

Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis

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ABSTRACT: We used stable carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) isotope analysis to investigate linkages between sources of primary production and the pelagic and benthic components of the Northeast Water (NEW) Polynya off northeastern Greenland. Ice algae was enriched in ^{13}C (mean $\delta^{13}\text{C} = -18.6$ vs -27.9‰) and ^{15}N (mean $\delta^{15}\text{N} = 8.3$ vs 4.9‰) over particulate organic matter (POM) suggesting that the relative importance of these sources might be traced isotopically. Most grazing crustaceans and filter-feeding bivalves had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in the range of -21 to -23‰ and 7 to 9‰ , respectively, indicating a direct pathway from POM. Close benthic-pelagic coupling was also confirmed for other benthic organisms examined with the exception of the predatory or deposit feeding echinoderms *Ophioclin*, *Ophiacantha* and *Pontaster*. Compared with other Arctic and temperate marine food webs, stable-carbon isotope values for the NEW Polynya were depleted in ^{13}C . A $\delta^{15}\text{N}$ trophic model that incorporated taxon-specific isotopic fractionation factors indicated that the NEW Polynya consisted of 4.5 to 5 trophic levels. Stable-isotope analysis may be well suited to establishing the importance of polynyas as sites of high primary productivity and tight benthic-pelagic coupling relative to regions of more permanent ice cover.

KEY WORDS: Polynya · Stable isotopes · Carbon-13 · Nitrogen-15 · Ice algae · Primary production

INTRODUCTION

Marine benthic communities are generally dependent on primary production in the overlying water column for their energy. Consequently, the distribution and abundance of benthic organisms are often dependent on water column processes which affect the transfer of organic material between benthic and pelagic systems (Davis & Payne 1984, Fowler & Knauer 1986, Townsend & Cammen 1988). In general, pelagic-benthic coupling appears to be particularly tight in the Arctic (reviewed by Carey 1991 and Grebmeier &

Barry 1991) where it has been suggested that a greater portion of biogenic material may reach the bottom than at lower latitudes (Petersen & Curtis 1980). In the few studies of biogenic sedimentation in boreal and Arctic systems, a large portion (30 to 96%) of the carbon fixed annually fell ungrazed to the benthos (Atkinson & Wacasey 1987, Wassman 1991); this percentage is considerably higher than that reaching the benthos at lower latitudes (Smetacek 1980, Suess 1980, Forsskall et al. 1982, Davis & Payne 1984). For similar depth and substrate types, benthic biomass in the Arctic appears to be greater than at lower latitudes (Petersen & Curtis 1980, Rowe 1983), suggesting that a greater proportion of the primary productivity may be cycled through the benthos in the Arctic than in temperate or tropical regions.

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Oceanographic discontinuities can have a large effect on phytoplankton productivity, and therefore may affect benthic dynamics. As recurring mesoscale areas of open water within areas of pack ice, polynyas are one of the most conspicuous oceanographic features in polar regions and are important components of the Arctic ecosystem (Stirling 1980, Dunbar 1987, Massom 1988). These areas are also characterized by high levels of primary productivity (Baumann 1989). Benthic communities under polynyas may, therefore, be very different from communities under nearby ice covered areas (Ambrose & Renaud 1995).

Tracing sources of primary productivity supporting food webs is a difficult task, particularly in polar marine ecosystems where long-term sampling of food web components may often be impossible. Even where organic material in stomachs can be identified, several limitations of conventional dietary approaches can confound such analyses (Hyslop 1980). The value of measuring naturally occurring stable isotopes of carbon and nitrogen within marine food webs is based on the observation that these isotopes often undergo predictable step-wise enrichments between trophic levels (Rau 1982, Wada et al. 1987, Fry 1988). Compared to conventional dietary analyses which only provide a measure of ingested food, stable isotope analysis of food web structure has the advantage of providing time-integrated averages of assimilated foods and, thus, represents a complimentary method for delineating patterns of trophic structure and energy flow (Fry 1988, Owens 1988, Harrigan et al. 1989, Hobson & Welch 1992, Rau et al. 1992). Where 2 isotopically distinct sources of primary productivity are available to marine food webs, stable isotope analysis may also provide information on the relative importance of each source (reviewed by Fry & Sherr 1988) and the power of this approach is improved if several isotopes are measured simultaneously (Harrigan et al. 1989).

