Trophic relationships and isotopic gradients among arctic and subarctic marine fauna*

Kenneth H. Dunton[1], Susan M. Saupe[2], Alexander N. Golikov[3], Donald M. Schell[2], Susan V. Schonberg[1]

[1] Marine Science Institute, The University of Texas at Austin, Port Aransas, Texas 78373-1267, USA
[2] Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99775, USA
[3] Zoological Institute, The Soviet Academy of Sciences, Leningrad 199164, USSR

ABSTRACT: Stable carbon and nitrogen isotope measurements of benthic fauna were used to identify an isotopic gradient in plankton along the subarctic and arctic coast of Alaska, and to study food web relationships in 3 geographically distinct arctic environments: the southeast Bering, the Chukchi and the eastern Beaufort Seas. Isotope measurements were also made of selected fauna from the western Beaufort Sea and from the East Siberian Sea. Results show a pronounced difference in the carbon isotope composition of suspension feeders collected in the southeastern Bering, Chukchi and western Beaufort Seas ($\delta^{13}C = -19$ to $-20\%_0$) compared to the eastern Alaskan Beaufort and East Siberian Seas (-25 to $-26\%_0$). This geographic difference is greatest at lower trophic levels but is observed throughout the food web as a progressive decrease in ^{13}C content of fauna from the southeast Bering to the eastern Beaufort Sea. Predatory and omnivorous gastropods were ^{13}C-enriched relative to most organisms at most geographic locations, occupying a trophic level equivalent to that of demersal fishes. Trophic relationships among fauna from the different geographical areas were similar. In the Chukchi Sea, $\delta^{13}C$ and $\delta^{15}N$ values fell in a narrow range compared to other regions studied. The ^{13}C enrichment of secondary consumers in the Chukchi relative to that of zooplankton was also small. This may reflect shorter food chains, which in the Chukchi Sea is related to a more direct coupling of benthic consumers to the very high pelagic primary production, little of which is grazed before reaching the sea bed.

INTRODUCTION

Geographic gradients in the isotopic composition of marine zooplankton provide natural markers valuable for tracing migrational patterns and feeding habits of their predators (Schell et al. 1989). A pronounced difference in zooplankton $\delta^{13}C$ values between the Bering and eastern Beaufort Sea is reflected in the isotopic composition of the migratory bowhead whale (Saupe et al. in press). Analysis of these isotopic variations have contributed significantly to understanding the natural history of this animal (Schell et al. in press).

A gradient in zooplankton carbon isotope composition along the north Alaskan arctic coast by Dunton (1985) was confirmed by Saupe et al. (in press). Dunton (1985) found that $\delta^{13}C$ values of calanoid copepods collected in September 1977 decreased from -23.5 to $-25.4\%_0$ between the northeastern Chukchi Sea (158° W) and the US-Canadian border (141° W) along the Beaufort Sea coast. Saupe et al. (in press) found a similar trend in mean $\delta^{13}C$ values from samples collected along the same coastline in October 1986 (-22.8 to $-26.2\%_0$). They found that calanoid copepods were isotopically enriched in ^{13}C in the southern Chukchi and northern Bering Seas, with mean $\delta^{13}C$ values of -20.7 and $-21.1\%_0$ respectively.

The zooplankton $\delta^{13}C$ values recorded by Dunton (1985) and Saupe et al. (in press) from the Chukchi and western Beaufort Sea agree with those reported by Rau et al. (1982) for western Beaufort Sea plankton (-21.5 and $-22.4\%_0$). Rau et al. (1982) used these results to compare latitudinal trends in plankton $^{13}C:^{12}C$ ratios between northern and southern oceans and found that, although the plankton in both hemispheres showed depletions in ^{13}C with increasing latitude, the depletions were significantly less progressing toward the Arctic (about $-22\%_0$) compared to the Antarctic (-26 to

$-28\,‰$). Saupe et al. (in press) found $\delta^{13}C$ values of unsorted zooplankton collected in the eastern Beaufort Sea to be ^{13}C depleted by as much as $-29.2\,‰$.

The existence of a gradient in plankton $^{13}C:^{12}C$ ratios between the Bering and eastern Beaufort Sea might be questioned on the basis that (1) the isotopic measurements are of short-lived zooplankters, and (2) zooplankton biomass and species composition differ spatially and temporally across this range. The object of this research was to further define this isotopic gradient through $^{13}C.^{12}C$ analyses of benthic and epibenthic consumers that are relatively long-lived, possess a variety of feeding strategies, and which are common between the southeast Bering and eastern Beaufort Sea. The collection of similar species from Chauna Bay, East Siberian Sea, 1000 km west of Alaska, provided a benchmark from which to compare $\delta^{13}C$ values from an arctic region not likely influenced by the intrusion of Bering Sea and Alaskan coastal water (Walsh et al. in press). Measurement of both $\delta^{13}C$ and $\delta^{15}N$ values of fauna from several arctic and sub-arctic areas also provided a unique opportunity to compare food webs in areas having substantially different rates of annual primary production, from less than $50\,g\ C\ m^{-2}\,yr^{-1}$ (Beaufort Sea; Horner 1984) to $300\,g\ C\ m^{-2}\,yr^{-1}$ (Bering Sea; Walsh et al. in press).

