



PERGAMON

Deep-Sea Research II 49 (2002) 5131–5150

DEEP-SEA RESEARCH  
PART II

www.elsevier.com/locate/dsr2

# A stable isotope ( $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$ ) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants

Keith A. Hobson<sup>a,\*</sup>, Aaron Fisk<sup>b</sup>, Nina Karnovsky<sup>c</sup>, Meike Holst<sup>d</sup>,  
Jean-Marc Gagnon<sup>e</sup>, Martin Fortier<sup>f</sup>

<sup>a</sup> *Prairie and Northern Wildlife Research Center, Canadian Wildlife Service, Saskatoon, SK, Canada, S7N 0X4*

<sup>b</sup> *Chemistry Department, Carleton University, Ottawa, ON, Canada, K1S 5B6*

<sup>c</sup> *Department of Ecology and Evolutionary Biology, University of California at Irvine, Irvine, CA 92697-2525, USA*

<sup>d</sup> *Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada, T6G 2E9*

<sup>e</sup> *Canadian Museum of Nature, P.O. Box 3443 STN "D", Ottawa, ON, Canada, K1P 6P4*

<sup>f</sup> *GIROQ, Département de Biologie, Université Laval, Québec, QC, Canada, G1K 7P4*

Received 27 September 2000; received in revised form 6 April 2001; accepted 7 November 2001

## Abstract

The North Water Polynya is an area of high biological activity that supports large numbers of higher trophic-level organisms such as seabirds and marine mammals. An overall objective of the Upper Trophic-Level Group of the International North Water Polynya Study (NOW) was to evaluate carbon and contaminant flux through these high trophic-level (TL) consumers. Crucial to an evaluation of the role of such consumers, however, was the establishment of primary trophic linkages within the North Water food web. We used  $\delta^{15}\text{N}$  values of food web components from particulate organic matter (POM) through polar bears (*Ursus maritimus*) to create a trophic-level model based on the assumptions that *Calanus hyperboreus* occupies TL 2.0 and there is a 2.4‰ trophic enrichment in  $^{15}\text{N}$  between birds and their diets, and a 3.8‰ trophic enrichment for all other components. This model placed the planktivorous dovekie (*Alle alle*) at TL 3.3, ringed seal (*Phoca hispida*) at TL 4.5, and polar bear at TL 5.5. The copepods *C. hyperboreus*, *Chiridius glacialis* and *Euchaeta glacialis* formed a trophic continuum (TL 2.0–3.0) from primary herbivore through omnivore to primary carnivore. Invertebrates were generally sorted according to planktonic, benthic and epibenthic feeding groups. Seabirds formed three trophic groups, with dovekie occupying the lowest, black-legged kittiwake (*Rissa tridactyla*), northern fulmar (*Fulmarus glacialis*), thick-billed murre (*Uria aalge*), and ivory gull (*Pagophila eburnea*) intermediate (TL 3.9–4.0), and glaucous gull (*Larus hyperboreus*) the highest (TL 4.6) trophic positions. Among marine mammals, walrus (*Odobenus rosmarus*) occupied the lowest (TL 3.2) and bearded seal (*Erignathus barbatus*), ringed seal, beluga whale (*Delphinapterus leucas*), and narwhal (*Monodon monoceros*) intermediate positions (TL 4.1–4.6). In addition to arctic cod (*Boreogadus saida*), we suggest that lower trophic-level prey, in particular the amphipod *Themisto libellula*, contribute fundamentally in transferring energy and carbon flux to higher trophic-level seabirds and marine mammals. We measured PCB 153 among selected organisms to investigate the behavior of bioaccumulating contaminants within the food web. Our isotopic model confirmed the trophic magnification of PCB 153 in this high-Arctic food web due to a strong correlation between contaminant concentration and organism  $\delta^{15}\text{N}$  values, demonstrating the utility of combining isotopic and contaminant approaches to food-web studies. Stable-carbon isotope analysis confirmed an

\*Corresponding author. Tel.: +1-306-975-4102; fax: +1-306-975-4089.

E-mail addresses: keith.hobson@ec.gc.ca (K.A. Hobson).

enrichment in  $^{13}\text{C}$  between POM and ice algae ( $-22.3$  vs.  $-17.7\%$ ). Benthic organisms were generally enriched in  $^{13}\text{C}$  compared to pelagic species. We discuss individual species isotopic data and the general utility of our stable isotope model for defining carbon flux and contaminant flow through the North Water food web.