Studies of high latitude marine food webs suggest that stable carbon isotope analysis may be useful in elucidating the degree to which benthic consumers are coupled to pelagic primary production (McConnaughey & McRoy 1979, Dunton et al. 1989). Close coupling of consumers with pelagic primary productivity results in less ^{13}C enrichment in consumer tissues compared with these links in deposit feeders and detrital-based food webs. This distinction has been observed in a study of higher trophic level vertebrates relying on pelagic versus benthic prey (Hobson et al. 1994). In this study, we used stable isotope analysis to investigate trophic relationships within, and sources of primary productivity for, the marine food web of the Northeast Water (NEW) Polynya off northeastern Greenland. The purpose of our investigation was to use stable carbon isotope analysis to evaluate the

degree of coupling between pelagic primary production and the benthos. We hypothesized that significant inputs of carbon from bacterial or meiofaunal sources, or from ice algae, would result in greater ^{13}C enrichment of benthic organisms than that expected from direct phytoplankton input. We also used stable-nitrogen isotope analysis to delineate trophic relationships within the NEW Polynya in order to confirm individual species feeding patterns.

STUDY AREA AND METHODS

The NEW Polynya is largely a summer polynya centered off Nordostrundingen, northeast Greenland (Parkinson et al. 1987; Fig. 1A). The polynya varies in size and position among years but lies between 77° and 81° N latitude and 5° and 15° W longitude. At its maximal extent, the polynya is bound by the coast on the west, the shoreward edge of the south-flowing East Greenland Current on the east and ice on the south. The NEW Polynya is a consistent annual feature opening for the summer in April or May and closing in September. Throughout the winter, parts of the polynya may periodically open and close (Schneider & Budeus 1995).

The bathymetry and water circulation on this section of the Greenland shelf are complex (Fig. 1B). The polynya is often centered over 2 shallow banks. The southern and larger of the two, Belgica Bank, is bound on the north, south, and west by troughs with average water depths of 300 m and some depths exceeding 500 m (Fig. 1B). Most of the samples for isotopic analysis were collected from the northern bank or from the northern trough, areas which experience open water every summer and which are located well within the polynya. Circulation of surface water (<160 m deep) in the polynya is dominated by an anticyclonic gyre which encompasses the northern portion of Belgica Bank and the northern trough (Budeus & Schneider 1995, T. Hopkins pers. comm.). This is a recirculating system with little exchange to the north or east (T. Hopkins pers. comm., G. Budeus pers. comm.). A smaller cyclonic gyre exists over the northern bank (T. Hopkins pers. comm.). For these reasons, we considered our sample to be typical of the polynya and not to be influenced by organisms or materials from other areas.

All samples were collected during June and July 1993. Particulate organic matter (POM) was obtained at 2 locations within the polynya on 5 July by filtering up to 27 l of seawater through a 0.06 mm screen and then onto precombusted GFF glass-fiber filters and stored frozen. Ice algae was obtained on 30 June and 8 July from under-ice surfaces using a scoop. Zooplankton were sampled using vertical tows of a plankton net and were held in seawater overnight to allow

the evacuation of gut contents prior to isotopic analysis. Benthic infauna and epifauna, epibenthic predators, and fishes were collected using box cores, epibenthic sledges and Agassiz trawls. Tissues from birds and polar bears were collected opportunistically by other researchers studying these groups.

When possible, we used muscle tissue for isotopic analysis. However, for most small invertebrates, tissues were obtained by combining a suitable number of whole specimens. Muscle tissue was dissected from bivalves, fish, and seabirds. Whole blood samples from polar bears were analysed. All tissues were freeze-dried and powdered with mortar and pestle or analytical mill. Samples comprised of whole organisms were then treated with 2 N HCl to remove carbonates. Because organisms may vary in their concentrations of isotopically lighter lipids (Attwood & Peterson 1989, Monteiro et al. 1991, Sholto-Douglas et al. 1991), lipids were removed from all samples using a Soxhlet apparatus for 4 to 6 h with chloroform as a solvent.

Samples for $^{13}\text{C}/^{12}\text{C}$ analysis were loaded into Vycor tubes with CuO and silver foil, sealed under vacuum and then combusted at 850°C for 6 h. A similar approach was used for $^{15}\text{N}/^{14}\text{N}$ analysis but samples were also loaded with copper wire and CaO to absorb carbon dioxide and facilitate direct transfer of N_2 to the

mass spectrometer without cryogenic separation. Both CO_2 and N_2 gases were analysed using a VG OPTIMA isotope-ratio mass spectrometer at the National Hydrology Research Institute in Saskatoon, Saskatchewan, Canada. Stable-isotope ratios were expressed in δ notation as parts per thousand (‰) according to the following relationship:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Standards for ^{13}C and ^{15}N are PDB and atmospheric N_2 (AIR), respectively. Replicates using laboratory standards indicate analytical errors of ± 0.1 and 0.3‰ for carbon and nitrogen samples, respectively.

