reach equilibrium. The proximity coefficient was adjusted to yield realistic population values. The densities of each age class initially increased and oscillated but came to equilibrium after about 120 iterations (Fig. 3). Each model iteration is equivalent to 1 yr. If the proximity coefficient was about 0.48, the predicted population of each age class of *Ampelisca macrocephala* approached
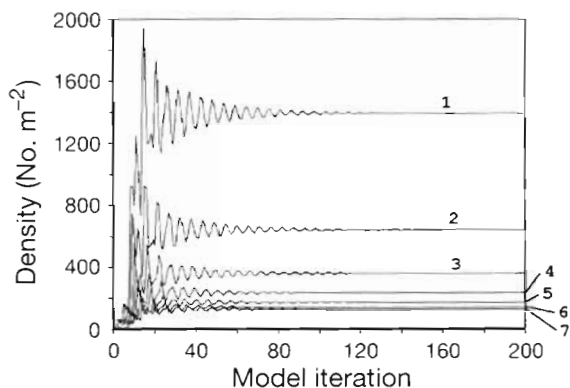
Fig. 3. *Ampelisca macrocephala*. Model prediction of age class densities, assuming space competition determines age class size. Lines 1 to 7 indicate age classes 1 to 7 respectively

the mean values measured at 6 stations for 6 cruises, although model predictions were slightly higher for age classes 1 and 7 (Table 3). Age class 1 was probably undersampled due to loss through the sieves during collection, and population losses in age class 7 may be higher than predicted due to senescent mortality. The model results suggest that age-related mortality caused by competition for space has the potential to set the relative abundance of each age class of *A. macrocephala*.

The proximity coefficient required by the model (0.48) exceeds the antenna length of *Ampelisca macrocephala* (0.35 of body length) because the model does not include *A. birulai* and *Byblis* spp., the other 2 abundant ampeliscids in the Chirikov Basin. The model was therefore refined to include the latter 2 taxa and to incorporate the effects of density independent predation mortality as well as competition between taxa. Predation was estimated by removing a constant percentage of individuals from all year classes each year. A growth rate of 4 mm yr^{-1} and fecundity of 12 eggs female^{-1} was used for *A. birulai*, with maturity occurring in the third year. Values used for *Byblis* were

Table 3. *Ampelisca macrocephala*. Mean no. m^{-2} of amphipods in 7 age classes at 6 stations over 3 yr, and age-frequency distribution (no. m^{-2}) projected by the model after reaching equilibrium with a proximity coefficient (proportion of body length) of 0.48

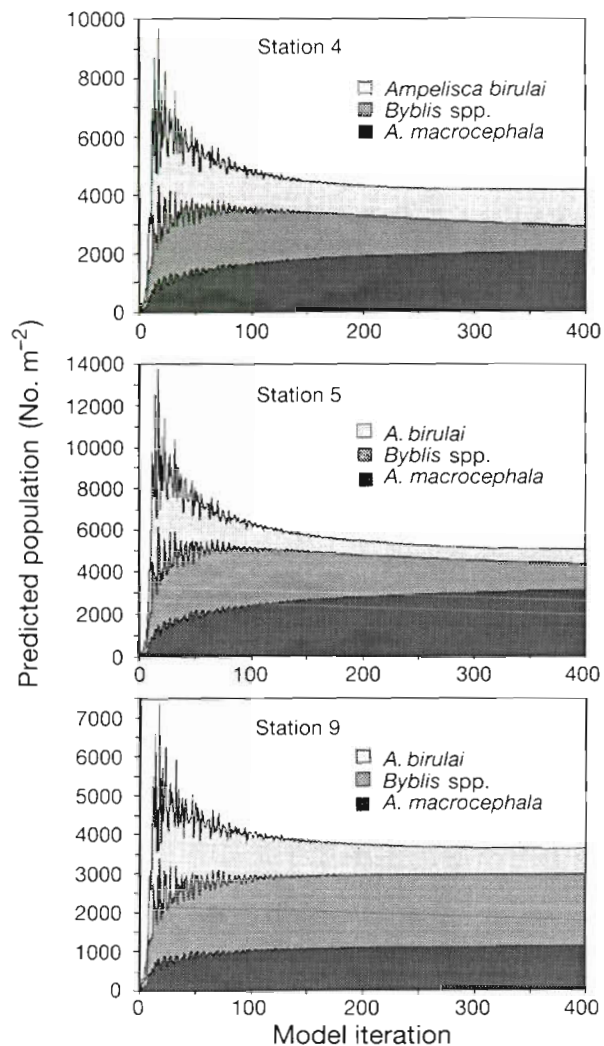|	Age class						
	1	2	3	4	5	6	7
Mean	972	678	355	213	158	150	71
(SD)	(593)	(410)	(299)	(136)	(89)	(64)	(42)
Model	1392	643	362	236	175	143	130