© 2002 Elsevier Science Ltd. All rights reserved.

## 1. Introduction

In contrast to the Northeast Water Polynya off eastern Greenland, the North Water of northern Baffin Bay is an area of immense biological activity, with high populations of seabirds and marine mammals (Stirling, 1980; Falk et al., 1997). Populations of dovekie (*Alle alle*), a small planktivorous seabird, alone are estimated to range from 14 to 30 million pairs (Salmonsén, 1981; Nettleship and Evans, 1985; Boertman and Mosbech, 1998). The polynya also is thought to support large numbers of beluga (*Delphinapterus leucas*), narwhal (*Monodon monoceros*), and seals (Finley and Renaud, 1980; Stirling, 1980; Stirling et al., 1981; Richard et al., 1998), and is used seasonally by the endangered eastern population of the bowhead whale (*Balaena mysticetus*; Holst and Stirling, 1999). Most of these animals are used by aboriginal peoples of both Canada and Greenland for food and so are also important from an economic and contaminants perspective (Muir et al., 1988; Braune, 1994). However, such populations of animals represent but the most conspicuous components of a highly productive marine food web consisting of at least five trophic levels (Hobson and Welch, 1992a). What role all components of the North Water food web play in energy or contaminant flux is currently unknown.

A fundamental requirement to understanding energy flow through complex marine food webs from primary carbon fixation through upper trophic-level consumers is knowledge of trophic linkages among organisms. Such knowledge is also key to modeling the flux of persistent contaminants that may bioaccumulate or biomagnify in marine food webs (Muir et al., 1995; Jarman et al., 1996, 1997; Atwell et al., 1998). An important objective of the International North Water Polynya Study (NOW) was to establish a trophic food web model in order to understand basic aspects of the ecology

of key groups of organisms and to provide a template to assist in the modeling of energy and contaminant flow. In the last decade, tracing sources of primary productivity to and relative trophic level of organisms in marine food webs has been advanced by the use of measurements of naturally occurring stable isotopes of elements such as carbon ( $^{13}\text{C}/^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) (Michener and Schell, 1994). This approach is based on the principle that the stable isotope ratios in consumer tissues can be related in a predictive way to those in their diet (DeNiro and Epstein, 1978, 1981). For carbon, there appears to be little (i.e. approx. 1‰) or no change in the relative abundance of  $^{13}\text{C}$  between trophic levels following the primary producer to primary consumer link (Hobson and Welch, 1992a), so that this isotope is useful as an indicator of sources of primary productivity in simple systems where two isotopically distinct sources are present (e.g., phytoplankton vs. ice algae) (Hobson et al., 1995). Stable-carbon isotope values are also relatively enriched in benthic or inshore food webs relative to pelagic food webs (Hobson and Welch, 1992a; Hobson et al., 1994; France, 1995a). For nitrogen, enrichment in  $^{15}\text{N}$  occurs with trophic level, an effect that appears to be relatively constant and typically 3–4‰ (Michener and Schell, 1994). Relative trophic position thus can be modeled using stable-nitrogen isotope measurements alone, an approach that recently has provided insights to the behavior of contaminants in marine food webs (Broman et al., 1992; Rolff et al., 1993; Atwell et al., 1998). The combined use of stable-carbon and stable-nitrogen isotope measurements of marine organisms, together with more conventional dietary approaches, can thus be used to provide important new information on trophic relationships and feeding ecology, including spatial use of habitat (Hobson and Welch, 1992a; Hobson et al., 1994; Michener and Schell, 1994; Kelly, 2000; Lawson and Hobson, 2000).

Following the isotopic research conducted in the Northeast Water Polynya (Hobson et al., 1995), this paper presents the results of an isotopic survey of the North Water food web, from particulate organic material (POM) through seals and seabirds. We intend this as a broad overview to provide a model of trophic relationships among key organisms. We used stable-carbon isotope measurements to interpret sources of primary productivity and stable-nitrogen isotope analysis to provide estimates of relative trophic position. We also address the utility of this information for the broader NOW objectives of modeling carbon flux and contaminant flow through the food web. Future papers will deal with various taxa in more detail, as well as more specific questions of spatial and temporal patterns in stable isotope signatures (e.g., Schell et al., 1998).