Based on the findings of Hobson & Welch (1992), we generally applied an ^{15}N trophic-enrichment factor of $+3.8\text{‰}$ to obtain trophic level estimates according to the relationship:

$$TL = (D - 4.9)/3.8 + 1$$

where D is the $\delta^{15}\text{N}$ value of the organism, 4.9 refers to the mean value of POM, and TL is the organism's trophic level (see Table 1). We also used this relationship to determine trophic level for polar bears even though we examined bear blood and not muscle. Since

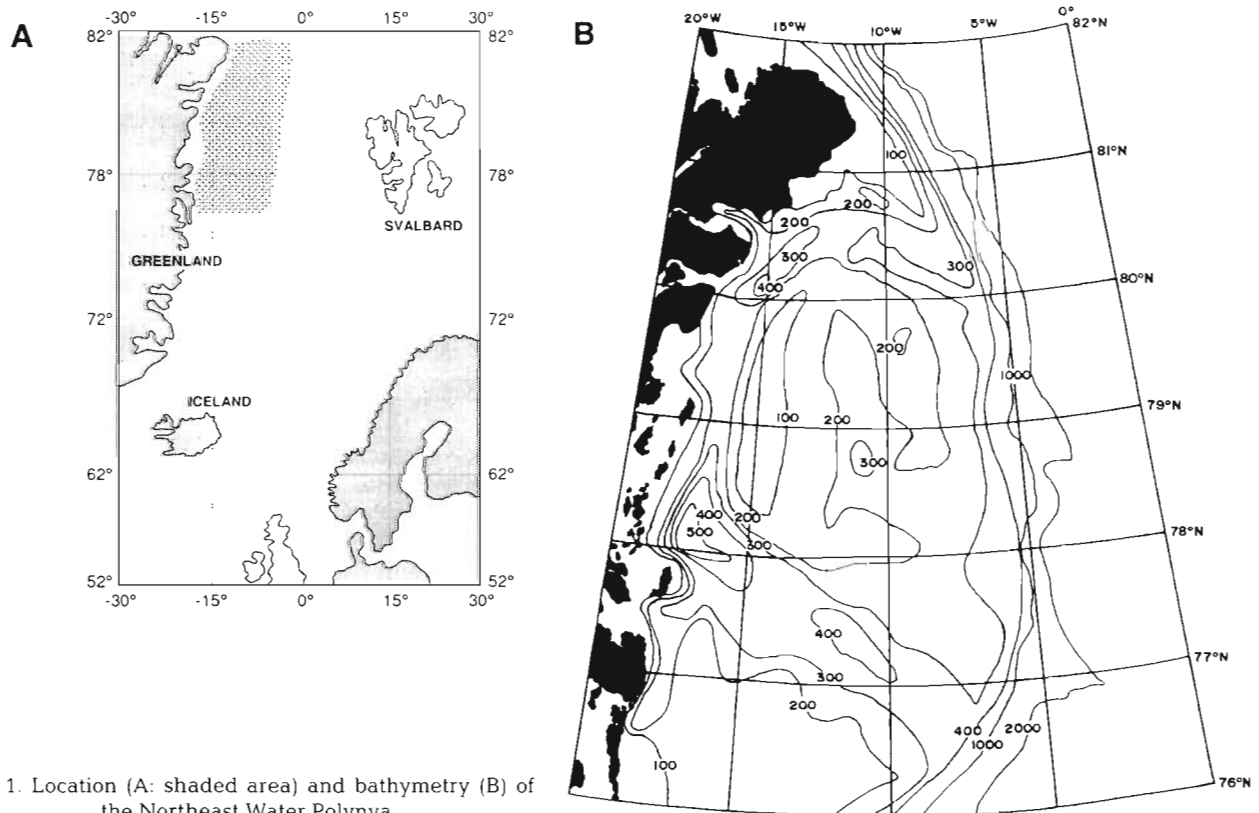


Fig. 1. Location (A: shaded area) and bathymetry (B) of the Northeast Water Polynya

Table 1 Location, depth, stable-carbon and nitrogen isotope values (mean \pm SD) and estimated trophic level for components of the NEW Polynya marine food web. TL: trophic level