Fig. 4. Model simulations of ampeliscid densities at Stns 4, 5 and 9 over 400 model iterations

4 mm yr^{-1} and 25 eggs female^{-1} with maturation in the fifth year. Initial densities of all 3 species were set below 10 ind. m^{-2} per age class. Fecundity, the proximity coefficient, and predation mortality were adjusted to bring simulated populations after 400 model iterations to levels approximately equal to average values observed at 3 stations over 6 cruises (Fig. 4, Table 4). For graphic clarity, only the total densities of the 3 species were plotted.

To obtain realistic population estimates for all 3 species at these stations, the fecundity of *Byblis gaimardi* and *Ampelisca birulai* had to be elevated to 35 and 17.5 eggs female^{-1} respectively. Therefore, the maximum fecundity values determined from field samples were probably representative, with lower numbers resulting from egg losses during collection. With the above fecundity values held constant, small variations in the

Table 4. *Ampelisca macrocephala, A. birulai, Byblis* spp. Mean densities (no. m^{-2}) for each age class of the 3 dominant ampeliscid taxa at 3 stations in the northern Bering Sea relative to model projections. Model parameters for each station are also shown

Model parameters		Station	
	4	5	9
Fecundity (eggs ind.$^{-1}$)			
A. macrocephala	36.6	35.9	34.2
A. birulai	17.5	17.5	17.5
Byblis spp.	35.0	35.0	35.0
Proximity coefficient	0.35	0.30	0.40
Predation	0.14	0.12	0.14

Station		Age class						
		1	2	3	4	5	6	7
Ampelisca macrocephala								
4	Mean	951	573	241	149	93	114	48
	(SD)	(291)	(212)	(76)	(47)	(35)	(29)	(21)
	Model	906	441	255	170	125	101	83
5	Mean	1279	492	389	232	199	143	32
	(SD)	(404)	(231)	(282)	(160)	(99)	(50)	(20)
	Model	1362	665	383	254	189	153	129
9	Mean	406	166	132	77	83	75	21
	(SD)	(219)	(52)	(60)	(31)	(46)	(34)	(13)
	Model	489	238	138	93	69	56	47
Ampelisca birulai								
4	Mean	1005	429	208				
	(SD)	(265)	(155)	(93)				
	Model	717	350	201				
5	Mean	290	175	53				
	(SD)	(176)	(116)	(30)				
	Model	409	190	108				
9	Mean	302	183	67				
	(SD)	(158)	(116)	(27)				
	Model	376	184	106				
Byblis spp.								
4	Mean	474	330	103	69	39		
	(SD)	(221)	(182)	(75)	(26)	(3)		
	Model	397	194	112	75	55		
5	Mean	991	570	177	63	45		
	(SD)	(937)	(292)	(75)	(32)	(31)		
	Model	583	285	165	109	81		
9	Mean	1068	542	252	205	102		
	(SD)	(718)	(201)	(114)	(161)	(70)		
	Model	884	430	250	167	125		

fecundity of *A. macrocephala*, the proximity coefficient and predation mortality yielded population estimates approximately equivalent to average values measured at the 3 stations (Table 4). The proximity coefficient ranged from 0.30 to 0.40 and was lowest at Stn 5, where *A. macrocephala* populations were greatest, and highest at Stn 9, where *Byblis* spp. dominated. A small decrease in *A. macrocephala* fecundity relative to *Byblis* spp. fecundity is sufficient for the latter species to out-

compete the former *A. birulai* densities were highest at Stn 4, where predation was highest and *A. macrocephala* densities exceeded *Byblis* spp. densities.