MATERIALS AND METHODS

Study area. Samples were collected from stations located at each of the 5 major geographic areas shown in Fig. 1. Nearly all fauna were collected within 20 km of the coastline in water depths ranging between 5 and 50 m. The letters in Fig. 1 correspond to animals collected from: (A) the north Aleutian Shelf, southeast Bering Sea, mostly between May and July 1985 from trawls deployed along 5 transects at 10 stations; (B) the eastern Chukchi Sea, in September 1983, from trawls deployed along 3 transects between Cape Lisburne and Wainright at 15 stations; (C) the western Alaskan Beaufort Sea, in February 1983, by diving at 2 sites near Cape Halkett; (D) the eastern Alaskan Beaufort Sea, mostly in August 1986 and August 1987, by diving at 6 locations between Prudhoe Bay and the US-Canadian border; and (E) in the East Siberian Sea, in August 1987, by diving at 1 site in Chauna Bay.

Isotopic analyses. White muscle tissue samples were dissected from fish that generally ranged between 10 and 30 cm long. Muscle tissue was also taken from adult shrimp, gastropods, bivalves and decapods. Other invertebrates were washed of debris and analyzed whole. Polychaetes, small crustaceans and ascidians were held alive for several hours to allow gut clearance prior to analysis. All animals were dried in
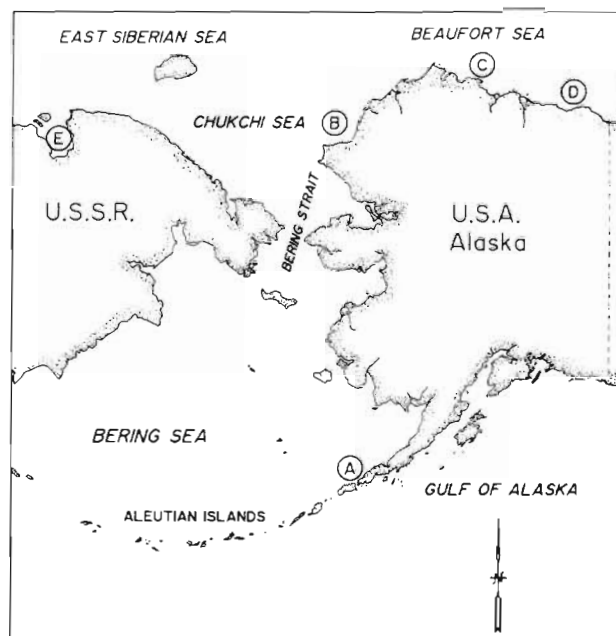

Fig. 1. Locations of collection sites. A: Southeast Bering Sea (north Aleutian Shelf); B: Chukchi Sea; C: western Alaskan Beaufort Sea; D: eastern Alaskan Beaufort Sea; E: East Siberian Sea

aluminum dishes at $50\,°C$. In many instances, small individuals of the same species collected at the same time were pooled to obtain sufficient material for isotopic analysis. These composites (which included several polychaete and crustacean species) consisted of at least 3 individuals.

Samples containing inorganic carbonates were soaked in $1\,N$ HCl for 4 to 6 h (or until bubbling stopped) to remove carbonates, rinsed in distilled water, and then dried at $50\,°C$. Subsamples of each organism or composite (8 to 10 mg) were manually ground in the presence of copper oxide and treated to yield pure CO_2 and N_2 for isotopic determination as described by Dunton & Schell (1987) for carbon and Minagawa et al. (1984) for nitrogen. Results are expressed as conventional $\delta^{13}C$ or $\delta^{15}N$ values, where the ratio of the sample is compared to that of a standard, where

$$\delta(‰) = \{(R_{sample}/R_{standard}) - 1\} \times 1000;$$
$$R = {}^{13}C:{}^{12}C\ \text{or}\ {}^{15}N:{}^{14}N,$$

and standards are PDB ($\delta^{13}C$) and nitrogen in air ($\delta^{15}N$). Replicate isotope analyses generally differed by $< 0.3\,\%$.

Animals were grouped by feeding type into 9 categories based on the results of earlier work with these species (Dunton & Schell 1987) and known feeding behavior: (1) NSB, non-selective benthic suspension feeders (bivalves and ascidians), (2) SBS, selective benthic suspension feeders (sponges, hydrozoans, soft

corals, and bryozoans); (3) BOC, benthic omnivorous crustaceans (crabs and isopods); (4) EOC, epibenthic omnivorous crustaceans (amphipods and shrimp); (5) PF, pelagic fish (Pacific and Arctic cod); (6) PO, polychaete omnivores; (7) MO, molluscan omnivores (mostly *Buccinum*, *Neptunea* and *Plicifusus*); (8) MP, molluscan predators (mostly *Natica*); and (9) BF, demersal fish (sole, sculpins and snailfishes).