Sample	N	Location	Sample depth (m)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TL (mean)
Algae						
POM	3	80° 27' N, 13° 40' W	6	-27.7 \pm 0.6	4.8 \pm 0.2	1.0
POM	2	80° 27' N, 13° 40' W	16	-28.4	5.0	
Ice algae	2	77° 10' N, 10° 28' W	Surface	-18.7	8.2	
Ice algae	1	79° 57' N, 15° 05' W	Surface	-18.4	8.4	
<i>Phycodryps</i> sp.	1 ^a	81° 00' N, 12° 54' W	48	-37.1	4.6	
Crustaceans						
<i>Calanus hyperboreus</i>	4 ^a	77° 10' N, 10° 29' W	0–200	-22.7 \pm 0.1	7.6 \pm 0.7	1.7
<i>Calanus gracilis</i>	1 ^a	79° 57' N, 15° 47' W	0–70	-22.3	8.2	1.9
<i>Themisto</i> sp.	1 ^a	80° 08' N, 15° 47' W	0–70	-24.2	10.4	2.5
<i>Gammarus wilkitzkii</i>	1 ^a	80° 06' N, 10° 10' W	0–70	-23.0	9.3	2.2
<i>Anonyx</i> sp.	1 ^a	80° 59' N, 10° 59' W	59	-26.3	8.3	1.9
<i>Arcturus</i> sp.	3 ^a	81° 00' N, 12° 54' W	48	-24.0 \pm 0.4	8.2 \pm 0.2	1.9
<i>Spirontocaris</i> sp.	1 ^a	81° 00' N, 12° 54' W	48	-21.1	10.3	2.4
<i>Sclerocrangon terox</i>	1 ^a	80° 01' N, 6° 43' W	310	-23.3	16.3	4.0
Bivalves						
<i>Arctinula groenlandica</i>	8	81° 13' N, 11° 31' W	45	-22.0 \pm 0.4	9.7 \pm 0.1	2.3
<i>Astarte crenata</i>	5	80° 06' N, 10° 42' W	194	-21.3 \pm 0.2	11.9 \pm 0.1	2.8
Gastropod						
<i>Clione</i> sp.	5	79° 57' N, 15° 47' W	0–70	-20.2 \pm 0.6	9.8 \pm 0.3	2.3
Echinoderms						
<i>Ophiopleura borealis</i>	8	80° 01' N, 6° 43' W	310	-21.1 \pm 0.6	11.8 \pm 0.6	2.8
<i>Ophioctin sericeum</i>	33	80° 01' N, 6° 43' W	310	-18.5 \pm 1.1	11.7 \pm 0.2	2.8
<i>Ophiacantha bidentata</i>	3	80° 59' N, 10° 59' W	59	-18.0 \pm 0.5	12.9 \pm 0.1	3.1
<i>Ophioscolex glacialis</i>	6	80° 01' N, 6° 43' W	310	-22.3 \pm 0.5	11.7 \pm 0.5	2.8
<i>Ophiura sarsia</i>	2 ^a	79° 53' N, 10° 56' W	169	-22.0	11.9	2.8
<i>Pontaster tenuispinus</i>	5	79° 55' N, 15° 00' W	165	-19.4 \pm 2.2	13.2 \pm 0.5	3.2
<i>Heliometra glacialis</i>	7	79° 55' N, 15° 00' W	165	-22.3 \pm 0.6	12.3 \pm 0.5	3.0
Polychaetes						
<i>Nephtys</i> sp.	5	80° 29' N, 13° 30' W	279	-20.8 \pm 0.3	12.8 \pm 0.4	3.1
Maldanidae	4	77° 10' N, 10° 29' W	482	-21.7 \pm 0.4	12.5 \pm 0.4	3.0
Pisces						
<i>Arctediceilus europeus</i>	3	80° 29' N, 13° 30' W	279	-20.1 \pm 0.5	14.4 \pm 0.4	3.5
	2	80° 01' N, 6° 43' W	310	-19.7	15.6	3.8
<i>Boreogadus saida</i>	1	80° 40' N, 13° 13' W	220	-22.4	13.5	3.3
	1	80° 59' N, 11° 34' W	99	-21.6	13.7	3.3
	1	80° 35' N, 9° 21' W	264	-21.7	12.9	3.1
<i>Icelus bicornis</i>	5	80° 39' N, 11° 34' W	99	-21.0 \pm 0.2	13.7 \pm 0.4	3.3
<i>Liparis koefoedi</i>	7	80° 59' N, 10° 59' W	59	-20.5 \pm 0.3	12.8 \pm 0.6	3.1
<i>Lycodes rossi</i>	3	80° 01' N, 6° 43' W	310	-20.5 \pm 0.3	15.3 \pm 0.6	3.7
<i>Micromesistius poutassou</i>	3	80° 29' N, 13° 30' W	279	-21.3 \pm 0.2	13.1 \pm 0.4	3.2
	3	80° 01' N, 6° 43' W	310	-21.4	12.7	3.1
<i>Sebastes marinus</i>	1	80° 01' N, 6° 43' W	310	-21.4	14.5	3.5
<i>Triglops nybelini</i>	5	ND	ND	-20.5 \pm 0.5	13.6 \pm 0.2	3.3
Birds						
<i>Larus hyperboreus</i>	1	80° 38' N, 13° 43' W		-18.3	14.7	4.0
<i>Somateria mollissima</i>	5	80° 38' N, 13° 43' W		-18.4 \pm 0.4	12.3 \pm 0.3	3.3
<i>Somateria spectabilis</i>	5	80° 38' N, 13° 43' W		-19.2 \pm 0.1	12.8 \pm 0.3	3.5
Mammals						
<i>Ursus maritimus</i>	5	^b		-19.4 \pm 0.7	18.6 \pm 0.8	4.6