Average values of model parameters for the ampeliscid bed during the 3 yr study were computed as follows. The population of each taxon in each age class was averaged for the 6 stations and cruises listed in Table 2. Model parameters were then adjusted to yield predicted population densities in approximate agreement with field data after 400 iterations (Table 5). Predation mortality was set at 13 % of each population per year, the proximity coefficient was set at 0.35 and *Ampelisca macrocephala* fecundity was set at 36 eggs female^{-1}. Under these conditions, the model predicts an AFDW biomass for all taxa of 43 g m^{-2} compared with field estimates of 38 g m^{-2}, computed from the AFDW regression and population data for the above 6 stations and cruises. The model predicts an AFDW production of 26 g m^{-2} yr^{-1}, assuming constant mortality over the production season, compared with measured estimates of 25 g m^{-2} yr^{-1} for a 6 mo production period (Highsmith & Coyle 1992). The model predicts ampeliscid carbon consumption rates of 39 to 56 g C m^{-2} yr^{-1} compared with measured estimates of 55 g C m^{-2} yr^{-1} for the macrofaunal benthic community in the Chirikov Basin (Walsh et al. 1989). The model predicts a total AFDW loss to predation of 5.6 g m^{-2} yr^{-1}. Annual consumption of ampeliscids by gray whales is approximately 4.6 g m^{-2} yr^{-1}, converted from kcal to AFDW (Highsmith & Coyle 1992).

The effect of an oscillation in predation rates, such as might have occurred due to gray whale hunting in the 19th through the mid-20th centuries (Henderson 1984) and the subsequent recovery of whale populations (Reilly et al. 1983), was simulated by a sine wave per-

Table 5. Mean densities (no. m^{-2}) in each age class of the 3 dominant ampeliscid taxa at 6 stations during 6 cruises, and corresponding model predictions

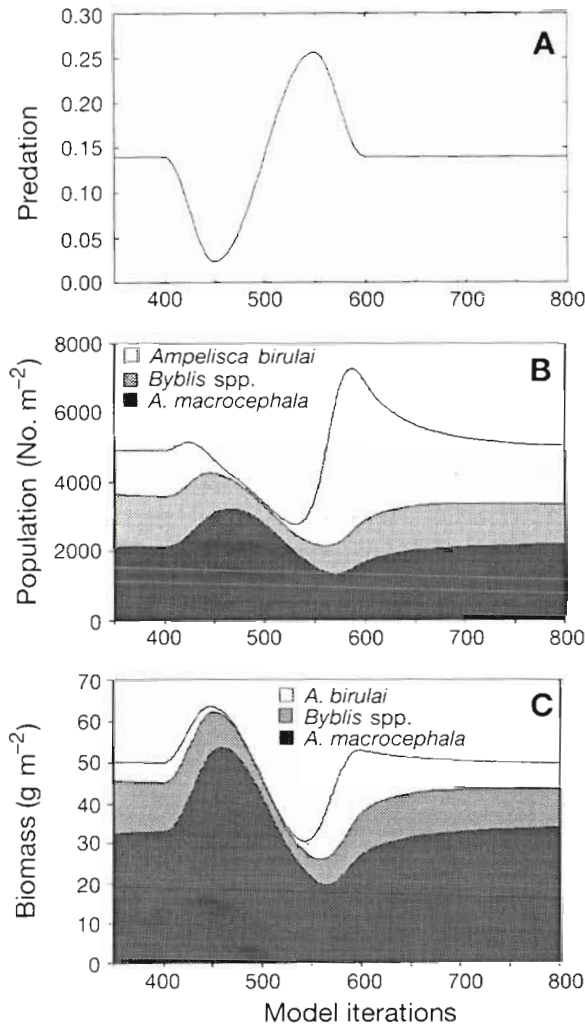|	Age class						
	1	2	3	4	5	6	7
Ampelisca macrocephala							
Mean	973	678	355	214	158	150	71
(SD)	(593)	(411)	(229)	(137)	(89)	(64)	(43)
Model pred.	1262	615	356	237	175	142	119
Ampelisca birulai							
Mean	566	306	108				
(SD)	(391)	(192)	(74)				
Model pred.	659	319	181				
Byblis spp.							
Mean	736	434	197	123	70		
(SD)	(632)	(263)	(143)	(110)	(58)		
Model pred.	660	322	187	125	92		