RESULTS

^{13}C:^{12}C ratios of fauna

^{13}C content generally increased at ascending trophic levels in the Bering, Chukchi and eastern Beaufort Seas (Fig. 2). The mean δ^{13}C values of animal species
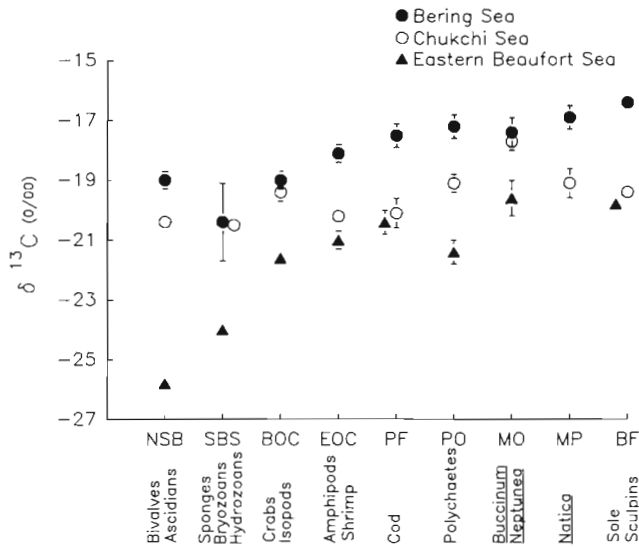

Fig. 2. δ^{13}C values ($\bar{x}$ ± SE, n ≥ 4 for all points) of Alaska fauna from the southeast Bering, Chukchi and eastern Beaufort Seas. Animals are grouped according to feeding strategy. For abbreviations see 'Materials and methods'

collected at all 5 locations are shown in Table 1. ^{13}C content of the food webs generally decreased progressing from the southeast Bering to the eastern Beaufort seas, with consistent differences in mean feeding group δ^{13}C values between geographic areas. Animals were ^{13}C-enriched in the Bering Sea and ^{13}C-depleted in the eastern Beaufort Sea, with the Chukchi Sea fauna intermediate between the 2 extremes (Fig. 2). The differences in δ^{13}C between regions were greatest at the lower trophic levels. In the eastern Beaufort Sea, the mean δ^{13}C values of non-selective (−25.8‰) and selective (−24.0‰) benthic suspension feeders, benthic omnivorous crustaceans (−21.6‰), polychaetes (−21.4‰) and molluscan omnivores (−19.6‰)

were significantly lower (p < 0.05, 1-way ANOVA) than for the same species from either the Chukchi or Bering Seas. At higher trophic levels, the difference in δ^{13}C values between the eastern Beaufort and Chukchi Seas remained below 2.5‰, considerably less than the initial 6.4‰ difference found in non-selective suspension feeders. The range of all feeding group mean δ^{13}C values were lowest in the Chukchi Sea (−18.2 to −20.5‰), highest in the eastern Beaufort Sea (−19.6 to 25.8‰), and intermediate in the southeast Bering Sea (−16.4 to −20.4‰).

Comparisons of the geographic trends in the carbon isotope ratios of filter feeders and secondary consumers common to the eastern and western Beaufort, Chukchi and southeast Bering Seas are shown in Fig. 3. The δ^{13}C values of filter feeders in the eastern Beaufort were significantly lower (p < 0.05, 1-way ANOVA) than those from all other areas. Geographic differences among secondary consumers were not as pronounced, although a trend of increasing ^{13}C depletion is apparent from the southeast Bering to the eastern Beaufort Sea. Filter feeders and secondary consumers in the western Beaufort Sea were closer in isotopic composi-
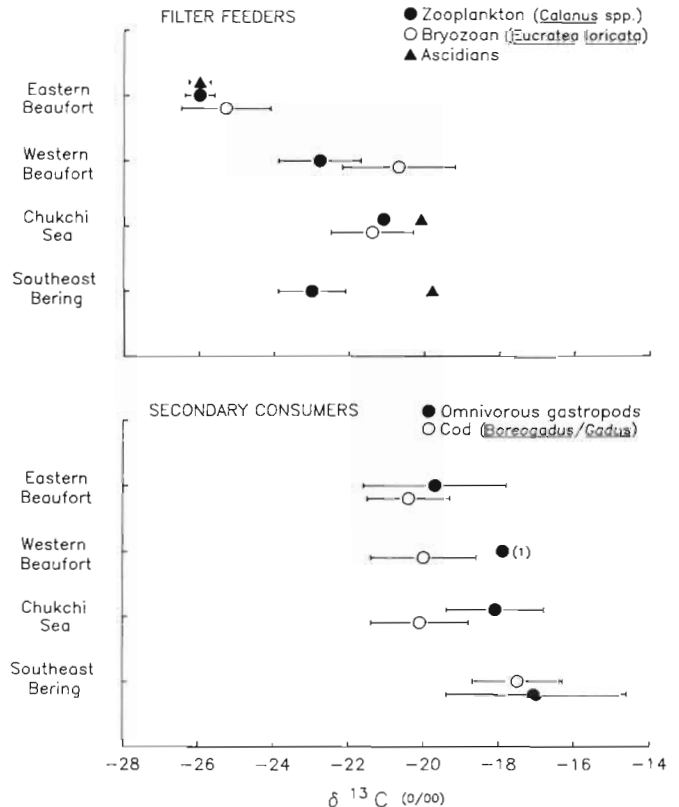