^aCombined sample of several individuals (see 'Methods')

^bLocations of polar bear captures ranged from 79° 07' to 80° 44' N and 10° 57' to 19° 20' W

captive-rearing studies on birds suggest a diet-tissue isotopic fractionation factor of +2.4‰ is appropriate for these taxa (Hobson & Clark 1992), we used this value and the relationships $TL_{\text{bird}} = TL_{\text{prey}} + 1$ and $D_{\text{prey}} = D_{\text{bird}} - 2.4$ in order to modify the above equation to:

$$TL_{\text{bird}} = (D_{\text{bird}} - 7.3)/3.8 + 2$$

RESULTS

Our isotopic analyses revealed a considerable range in both ^{13}C and ^{15}N values for food web components of the NEW Polynya (Table 1). Average stable carbon isotope ratios ranged from -37.1‰ for the macroalgae *Phycodryx* through -18.0‰ for the echinoderm *Ophiacantha*. Ice algae was enriched considerably in ^{13}C over POM indicating that stable carbon isotope analysis may be used to discern the relative contributions of these sources of primary production. Considerable overlap in ^{13}C values throughout the food web was apparent with no clear pattern of trophic enrichment after the second trophic level (Fig. 2). Some organisms, particularly the bivalve *Astarte crenata*, and the echinoderms *Ophioclin*, *Ophiacantha* and *Pontaster* were notably enriched in ^{13}C compared to conphyletics.

The mean POM $\delta^{13}\text{C}$ value of -27.9‰ was considerably lower than values recorded for other regions of the Arctic. In order to determine if this low $\delta^{13}\text{C}$ value for primary productivity in the NEW Polynya was transferred characteristically throughout the food web, we contrasted our data with patterns of $\delta^{13}\text{C}$ distribution in other published studies of high latitude (western Bering Sea: McConnaughey & McRoy 1979, Chukchi Sea: Dunton et al. 1989, Lancaster Sound: Hobson & Welch 1992) or cold-temperate (Scotia Sea: Mills et al. 1984, Georges Bank: Fry 1988) marine systems (Fig. 3). We classified organisms primarily into pelagic versus benthic categories, and secondarily into the general feeding categories of POM grazers, planktivorous fish, benthic filter feeders and benthic omnivores. Throughout these components of the food web, organisms from the NEW Polynya were consistently less enriched in ^{13}C compared to the other areas (Fig. 3). Within the pelagic zone, all studies showed a strong positive shift in $\delta^{13}\text{C}$ between POM and POM grazers generally followed by a smaller enrichment to planktivorous fish. Within the benthos, omnivores were generally enriched over filter feeders. In the 5 cases where POM grazers could be compared to benthic filter feeders within the same system, the NEW Polynya and Lancaster Sound studies showed little difference in mean $\delta^{13}\text{C}$ values whereas the Scotia shelf, Georges Bank, and western Bering Sea studies showed higher ^{13}C enrichment between these feeding groups (Fig. 3).

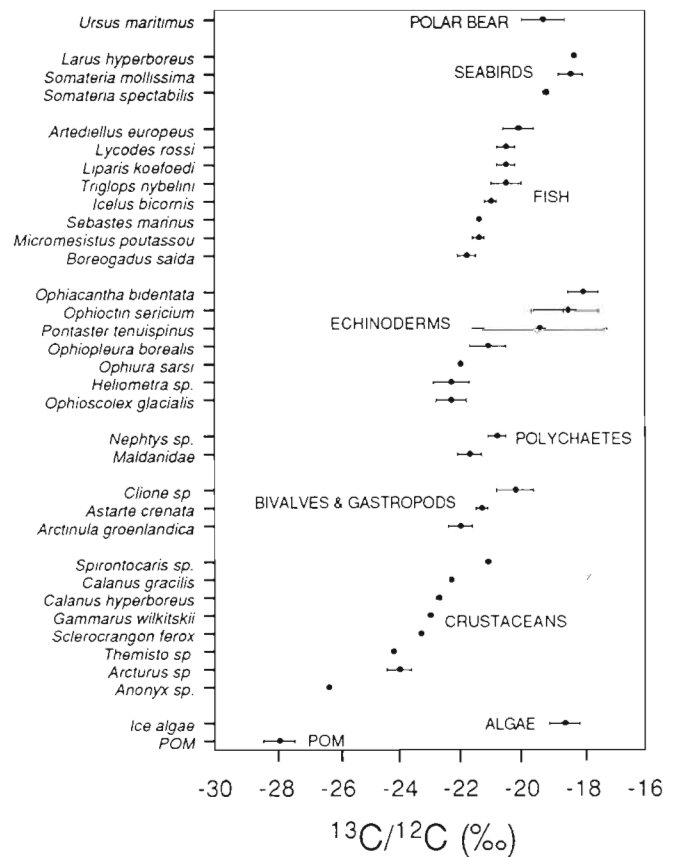


Fig. 2. Distribution of stable-carbon isotope ratios (mean \pm SD) among food web components of the Northeast Water Polynya