Fig. 5. Model simulation of the effect of a sine wave perturbation in predation rates on ampeliscid population and biomass after 400 model iterations. (A) Predation rates as a percentage of population; (B) ampeliscid populations; (C) ash free dry weight biomass

turbation in predation losses. Exact gray whale population data during the unregulated whaling period are not available. Historical catch data, however, indicate that the California gray whale population was reduced to about one-fourth of prewhaling numbers, from 20 000 to 5000 animals (Henderson 1984). At the current rate of population growth, about 3 % yr^{-1}, whales may take up to 25 % of annual amphipod production by the year 2000 (Highsmith & Coyle 1992). Model predictions, however, indicate that such removal rates are not sustainable. Simulations with a prewhaling predation rate of 14 % yielded predicted ampeliscid densities during the late stages of whale recovery roughly equivalent to our field estimates. The amphipod model was initially run for 400 iterations with predation rate

held constant at 14 % of the total ampeliscid population per year. Between iterations 400 and 450 the predation rate was gradually decreased to about 3 % of the population per year. Predation losses were then increased symmetrically from 3 % to 26 % yr^{-1} between iterations 450 and 550, and allowed to returned to 14 % between iterations 550 and 600 (Fig. 5A). Decreased predation produced an increase in Ampelisca macrocephala density, a crash in the A. birulai population and a less severe dip in the Byblis spp. population (Fig. 5B). With a reduction in predation losses, the smaller amphipods in the simulation were unable to compete effectively for space with the larger individuals. After predation rates were increased between iterations 450 and 550, A. birulai densities rapidly increased and Byblis spp. began a slower rebound. By iteration 600, when predation again reached 14 % of the total population per year, A. birulai densities were more than double their initial value before iteration 400. Over the next 150 iterations, A. birulai populations underwent a gradual decline, as Byblis spp. and A. macrocephala densities approached their initial values prior to iteration 400. Despite the substantial population variations, the largest species, A. macrocephala, dominated amphipod biomass during the entire period (Fig. 5C). Since 1 model iteration is equivalent to 1 yr, the model predicts that perturbations in predation will have long-term effects (tens to hundreds of years) on these slow-maturing Arctic populations.

The simulated oscillation in predation caused an opposite fluctuation in ampeliscid carbon consumption and production, with amplitudes of only about 20 % (Fig. 6A, B). When predation losses were returned to the equilibrium value at iteration 600, production and carbon consumption levels were nearly identical to those before the perturbation. When predation was maximum, the space occupied by ampeliscids underwent about a 50 % decline (Fig. 6C).

Based on recent estimates of gray whale population growth, the whales should take 1.7 times more ampeliscids by the year 2000 (Highsmith & Coyle 1992). If the predation rate had been held at the maximum of 26 % of the population in the simulation, the densities and biomass of Ampelisca macrocephala, A. birulai and Byblis spp. after 800 iterations would have been 50, 7600 and 1650 ind. m^{-2}, and 7, 20 and 13 g m^{-2} respectively. Thus, A. macrocephala would have been essentially eliminated from the population. Total production at equilibrium following sustained predation at 26 % would be lower than before, and roughly 65 % of the production would be due to A. birulai, the smallest ampeliscid with the highest reproductive potential. This scenario is unlikely, however, because these changes in ampeliscid densities would result in lower biomass and probably food limitation of the gray
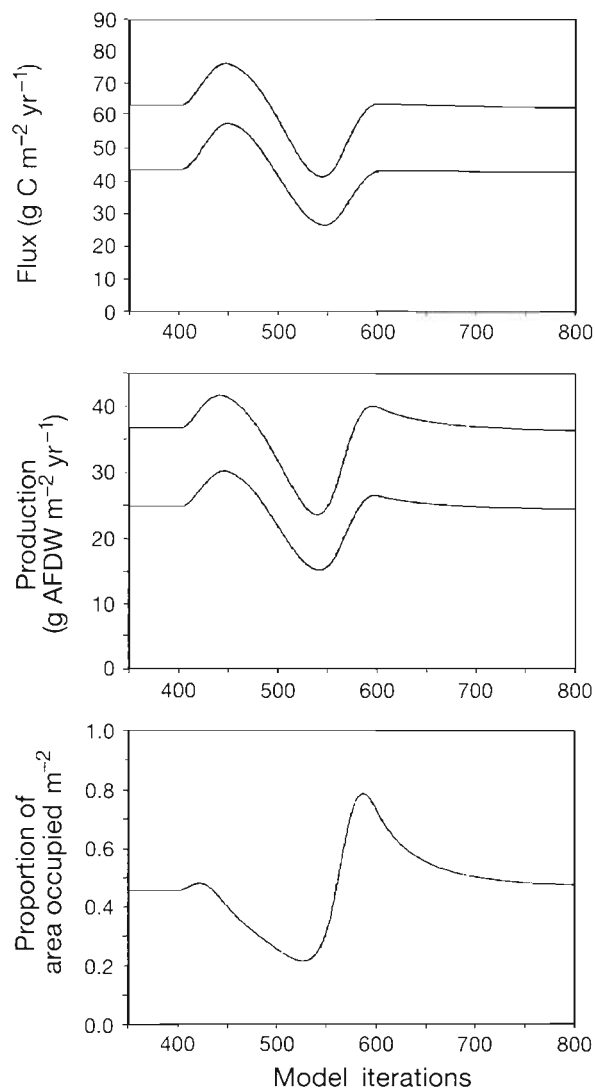
Fig. 6. Model simulation of the effect of a sine wave perturbation in predation rates on the carbon flux to the ampeliscid population, ash free dry weight production and maximum area occupied by ampeliscids. (A) Carbon flux. Upper line: maximum possible if all individuals survived to the next age class; lower line: flux if population is in approximate steady state. (B) Production. Line designations same as above. (C) Maximum possible area occupied ($m^2 m^{-2}$ of surface area)