Fig. 3. δ^{13}C values ($\bar{x}$ ± 95 % confidence limits) for filter feeders and secondary consumers common to 4 geographic areas in Alaska. Omnivorous gastropods include only *Buccinum* and *Neptunea* spp. Zooplankton data from Saupe (1989) and Saupe et al. (in press)

Table 1. $\delta^{13}C$ values (‰) of fauna collected at 5 locations in Alaskan and Siberian waters. Values are $\bar{x} \pm SE$ (n) for n > 1

Organism	Bering Sea	Chukchi Sea	W. Beaufort Sea	E. Beaufort Sea	E. Siberian Sea
PORIFERA					
Halichondria panicea		−20.6 ± 0.2(3)		−23.7 ± 0.5(5)	
Haliclona gracilis				−24.5 ± 0.3(12)	
Phakettia cribrosa		−19.3		−23.4 ± 0.1(12)	
Suberites domicula	−23.6 ± 1.0(2)			−22.3 ± 0.2(8)	
CNIDARIA					
Hydrozoa					
Sertularia spp.	−20.7 ± 0.5(2)	−20.4		−25.5 ± 0.6(3)	
Thuiaria sp.		−19.7		−26.7	
Anthozoa					
Gersemia rubiformis		−20.9 ± 0.2(3)		−23.4 ± 0.3(8)	
Unidentified anemone	−19.6				
ANNELIDA					
Polychaeta					
Antinoella badia		−20.2 ± 0.4(2)			
Axiothella catenata		−17.8			
Chaetozone setosa				−21.5	
Cistenides granulata					−23.1 ± 0.0(2)
Eunoe depressa		−19.1 ± 0.3(2)			
Flabelligeridae				−19.6	
Gattyana ciliata		−18.8			
Harmothoe imbricata		−19.4			
Lumbrineris sp.		−19.6			
Nephtys caeca	−16.5 ± 0.2(5)				
Nicolea zostericola				−22.0	
Scalibregma inflatum		−17.6			
Scoloplos armiger				−21.4	
Terebellides stroemi				−21.8 ± 0.1(2)	
MOLLUSCA					
Gastropoda					
Buccinum spp.	−17.6 ± 0.4(2)	−17.7 ± 0.3(3)	−17.9	−19.9	
Bulbus fragilis		−19.8 ± 1.0(2)			
Margarites costalis		−17.0 ± 0.1(3)			
Natica clausa[a]	−17.1 ± 0.5(4)	−17.9 ± 0.2(3)			
Neptunea spp.	−16.0	−18.5 ± 1.0(3)		−19.6 ± 0.9(4)	−22.1
Plicifusus kroyeri	−18.3			−19.5	
Polinices pallidus[b]	−16.2	−19.3 ± 1.1(2)			
Solariella obscura		−17.6			
Velutina undata		−21.0			
Polyplacophora					
Amicula vestita		−17.6 ± 0.5(4)			
Bivalvia					
Astarte borealis[c]	−19.7 ± 0.4(3)				−24.7 ± 0.3(4)
Clinocardium ciliatum[d]	−19.0	−20.0			
Cyclocardia crebricostata	−18.8 ± 0.4(4)				
Hiatella arctica		−20.4 ± 0.1(3)			
Musculus corrugatus				−25.5 ± 0.2(6)	
Mytilus edulis		−21.1 ± 0.2(2)			
Serripes groenlandicus		−20.2 ± 0.0(3)			
Yoldia hyperborea		−20.1			
ARTHROPODA					
Crustacea-Cirripedia					
Balanus crenatus	−19.1	−21.6	−19.8 ± 0.0(2)		
Crustacea-Malacostraca					
Isopoda					
Saduria entomon	−18.4	−19.6	−19.2 ± 0.3(3)	−21.6 ± 0.1(14)	−23.2
Tecticeps sp.		−20.0 ± 0.4(2)			

Table 1 (continued)