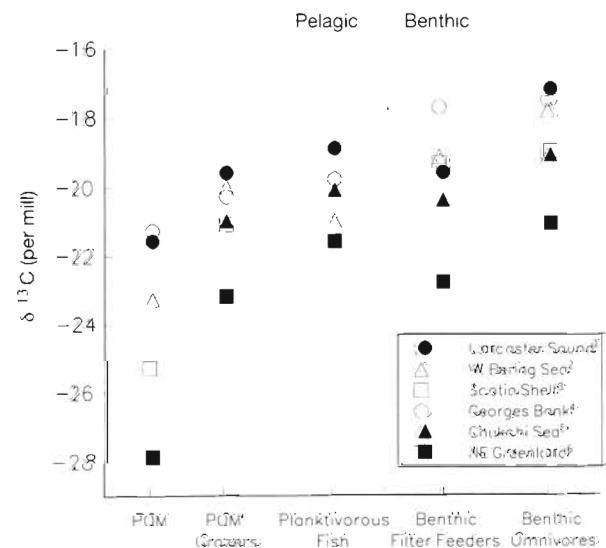


Fig. 3. Average $\delta^{13}\text{C}$ values for selected food web components reported in this study and other Arctic and temperate isotopic investigations. References for data: ¹Hobson & Welch (1992), ²McConnaughey & McRoy (1979), ³Mills et al. (1984), ⁴Fry (1988), ⁵Dunton et al. (1989), ⁶this study

Within species, ^{15}N values were generally less variable than ^{13}C and a step-wise increase with trophic level ranged from an average of 4.9‰ for POM through 18.6‰ for polar bear blood (Table 1, Fig. 4) suggesting a food web consisting of approximately 5 trophic levels. Stable-nitrogen isotope values for POM were similar to those found at other arctic locations (reviewed by Hobson & Welch 1992) and were considerably less enriched than ice algae. This indicates that $\delta^{15}\text{N}$ measurements might also be used to delineate relative inputs of ice algae and POM to the benthos.

DISCUSSION

Benthic-pelagic coupling

Our isotopic investigations of the NEW Polynya support the hypothesis that a major component of the benthic community was supported primarily by ungrazed POM reaching the benthos. Carbon evidence for this is the similarity in $\delta^{13}\text{C}$ values between pelagic POM-based feeders (e.g. *Calanus* spp., *Themisto* sp.) and benthic filter feeders (*Arctinula groenlandica*, *Helio-*

metra sp.); (Table 1, Fig. 3). Similar results have been found in isotopic investigations of marine food webs in Lancaster Sound (Hobson & Welch 1992), the west Bering Sea (McConnaughey & McRoy 1979), and the eastern Chukchi Sea (Grebmeier et al. 1988, Dunton et al. 1989; Fig. 3). Benthic organisms in systems exhibiting weaker benthic-pelagic coupling would be expected to be substantially enriched in ^{13}C relative to both POM and POM grazers. Stable-carbon isotope values of the bottom nepheloid layer of the sediments sampled in midsummer were primarily in the range of -24 to -23‰ (H. Notholt pers. comm.) and this again reflects the presence of ungrazed POM reaching the benthos.

We observed greater enrichment in ^{13}C between POM and POM grazers than between higher trophic levels, a pattern common to other high latitude marine food webs (Fig. 3). It is not clear why this pattern exists. One possibility may be the presence of a strong microbial loop in which fixed carbon is first cycled through flagellates and microzooplankton before being consumed by zooplankton.

In our study, POM and ice algae were the only possible sources of significant primary production in the NEW Polynya. The red alga *Phycodryis*, while having a distinct and highly negative $\delta^{13}\text{C}$ value (Table 1), likely contributed little carbon to the food web because it is restricted to shallow (<50 m) water and many of the animals in this study were collected considerable distances from shallow banktops. The difference in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between POM and ice algae (Table 1) permitted further insight into the relative input of these sources to the food web. While it is possible that ice algae contributed to the 5‰ enrichment in ^{13}C we observed between POM and POM grazers, the contribution was minimal since most grazing crustaceans and filter-feeding bivalves had $\delta^{15}\text{N}$ values in the range of 7 to 9‰ (Table 1). This is consistent with direct feeding on POM and not the isotopically heavier ice algae. Stable-carbon isotope values for these organisms were typically in the range of -21 to -23‰, which is consistent with a general depletion of ^{13}C in food webs with latitude in the northern hemisphere (Fontugne & Duplessy 1981, Rau et al. 1982, 1989, Dunton & Schell 1987). Low $\delta^{13}\text{C}$ values were generally maintained through the food web, including fishes and benthic invertebrates, again confirming the importance of POM as a food source for the entire food web. The only notable exception to this pattern was some enrichment of ^{13}C observed in the benthic deposit-feeding echinoderms, *Ophioclin*, *Ophiacantha*, and *Pontaster* (Table 1). Stable carbon isotope analysis, therefore, provides a complimentary data set supporting the evidence of benthic-pelagic coupling emerging from studies of the NEW Polynya. Ambrose & Renaud