whales, causing their populations to decline, switch to other prey or forage elsewhere, thus reducing predation rates.

The actual ampeliscid density at which the gray whale population would become food limited is unknown. Since ampeliscids appear to have a patchy distribution, they may be an effective food source at lower average concentrations than might be predicted, if the whales can locate the patches. Nevertheless, the model does demonstrate the ampeliscid population trends likely to occur due to changes in whale predation.

DISCUSSION

The Chirikov Basin is an unusually productive region due to the transport of nutrient-rich Anadyr water northward from the Cape Navarin region through the Gulf of Anadyr and into the northern Bering Sea (Hansell et al. 1989, 1993, Springer & McRoy 1993). The northward transport is due to differences in sea level between the Arctic Ocean and Bering Sea (Coachman 1993). Although some interannual differences in residence time of Anadyr Water in the Chirikov Basin can occur due to wind patterns in the Bering Strait regions, the overall transport during the production season is consistently northward (Coachman 1993). Because of the consistent northward transport of nutrient-rich water into the Chirikov Basin throughout the summer, the region has been likened to a continuous culture system (Sambroto et al. 1984). Total annual carbon production rates may be as high as 720 to 840 g C $m^{-2} yr^{-1}$ (Springer & McRoy 1993), with new production rates of about 288 g $m^{-2} yr^{-1}$ in the Chirikov Basin (Hansell et al. 1993). The above production rates also show remarkable interannual continuity (Hansell et al. 1993). In addition to local production, substantial amounts of phytoplankton appear to be transported into the Chirikov Basin in the Anadyr water (Hansell et al. 1989). The combination of advection and high production leads to high carbon flux to the benthos, thus permitting dense concentrations of large ampeliscids to occur, which in turn provides favorable foraging habitat for gray whales. Benthic faunal structure and biomass have not changed significantly over a decade (Grebmeier et al. 1989), an additional indication of a persistent food supply to the benthos.

The relationship between ampeliscid size, carbon flux requirements, growth and molting rates limits the geographic distribution of large ampeliscids to cold, highly productive waters (Highsmith & Coyle 1991). If molting rates and maturation accelerate due to increasing temperature and the number of molts to maturity is constant, as indicated in the literature (Highsmith & Coyle 1991), temperate ampeliscids would require greater carbon flux to the seafloor to reach the same size as polar species because they would have to grow faster between the more frequent molts. Numerical comparisons of carbon flux requirements by faster-maturing temperate species and Arctic ampeliscids can be made by summing carbon flux estimates (Table 1) in adjacent age classes. For example, individuals maturing at 10 to 12 mo of age and 12 mm length in 2 to 18°C water (near the Isle of Man and near Helgoland; Klein et al. 1975, Hastings 1981, Highsmith & Coyle 1991) would require a minimum of about 116 to 168 g C $m^{-2} yr^{-1}$ depending on antenna