Organism	Bering Sea	Chukchi Sea	W. Beaufort Sea	E. Beaufort Sea	E. Siberian Sea
Amphipoda					
Acanthostephia behregensis		−19.5 ± 0.2(4)		−19.7 ± 0.5(4)	
Anonyx sarsi/nugax	−20.1 ± 1.6(2)	−21.1 ± 0.2(7)		−22.8 ± 1.2(2)	
Atylus carinatus		−21.8		−20.6 ± 0.5(8)	
Boeckosimus affinis				−22.9 ± 0.4(2)	
Gammaracanthus loricatus					−21.1 ± 0.3(3)
Gammarus setosus				−20.2	−23.3 ± 0.2(2)
Onisimus litoralis				−22.2	
Weyprechtia sp.		−19.0			
Decapoda					
Cancer pygmaeus	−19.0				
Chionoecetes opilio	−19.0	−18.6 ± 0.2(2)			
Crangon dalli	−17.9 ± 0.2(15)				
Hyas coarctatus alutaceus		−18.6			
Nectocrangon spp.		−19.5 ± 0.1(6)			
Pagurus trigonocheirus	−18.8 ± 0.4(3)	−20.3	−18.4		
BRYOZOA					
Alcyonidium gelatinosum		−20.6 ± 0.0(2)		−25.8 ± 0.3(2)	
Carbasea carbasea				−25.3	
Eucratea loricata		−21.4 ± 0.3(2)	−20.7 ± 0.4(3)	−25.7 ± 0.4(8)	
Flustra spp.		−19.1 ± 0.0(2)		−23.9 ± 0.5(3)	
Flustrella sp.	−17.0 ± 1.4(2)	−21.1	−20.4	−23.2 ± 0.7(4)	
ECHINODERMATA					
Asteroidea					
Leptasterias spp.	−17.5 ± 0.5(2)	−20.6			
Ophiuroidea					
Ophelia limacina	−18.0 ± 0.6(5)				
Stegophiura nodosa		−18.8 ± 0.1(2)		−21.0 ± 0.6(2)	
Holothuroidea					
Cucumaria sp.	−17.0				
UROCHORDATA					
Ascidiacea					
Boltenia ovifera	−19.8	−20.1 ± 0.0(2)			
Chelyosoma macleayanum		−21.1			
Mogula griffithsii			−26.1 ± 0.1(6)		
Rhizomogula globularis			−25.8 ± 0.3(3)	−24.5 ± 0.2(4)	
VERTEBRATA					
Osteichthyes					
Boreogadus saida		−20.1 ± 0.5(5)	−20.0 ± 0.4(4)	−20.4 ± 0.5(8)	
Gadus macrocephalus	−17.5 ± 0.4(5)				
Hippoglossoides elassodon		−15.9			
Hippoglossus stenolepis	−17.1				
Lepidopsetta bilineata	−17.0 ± 0.5(6)				
Leptocottus armatus	−15.4 ± 0.4(4)				
Limanda aspera	−16.6 ± 0.2(11)				
Liopsetta glacialis				−19.9 ± 0.2(2)	
Liparis spp.		−20.5		−19.5	
Lycodes sp.		−19.2			
Mallatus villosus				−20.7 ± 0.3(2)	
Myoxocephalus quadricornis	−14.8	−19.2 ± 0.3(7)		−19.8 ± 0.2(4)	
Paraliparis deani	−18.1				
Platichthys stellatus	−16.1 ± 0.6(6)				

[a] *Natica* = *Cryptonatica*
[b] *Polinices* = *Lunatia*
[c] *Astarte* = *Iridontia*
[d] *Clinocardium* = *Ciliatocardium*
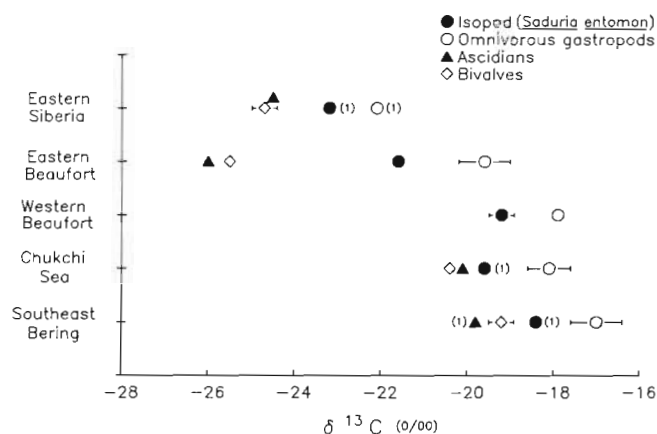
Fig. 4. δ¹³C values ($\bar{x} \pm$ SE, n $\geq$ 3 except where noted) for species common to Siberian and Alaskan coastal waters. Omnivorous gastropods include *Buccinum* and *Neptunea* spp. Compositions of remaining groups are listed in Table 1

tion to those from the Chukchi and southeast Bering Seas than to the same species in the geographically closer eastern Beaufort Sea. In contrast, East Siberian Sea species were noticeably depleted in ¹³C (Table 1; Fig. 4) compared to the same organisms from the western Beaufort, Chukchi and southeast Bering Seas. The δ¹³C values of eastern Siberian species most closely resembled those from the eastern Beaufort Sea (Fig. 4).

¹⁵N:¹⁴N ratios of fauna

Analysis of nitrogen stable isotope ratios showed general trends of increasing δ¹⁵N with trophic level but failed to show large or distinct geographic differences except for zooplankton (Table 2). The mean δ¹⁵N value of calanoid copepods from the eastern Beaufort Sea (9.4‰) was significantly lower (p < 0.05, t-test) than the mean value for copepods from the western Beaufort Sea (11.4‰). Chukchi and southeast Bering Sea copepods were also ¹⁵N enriched relative to Beaufort Sea copepods with δ¹⁵N values that averaged 11.2‰ for 3 samples (Table 2). δ¹⁵N data generally agreed with δ¹³C results on the relative trophic positions of organisms among the various food webs. The omnivorous gastropod *Buccinum* and benthic fishes were usually most enriched in ¹³C and ¹⁵N, while omnivorous demersal crustaceans displayed the least ¹³C and ¹⁵N enrichments (Fig. 5). The range in δ¹⁵N values was smallest in the Chukchi Sea (11.1 to 15.2‰), highest in the eastern Beaufort Sea (9.4 to 15.2‰), and intermediate in the southeast Bering Sea (11.2 to 16.2‰).