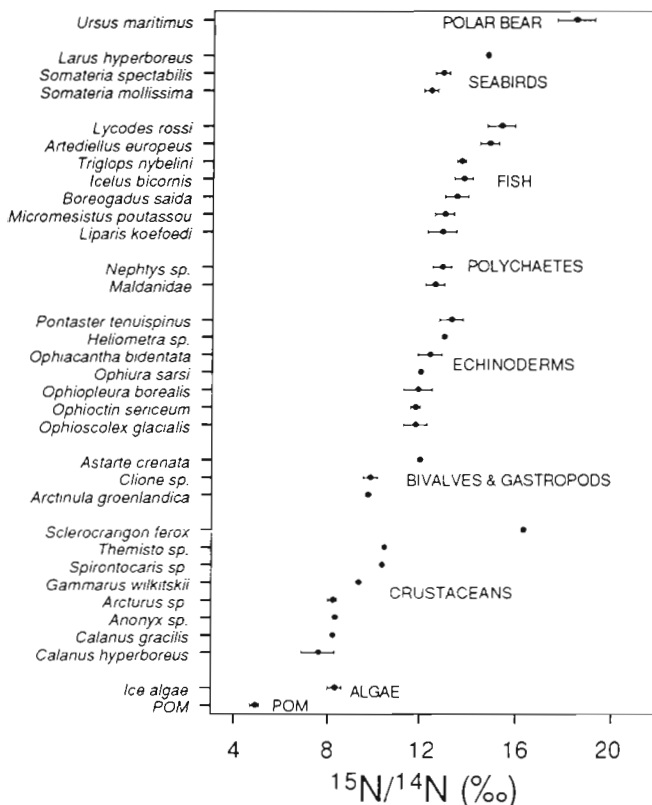


Fig. 4. Distribution of stable-nitrogen isotope ratios (mean \pm SD) among food web components of the Northeast Water Polynya

(1995) suggested that benthic and pelagic processes in the NEW Polynya are tightly linked based on strong correlations between sediment pigment concentrations and both water column pigment concentrations and benthic biomass. Additionally, low water column and sedimentary microbial activity (NEWATER 1993) and reduced zooplankton grazing (K. Daly pers. comm.) increases the likelihood that POM reaches benthic food webs relatively intact.

Mechanisms controlling $\delta^{13}\text{C}$ fractionation between inorganic substrates and marine algae are not well understood (Fry & Sherr 1988). However, isotope fractionation associated with carbon fixation may differ between POM and ice algae due to local differences in the availability of CO_2 for photosynthesis. The enriched ice-algal $\delta^{13}\text{C}$ values relative to those of POM might also be caused by a more general phenomenon: that isotopic discrimination in aquatic plants is related to the thickness of diffusive boundary layers that ultimately determine the rate of CO_2 or HCO_3^- diffusion (Smith & Walker 1980). Well-defined boundary layers such as those associated with littoral or epontic algae lead to an entrapment of otherwise normally expelled or discriminated ^{13}C . The subsequent enrichment in ^{13}C of carbon available for photosynthesis would thus result in higher $\delta^{13}\text{C}$ values of ice algae carbon (Keeley & Sandquist 1992, see also Simenstad et al. 1993). Algae occurring in pelagic or turbulent water conditions such as those associated with POM are expected to have reduced boundary layers and consequently decreased $\delta^{13}\text{C}$ values. In a recent review of the literature, France (1995) determined that in marine coastal areas, littoral algae may be enriched by up to 10‰ (mean 6‰) relative to pelagic algae. The boundary layer which develops over attached algae within the littoral zone may be a key factor determining the observed enrichment in ^{13}C of benthic organisms that was previously associated with bacterial or meiofaunal processes (McConnaughey & McRoy 1979, Dunton et al. 1989).

Trophic structure of the polynya

Our $\delta^{15}\text{N}$ trophic model for the NEW Polynya is in general agreement with our expectation of a 4 to 5 trophic level system in the high Arctic and demonstrates again the utility of the isotope approach to marine food web studies (Minagawa & Wada 1984, Fry 1988, Hobson & Welch 1992). Moreover, our model is among the first to apply more than one $\delta^{15}\text{N}$ trophic enrichment factor to various taxa within the food web based on evidence from captive-rearing studies (see also Hobson & Welch 1992, Hobson 1993). Undoubtedly, further refinements of this model will be appropriate as our understanding of processes resulting in

$\delta^{15}\text{N}$ trophic enrichment in marine food webs develops.