length, at least 1.7 times the rate required by *Ampelisca birulai* to mature at the same size in the Chirikov Basin in 2 yr. *A. macrocephala* would require a minimum of 481 g C m^{-2} yr^{-1} to mature at 20 to 28 mm length in temperate regions, assuming growth rates of about 8 mm yr^{-1}. *A. macrocephala* in the Øresund, mature in 1.5 (males) to 2 yr (females), but the females only reach about 18 mm length (Kanneworff 1965). These *A. macrocephala* would require a minimum of about 327 g C m^{-2} yr^{-1}, but may have utilized an alternative food source, as Kanneworff (1965) reported much animal material and algal detritus in the diets. In highly dense populations, where nearest neighbors are closer than the length of the second antenna, the above flux estimates would have to be even higher to sustain the same growth rates. Alternatively, the same species could survive at lower flux rates by simply maturing at a smaller size.

Carbon flux to the detritus pool is approximately 231 g C m^{-2} yr^{-1} in the Chirikov Basin under Anadyr water (Walsh et al. 1989), somewhat below the upper limit required for *Ampelisca macrocephala* to reach 28 mm length (Table 1). Carbon flux to macrobenthos in the Chirikov Basin is about 55 g C m^{-2} yr^{-1}, under Anadyr-Bering Shelf water (Walsh et al. 1989). The model predictions of ampeliscid population structure and biomass indicate a carbon utilization rate by ampeliscids of 39 to 57 g C m^{-2} yr^{-1}, roughly equivalent to the above estimate of carbon flux to macrobenthos. Total carbon flux to the detritus pool in Alaskan Coastal Water is only 30.5 g C m^{-2} yr^{-1} (Walsh et al. 1989), about 50% below that required by *A. birulai*, the most efficient ampeliscid forager in our study, to mature and reproduce (Table 1C). Carbon flux data and model predictions therefore indicate that ampeliscids cannot survive in areas of the Chirikov Basin overlain by Alaskan Coastal Water because carbon flux to the bottom is too low to sustain them.

Broad scale examination of benthic community structure in the Chirikov Basin confirms the absence of the ampeliscid community under Alaskan Coastal Water (Grebmeier et al. 1988, 1989). Although the sediment composition under Alaskan Coastal Water is somewhat different from that in the ampeliscid bed (Naidu 1988, Grebmeier et al. 1989), these sediment differences do not appear to explain the absence of ampeliscids under Alaskan Coastal Water because ampeliscids are present and sometimes abundant off Pt. Franklin (northern Chukchi Sea), where sediment composition is nearly identical to that under Alaskan Coastal Water in the Chirikov Basin (Klaus et al. 1990, Feder et al. 1991). Therefore, the absence of the ampeliscid community under Alaskan Coastal Water is probably due primarily to food limitation rather than sediment composition.

In field samples, *Ampelisca macrocephala* dominated ampeliscid populations at all sites within the ampeliscid bed, except at the southeast corner (64° N, 168° W), where *Byblis* spp. dominated. *Byblis* spp. dominance was simulated in the model by lowering the fecundity of *A. macrocephala* (Table 4). Decreases in *A. macrocephala* fecundity might result from lower carbon flux to the sea bed, as any decrease in carbon flux will influence the larger species before the smaller ones. Lower carbon sedimentation rates occur near the eastern edge of the ampeliscid bed, a transition zone between the Anadyr and less productive Alaskan Coastal Water masses (Walsh et al. 1989). Thus, lower carbon flux on the eastern edge of the Chirikov Basin may give *Byblis* spp. a competitive advantage, allowing it to dominate in that region.

Model simulations producing population estimates in approximate agreement with average ampeliscid densities observed in the Chirikov Basin from 1986 to 1988 require a predation loss of roughly 13% of the biomass per year, approximately 5.6 g AFDW m^{-2} yr^{-1}. Gray whales, major predators on ampeliscid populations, removed about 8 to 18% of the annual ampeliscid production between 1986 and 1988 (Highsmith & Coyle 1992), equivalent to approximately 2.4 to 5.4 g AFDW m^{-2} yr^{-1}. Other predators taking the remaining losses include fish, decapods and lysianassid amphipods (authors' unpubl. data). For steady state populations, maximum possible losses to predators would be 8.4 g dry wt m^{-2} yr^{-1} or about 4.2 g C m^{-2} yr^{-1}. Walsh et al. (1989) predict a carbon loss from benthic macrofauna to apex vertebrate predators of 5 g C m^{-2} yr^{-1} in Anadyr water.