DISCUSSION

Geographic trends in carbon isotope ratios

These results confirm the presence of the longitudinal gradient in zooplankton ¹³C:¹²C ratios reported by Dunton (1985) across the Alaskan Beaufort Sea, and the ¹³C depletion of eastern Beaufort Sea zooplankton relative to zooplankton from the Chukchi or Bering Sea (Saupe et al. in press). This geographic difference is most pronounced at lower trophic levels among sessile perennial benthic suspension feeders which directly consume phytoplankton or small zooplankters. The mean δ¹³C values of other feeding groups are also lowest in the eastern Beaufort Sea compared with the Chukchi or southeastern Bering Sea, but these differences are not as large. This may reflect trophic structure and energy transfer differences or indicate that another source of ¹³C enriched carbon is utilized by higher consumers, which is either not available or consumed by benthic suspension feeders.

Our isotopic measurements were primarily directed at benthic invertebrates, many of which are long-lived perennial species of restricted mobility. Our results
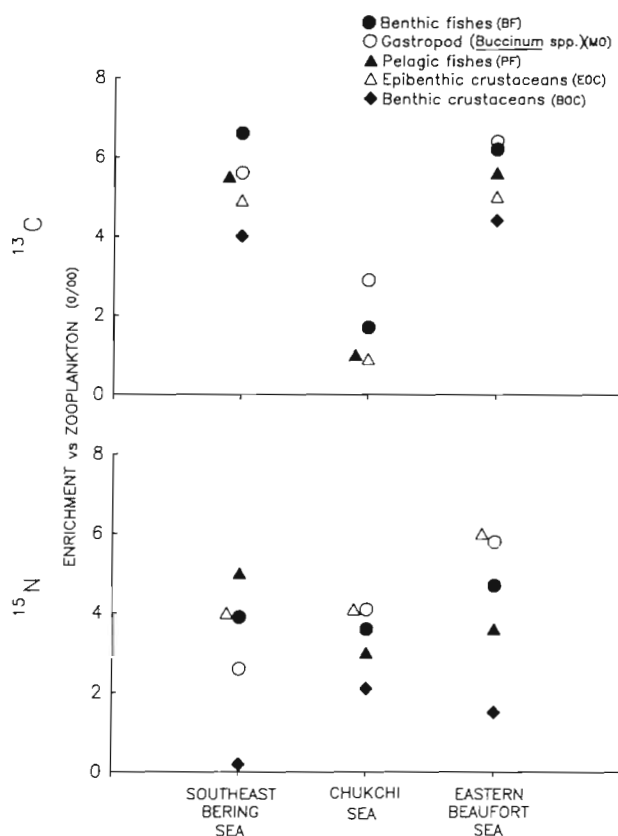

Fig. 5. Trophic ¹³C and ¹⁵N enrichments of secondary consumers versus zooplankton (*Calanus* spp.) from the southeast Bering, Chukchi and eastern Alaskan Beaufort Seas

Sea shelf, which include the intrusion of warm Bering Sea and Alaskan coastal water into the Beaufort Sea (Mountain 1974) and an upwelling in the eastern Beaufort Sea (Hufford 1974, Mountain 1974). Less is known about the East Siberian Sea where $\delta^{13}C$ values are similar to those of the eastern Beaufort.

Our data show that long-lived sessile benthic fauna of the same species can possess large isotopic differences within 2° latitude along a longitudinal gradient of only 300 km (western to eastern Beaufort Sea). Rau et al. (1982) analyzed 'arctic' zooplankton samples from the western Beaufort Sea to compare with antarctic species, and concluded that antarctic zooplankton had significantly more negative $\delta^{13}C$ values. Our results show that $\delta^{13}C$ values of calanoid copepods collected from the eastern Beaufort Sea range from −25 to −27‰, close to the range for unsorted zooplankton in south polar seas (Sackett et al. 1965, Eadie & Jeffrey 1973). Thus, the difference in the trends of plankton ^{13}C depletion with increasing latitude between both hemispheres may not be as significant as Rau et al. (1982) previously reported.

Geographic differences in food web structure

Carbon and nitrogen isotopic analyses revealed that trophic relationships among fauna were basically similar between the eastern Beaufort, Chukchi and Bering Seas. Isotope enrichment occurred with increasing trophic level, and there was general agreement in the

might be questioned on the basis that all samples were not collected in the same year and in the same season at all geographic locations. However, comparison of available carbon isotope data of species collected between seasons within the same year (southeast Bering Sea) or in same seasons between years (eastern Beaufort Sea) seldom revealed mean values that differed more than 1‰. Seasonal and annual differences were usually less than 0.4‰. Comparison of the $\delta^{13}C$ values of Bering Sea species analyzed in this study to the same species collected by McConnaughey & McRoy (1979) a decade earlier in the same region also revealed differences that averaged less than 1‰ in most cases. In addition, the food web relations described by McConnaughey & McRoy (1979) were nearly identical to those reported here; the most ^{13}C-enriched benthic invertebrates include predatory gastropods, the most ^{13}C-depleted, ascidians. Finally, the mean $\delta^{13}C$ values reported here are characterized by similar coefficients of variation as reported in other field studies of this type (Mills et al. 1984, Fry 1988).