In general, the trophic positions predicted by $\delta^{15}\text{N}$ are in good agreement with literature on fish and invertebrate gut contents and feeding behaviour. Based on the assumption that POM was the first trophic level, our sample of crustaceans included primarily POM grazers (i.e. TL 2), with the notable exception of a single *Sclerocrangon ferox* that occupied TL 4 and likely consumed small crustaceans and bivalves. The pectinid bivalve *Arctinula* was primarily a filter feeder, whereas *Astarte* with its more enriched $\delta^{15}\text{N}$ value was more likely a deposit feeder. Echinoderms and polychaetes generally occupied the third trophic level (Table 1) and this is consistent with benthic deposit feeding (e.g. *Ophioclin*, *Pontaster*; Mortenson 1927, Warner 1982, Pearson & Gage 1984) or predator/scavenger (e.g. *Ophiacantha*; Warner 1982, Pearson & Gage 1984) foraging niches. Fish ranged over a trophic level from primarily planktivorous species such as *Liparis*, *Boreogadus* and *Micromesistus* (TL 3.1 to 3.3; Briskina 1939, Green 1983) through *Arcticellus* and *Lycodes* (TL 3.5 to 3.8), which are predatory on larger benthic invertebrates and fishes (Briskina 1939, Klekowski & Weslawski 1990, von Dorrien 1993). Trophic-level estimates for both common *Somateria mollissima* and king *S. spectabilis* eiders were similar and were about a trophic level above their assumed bivalve prey (Godfrey 1986). Gut contents of the same birds analyzed in this study were similar, consisting primarily of bivalves (J. M. Weslawski pers. comm.). The trophic level estimate for *Larus hyperboreus* (TL 4.0, Table 1) is consistent with published studies of their preference for fish, bird chicks, and carrion (Ainley & Sanger 1979, Stempniewicz & Weslawski 1992).

Trophic level estimates for polar bears near the NEW Polynya were slightly lower than those obtained from Lancaster Sound (Hobson & Welch 1992). This may be due to the fact that trophic level estimates for bears at the NEW Polynya site were based on $\delta^{15}\text{N}$ analyses of blood instead of muscle, and it is not known to what extent isotope fractionation values differ for various bear tissues. Bear tissue samples were also obtained in late spring at the NEW Polynya site versus in winter for the Lancaster Sound study. It is possible that seals taken by bears differed in their trophic level between these seasons and locations. Seals depend on invertebrates as well as fish; and young seals, in particular, may consume more invertebrates than older seals and so may occupy a lower trophic position (Bradstreet et al. 1986, Hobson & Welch 1992). Our data suggest that seals taken by bears off northeastern Greenland occupied an average trophic level of about 3.6.

For some organisms, direct comparisons could be made between trophic level estimates for the NEW Polynya and Lancaster Sound food webs (Hobson &

Welch 1992). Trophic relationships of species may vary regionally but reasonable agreement in *TL* estimates was obtained for the invertebrates *Calanus hyperboreus* (1.7 vs 2.0) and *Gammarus wilkitzkii* (2.2 vs 2.6), for the fish *Boreogadus saida* (3.1 to 3.3 vs 3.6) and *Icelus bicornis* (3.3 vs 3.4), and for the birds *Somateria mollissima* (3.6 vs 3.4, Hobson 1993) and *Larus hyperboreus* (4.2 vs 4.4).

Further applications of stable-isotope analysis in polynya studies

In this study, we have shown that stable isotope analyses can be used to assess the linkage between the water column and benthic processes. There is a distinct difference in patterns of isotope enrichment between tightly coupled systems and those where microbial or meiofaunal pathways or benthic algae are more important, such as in Georges Bank (Fig. 3 and references within). Complementary studies documenting additional evidence for tight coupling linkages in the NEW Polynya (e.g. Ambrose & Renaud 1995) strengthen our findings. It is likely, therefore, that stable isotope techniques can be used to address questions of benthic-pelagic coupling in other systems and to make predictions on the relative importance of remineralization and detrital pathways in carbon cycling.

There is some disagreement in the literature regarding the importance of ice algae as a food source for the benthos (see Alexander & Chapman 1981, Carey 1987). While we do not dispute that for some period during the year it may constitute a large portion of the available carbon at the sea floor, ice algae does not appear to make a substantial contribution to the integrated diets of benthic organisms in the NEW Polynya. Studies are needed, however, to compare carbon sources for benthic organisms underlying permanent versus seasonal ice cover. Using stable isotope analysis to discern between 2 potential carbon sources is not new in ecology (see papers in Lajtha & Michener 1994), but the possibility that it may help resolve the fate and role of ice algae is a novel application of this technique.

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