Polar amplification of global warming may cause an increase in average annual temperatures in Arctic waters (Schlesinger & Mitchell 1987, Sarmiento et al. 1988), which could affect Arctic ampeliscid populations in 2 ways. Warmer bottom water temperatures should accelerate ampeliscid maturation rates (Highsmith & Coyle 1991). If carbon flux to the benthos remained constant or decreased, *Ampelisca macrocephala* would mature at a smaller size or be replaced by smaller taxa. Therefore, *A. erythrorhabdota*, *Byblis gaimardi*, *A. birulai* or some other taxon (e.g. *Echinarachnius parma*; Highsmith & Coyle 1991) would probably become the dominant primary consumer.

Many abundant commercial fish species from Bristol Bay are essentially excluded from more northern regions due to cold near-bottom water temperatures (Moiseyev 1964, Smith 1981, Bakkala 1981). Warmer conditions might permit them to extend their range northward into the Chirikov Basin, thus elevating predation on the ampeliscid community and increasing selective pressures for smaller, faster-maturing taxa. The immigration of additional temperate predator taxa

might also increase competition between gray whales, fish and decapod predators for the ampeliscid food resource.

LITERATURE CITED

Bakkala, R. G. (1981). Population characteristics and ecology of yellowfin sole. In: Hood, D. W., Clader, J. A. (ed.) The eastern Bering Sea shelf: oceanography and resources, Vol. 1. University of Washington Press, Seattle, p. 553–574

Blokhin, S. A., Vladimirov, V. L. (1981). Pitanie serykh kitov Kaliforniisko-Chukotskoi populyatsii v vodakh Chuktskogo poluostrogo v 1980 g. (The diet of the California-Chukotsk gray whale population in Chukchi Peninsula waters in 1980.) In: Nauchno-issledovatelskie raboty po morskim mlekopitayushchim severnoi chasti Tikhogo okeana v 1980/1981 gg. Proekt 02.05-61 Morskie mlekopitayushchie, Soglasheniya SSSR-ShA o sotrudnichestve v oblasti okhrany okruzhayushchei sredi. Moscow, p. 88–98

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

Coachman, L. K., Agaard, K., Tripp, R. B. (1975). Bering Strait. The regional physical oceanography. Univ. of Washington Press, Seattle

Coachman, L. K., Hansell, D. A. (eds.). (1993). ISHTAR. Inner shelf transfer and recycling in the Bering and Chukchi Seas. Cont. Shelf Res. 13(5/6): 473–704

Coyle, K. O., Highsmith, R. C. (1989). Arctic ampeliscid amphipods, three new species. J. Crust. Biol. 9: 157–175

Feder, H. M., Naidu, A. S., Hameedi, J. M., Jewett, S. C., Johnson, W. R. (1991). The Chukchi Sea continental shelf: benthos and environmental interactions. Final Report. Outer Continental Shelf Environmental Assessment Program, Vol. 68. U.S. Dept of Commerce, National Oceanic and Atmospheric Administrations, Washington, DC, p. 25–311

Grebmeier, J. M., Feder, H. M., McRoy, C. P. (1989). Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. II. Benthic community structure. Mar. Ecol. Prog. Ser. 51: 253–268

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. Mar. Ecol. Prog. Ser. 48: 57–67

Hansell, D. A., Goering, J. J., Walsh, J. J., McRoy, C. P., Coachman, L. K., Whitledge, T E. (1989). Summer phytoplankton production and transport along the shelf break in the Bering Sea. Cont. Shelf. Res. 9: 1058–1104

Hansell, D. A., Whitledge, T. E., Goering, J. J. (1993). Patterns of nitrate utilization and new production over the Bering-Chukchi shelf. Cont. Shelf Res. 13(5/6): 601–627

Hastings, M. N. (1981). The life cycle and productivity of an intertidal population of the amphipod *Ampelisca brevicornis.* Estuar. coast. Shelf Sci. 12: 665–667

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, New York, p. 159–186

Heron, G. A., Damker, D. M. (1986). A new nicothoid copepod parasitic on mysids from northwestern North America. J. Crust. Biol. 6(4): 652–665