The cause of the distinct geographical gradient in zooplankton and benthic fauna isotopic composition, which originates in the phytoplankton, is not understood. Mechanisms that may account for ^{13}C depletion in eastern Beaufort Sea phytoplankton have been discussed in relation to differential isotopic fractionation caused by temperature gradients and/or the variation in the isotopic composition of the inorganic carbon source (Dunton 1985). Both mechanisms are based on known oceanographic features of the Alaskan Beaufort

Table 2. $\delta^{15}N$ values (‰) of fauna collected at 4 locations in Alaskan coast. Values are $\bar{x} \pm SE$ (n) for n > 1

Organism	Bering Sea	Chukchi Sea	W. Beaufort Sea	E. Beaufort Sea
MOLLUSCA				
Gastropoda				
Buccinum spp.	13.8 ± 0.4(2)	15.2 ± 0.3(2)	17.1	15.2
ARTHROPODA				
Crustacea-Copepoda				
Calanus spp.	11.2 ± 0.6(2)	11.1	11.4 ± 0.1(6)	9.4 ± 0.3(6)
Crustacea-Malacostraca				
Isopoda				
Saduria entomon	10.1	14.4		10.9 ± 0.7(3)
Amphipoda				
Anonyx sarsi/nugax	16.9	15.2 ± 0.2(2)		15.4
Decapoda				
Crangon dalli	14.4 ± 0.4(2)			
Pagurus trigonocheirus	12.0 ± 0.2(2)	11.9	12.0	
VERTEBRATA				
Osteichthyes				
Boreogadus saida		14.1 ± 0.5(3)	12.6 ± 0.3(4)	13.0 ± 0.3(6)
Gadus macrocephalus	16.2 ± 1.3(3)			
Limanda aspera	15.0 ± 0.1(2)			
Liparis spp.		14.1		
Myoxocephalus quadricornis		15.0 ± 0.2(2)		14.1 ± 0.0(2)

Mar. Ecol. Prog. Ser. 56: 89–97, 1989

hierarchical order of the feeding groups as defined by both $\delta^{13}C$ and $\delta^{15}N$ data (Figs. 2 and 5). Because of the diversity and complexity of these systems, assigning trophic levels to various species is impractical, but it is apparent that omnivorous and predaceous gastropod invertebrates can occupy trophic levels equivalent to those possessed by demersal fishes. An analysis of food web structure in the southeast Bering Sea by McConnaughey & McRoy (1979) revealed a similar relationship in which predatory gastropods were the most ^{13}C-enriched invertebrate animals collected (including mammals and birds). Few offshore isotopic studies have included gastropods in food web analyses, and as a result, their role as one of the top benthic predators is often overlooked (Mills et al. 1984, Minagawa & Wada 1984).

Although the trophic relations among fauna from the different geographic areas were similar, the range of $\delta^{13}C$ values recorded in each system varied considerably. For example, the range in mean carbon isotope ratios among the 9 feeding groups (Fig. 2) was greatest in the eastern Beaufort (6‰), least in the Chukchi (2‰), and intermediate in the southeast Bering Sea (4‰). In addition, secondary consumers in the Chukchi Sea showed the least enrichment of ^{13}C relative to zooplankton, compared to Bering and Beaufort Sea fauna, which were nearly equal (Fig. 5).

These data suggest that Chukchi Sea benthic fauna are more closely coupled to primary production. There is some biological evidence to support this hypothesis. First, the northwestern Bering and Chukchi Seas are characterized by an extremely rich benthos (Grebmeier et al. 1988). This benthos is supported by primary production rates that average 250 to 300 g C m^{-2} yr^{-1} annually (Walsh et al. in press), compared to about half that for the southeast Bering Sea (Walsh & McRoy 1986, Walsh et al. in press), and 10 to 25 g C m^{-2} yr^{-1} for the Beaufort Sea (Alexander 1974, Horner 1984). Secondly, Coyle & Cooney (1988) found that the vast majority of spring carbon production in this area is ungrazed by zooplankton, presumably sinking directly to the seafloor. Grebmeier (1987) reported that nearly 70 % of the primary production produced in northern Bering and Chukchi Sea waters escapes pelagic consumption and falls to the seafloor, compared to 12 % for Alaskan coastal water which predominates in the southeast Bering Sea; the quality of the falling organic matter is also higher, as reflected in lower C/N ratios in Bering and Chukchi Sea sediments not overlain by Alaskan coastal water (Grebmeier et al. 1988).

The relative variations in $\delta^{15}N$ among fauna from the 3 geographic regions in this study were similar in direction as that noted for carbon. Although not as pronounced, the range in $\delta^{15}N$ values of secondary consumers varied from a high of about 6‰ in the eastern Beaufort Sea to a low of 4‰ in the Chukchi, with an intermediate value of 5‰ in the southeastern Bering Sea. No large differences were observed between the ^{15}N enrichment of consumers relative to zooplankton as in ^{13}C (Fig. 5), but this may reflect differing nitrogen fractionations during microbial transformations of available food. Generally, bacterial cells become enriched in ^{13}C relative to their substrate, but nitrogen assimilation by microflora can result in either ^{15}N depletion, ^{15}N enrichment, or no change, depending on the chemical nature of the substrate (Macko & Estep 1984). Thus, nitrogen isotopes may not be reliable food web tracers (or track ^{13}C enrichments) at *lower* trophic levels in detritus-based food webs.