Highsmith, R. C., Coyle, K. O. (1990). High productivity of northern Bering Sea 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. Am. Zool. 31: 861–873

Highsmith, R. C., Coyle, K. O. (1992). Productivity of arctic amphipods relative to gray whale energy requirements. Mar. Ecol. Prog. Ser. 83: 141–150

Hill, C. (1992). Interactions between year classes in the benthic amphipod *Monoporeia affinis:* effects on juvenile survival and growth. Oecologia 91: 157–162

Jensen, K. T., Kristensen, L. D. (1990). Field experiment on competition between *Corophium volutator* (Pallas) and *Corophium arenarium* Crawford (Crustacea: Amphipoda): effects on survival, reproduction and recruitment. J. exp. mar. Biol. Ecol. 137: 1–24

Kanneworff, E. (1965). Life cycle, food, and growth of the amphipod *Ampelisca macrocephala* Liljeborg from the Øresund. Ophelia 2(2): 305–318

Klaus, A. D., Oliver, J. S., Kvitek, R. G. (1990). The effects of gray whale, walrus, and ice gouging disturbance on benthic communities in the Bering Sea and Chukchi Sea, Alaska. Nat. Geogr. Res. 6(4): 470–484

Klein, G., Rachor, E., Gerlach, S. A. (1975). Dynamics of productivity of two populations of the benthic tube-dwelling amphipod *Ampelisca brevicornis* (Costa) in Helgoland Bight. Ophelia 14: 139–159

Moiseyev, P. A. (1964). Nekotorye itogi issledovaniy beringovomorskiy nauchno-promyslovoy ekspeditsii. In: Sovetskiye rybokhozyaystvennye issledovaniya v severovostochnoy chasti Tikhogo okeana, TINRO, No. 3. Pishchevaya Promyshlennost, Moscow, p. 7–29

Naidu, S. A. (1988). Marine surficial sediments. In: Bering, Chukchi and Beaufort Sea strategic assessment: data atlas No. 1.4. Office of Oceanography and Marine Assessment, National Oceanic and Atmospheric Administration, U.S. Dept of Commerce, Washington, DC

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, p. 423–450

Pielou, P. E. (1974). Population and community ecology. Gordon and Breach Science Publishers, New York

Reilly, S. B., Rice, E. W., Wolman, A. A. (1983). Population assessment of the gray whale, *Eschrichtius robustus,* from California shore censuses, 1967–1980. Fish. Bull. U.S. 81: 267–281

Sambroto, R. N., Goering, J. J., McRoy, C. P. (1984). Large yearly production of phytoplankton in the western Bering Strait. Science 244: 1147–1150

Sanders, H. L. (1956). Oceanography of Long Island Sound, 1952–1954. X. The biology of marine bottom communities. Bull. Bingham Oceanogr. Coll. 15: 345–414

Sarmiento, J. L., Toggweiler, J. R., Najja, R. (1988). Ocean carbon-cycle dynamics and atmospheric CO_2. Phil. Trans. R. Soc. Lond. 352: 3–21

Schlesinger, M. E., Mitchell, J. F. B. (1987). Climate model simulations of the equilibrium response to increased carbon dioxide. Rev. Geophys. 25: 760–798

Smith, G. B. (1981). The biology of walleye pollock. In: Hood, D. W., Calder, J. A. (eds.) The eastern Bering Sea shelf: oceanography and resources, Vol. 1 University of Washington Press, Seattle, p. 527–552

Springer, A. M., McRoy, C. P. (1993). The paradox of pelagic food webs in the northern Bering Sea. III. Patterns of primary production. Cont. Shelf Res. 13(5/6): 575–599

Stoker, S. W. (1981). Benthic invertebrate macrofauna of the eastern Bering/Chukchi continental shelf. In: Hood, D. W., Calder, J. A. (eds.) The eastern Bering Sea shelf: oceanography and resources, Vol. 2. Univ. of Washington Press, Seattle, p. 1069–1090

Strickland, J. D. H., Parsons, T. R. (1972). A practical handbook of seawater analysis. Bull. Fish. Res. Bd Can. 167

Walsh, J., and 19 co-authors (1989). Carbon and nitrogen cycling within the Bering/Chukchi Seas: source regions for organic matter affecting AOU demands of the Arctic Ocean. Prog. Oceanogr. 22: 277–359