Our results show the dual utility of stable carbon and nitrogen isotope ratios in food web studies. A knowledge of the feeding strategies of benthic and epibenthic fauna provides insight into understanding and interpreting isotopic variations in food webs, and the dynamic nature of trophic relationships among organisms. In this study, geographic gradients of the isotope ratios in benthic fauna indicate relative differences of benthic-pelagic coupling between food webs in different regions. These measurements also provide circumstantial evidence for transport of organic material from the northern Bering Sea to the Chukchi and western Beaufort Seas.

LITERATURE CITED

Alexander, V (1974). Primary productivity regimes of the nearshore Beaufort Sea, with reference to potential roles of ice biota. In: Reed, J. C., Sater, J. E. (eds.) The coast and shelf of the Beaufort Sea. Arct. Inst. N. Amer., Arlington, p. 609–632

Coyle, K. O., Cooney, R. T. (1988). Estimating carbon flux to pelagic grazers in the ice-edge zone of the eastern Bering Sea. Mar. Biol. 98: 299–306

Dunton, K. (1985). Zooplankton $^{13}C:^{12}C$ ratios in the Western Arctic Ocean: a longitudinal gradient. Ph.D. dissertation, Univ. Alaska, Fairbanks

Dunton, K., Schell, D. M. (1987). Dependence of consumers on macroalgal *(Laminaria solidungula)* carbon in an Arctic kelp community: $\delta^{13}C$ evidence. Mar. Biol. 93: 615–625

Eadie, B. J., Jeffrey, B. J. (1973). $\delta^{13}C$ analyses of oceanic particulate organic matter. Mar. Chem. 1: 199–209

Fry, B. (1988). Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. 33: 1027–1030

Grebmeier, J. M. (1987). The ecology of benthic carbon cycling in the northern Bering and Chukchi Seas. Ph.D. dissertation, Univ. Alaska, Fairbanks

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

Horner, R. (1984). Phytoplankton abundance, chlorophyll a, and primary productivity in the western Beaufort Sea. In: Barnes, P. W., Schell, D., Reimnitz, E. (eds.) The Alaskan Beaufort Sea: ecosystems and environments. Academic Press, Orlando, p. 295–310

Hufford, G. L. (1974). On apparent upwelling in the southern Beaufort Sea. J. geophys. Res. 79: 1305–1306

Macko, S. A., Estep, M. L. F. (1984). Microbial alteration of stable nitrogen and carbon isotopic compositions of organic matter. Org. Geochem. 6: 787–790

McConnaughey, T., McRoy, C. P. (1979). Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Mar. Biol. 53: 257–262

Mills, E. L., Pittman, K., Tan, F. C. (1984). Food-web structure on the Scotian Shelf, eastern Canada: a study using ^{13}C as a food-chain tracer. Rapp. P.-v. Réun. Cons. int. Explor Mer 183: 111–118

Minagawa, M., Wada, E. (1984). Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochim. Cosmochim. Acta 48: 1135–1140

Minagawa, M., Winter, D. A., Kaplan, I. R. (1984). Comparison of Kjeldahl and combustion methods for measurement of nitrogen isotope ratios in organic matter. Analyt. Chem. 56: 1859–1861

Mountain, D. G. (1974). Preliminary analysis of Beaufort shelf circulation in summer. In: Reed, J. C., Sater, J. E. (eds.) The coast and shelf of the Beaufort Sea. Arct. Inst. N. Amer., Arlington, p. 27–48

Rau, G. H., Sweeney, R. E., Kaplan, I. R. (1982). Plankton ^{13}C · ^{12}C ratio changes with latitude: differences between northern and southern oceans. Deep Sea Res. 29: 1035–1039

Sackett, W. M., Eckelmann, W. R., Bender, M. L., Be, A. W. H. (1965). Temperature dependence of carbon isotope composition in marine plankton and sediments. Science 148: 235–237

Saupe, S. M. (1989). Nutrient dynamics and carbon supply to the north Aleutian Shelf nearshore ecosystem. M.S. thesis, Univ. Alaska, Fairbanks

Saupe, S. M., Schell, D. M., Griffiths, W. (in press). δ^{13}C gradients in western arctic zooplankton. Mar. Biol.

Schell, D. M., Saupe, S. M., Haubenstock, N. (1989). Natural isotopic abundances in bowhead whale (Balaena mysticetus) baleen: markers of aging and habitat usage. In: Rundel, P. W. et al. (eds.) Stable isotopes in ecological research. Springer-Verlag, New York, p. 260–269

Schell, D. M., Saupe, S. M., Haubenstock, N. (in press). Bowhead whale (Balaena mysticetus) growth and feeding as estimated by δ^{13}C techniques. Mar. Biol.

Walsh, J. J., McRoy, C. P. (1986). Ecosystem analysis in the southeastern Bering Sea. Cont. Shelf Res. 5: 259–288

Walsh, J. J., and 20 co-authors (in press). Carbon and nitrogen cycling within the Bering/Chukchi Seas: source regions for organic matter affecting AOU demands of the Arctic Ocean. Prog. Oceanogr.