## 2. Methods

### 2.1. Field collections

Sampling of food web components was based primarily on collections made during the April–July 1998 NOW cruise onboard the CCGS *Pierre Radisson*. Samples of POM were obtained by filtering surface (<50 m) waters onto precombusted glass GFF filters and stored frozen. Ice-algae samples, obtained opportunistically during June from ice cores or from floating mats, were sieved through 0.1-mm screen to remove zooplankton and then frozen. Zooplankton samples were obtained primarily by towing a 4-m<sup>2</sup> zooplankton sampler from bottom to surface. The sampler consisted of four adjacent 1-m<sup>2</sup> frames supporting two 500- $\mu$ m and two 200- $\mu$ m mesh nets. Two small, 50- $\mu$ m mesh, 3-m long cylindrical nets with a 0.0075-m<sup>2</sup> aperture were also mounted on the sampler (Ringuette et al., 2002). Large macrozooplankton and young-of-the-year (YOY) fish larvae and juveniles were captured in double oblique hauls of a high filtering capacity two-net sampler (1 m<sup>2</sup> of 500- $\mu$ m mesh) in the surface layer (0–100 m). Subsamples of zooplankton were held in filtered seawater for 24 h to evacuate gut contents but, for logistical reasons, the majority of samples were sorted and frozen within 5 h after tows.

Samples of the benthic amphipod *A. nuxax* also were obtained using baited traps on the ocean floor at two stations. Traps contained squid or mackerel wrapped in nylon mesh to prevent the amphipods from feeding. Traps were deployed for 8–12 h. Benthic samples were obtained using box coring and crab traps. Crab traps were anchored to the ocean floor for 8–12 h and baited with squid or mackerel wrapped in nylon mesh.

Arctic cod (*Boreogadus saida*) adults were collected with hand-held nets when observed swimming near the surface in broken ice at one location. Thorny skates (*Raja radiata*) were captured by hook, baited with mackerel and squid, on long lines anchored to the ocean floor for 8–12 h. Fish were weighed and measured (fork length) and a subsample of muscle taken for isotopic analyses.

Seabirds were collected opportunistically by shotgun from a Zodiac inflatable motorboat launched from the *Pierre Radisson* at transect stations. Subsamples of muscle, liver, abdominal fat, bone and feathers were taken for stable isotope analysis. We used muscle tissues in this paper. Collections were made during the months of May, June, and July 1998. From 27 May to 28 June 1998, samples were collected by Inuit hunters from 99 ringed seals (*Phoca hispida*) taken near Grise Fiord, Nunavut, on the west side of the North Water (76°12 N, 83°06 W); between 9 May and 11 July 1998, 100 ringed seals were collected near Qaanaaq, Greenland, on the east side of the polynya (77°40 N, 69°00 W). Most seals were taken on landfast ice in near-shore areas. All tissue samples were frozen in the field. Beluga and narwhal samples were obtained from Inuit hunters from several western Greenland communities in 1997–1998 as part of a larger study organized by the National Environmental Research Institute in Denmark. Bowhead whale tissue was salvaged from three eastern Arctic animals as described in Hobson and Schell (1998). Stable isotope values for polar bears (*Ursus maritimus*) were based on those already reported by Hobson and Welch (1992a).

### 2.2. Stable isotope analysis

Prior to stable isotope analyses, all tissue samples were washed in distilled water and then

freeze-dried, powdered and treated with a 2:1 chloroform:methanol solution to remove lipids. Samples were then dried under a fume hood. Zooplankton, starfish, ice algae and POM samples were soaked in 0.1 N HCl to remove carbonates and allowed to dry without rinsing.

Stable-carbon and stable-nitrogen isotope assays were performed on 1-mg subsamples of homogenized materials by loading into tin cups and combusting at 1800°C in a Robo-Prep elemental analyzer. Resultant CO<sub>2</sub> and N<sub>2</sub> gases were then analyzed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer (CFIRMS) with every five unknowns separated by two laboratory standards. Stable isotope abundances were expressed in  $\delta$  notation as the deviation from standards in parts per thousand (‰) according to the following equation:

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

where  $X$  is <sup>13</sup>C or <sup>15</sup>N and  $R$  is the corresponding ratio <sup>13</sup>C/<sup>12</sup>C or <sup>15</sup>N/<sup>14</sup>N. The  $R_{\text{standard}}$  values were based on the PeeDee Belemnite (PDB) for <sup>13</sup>C and atmospheric N<sub>2</sub> (AIR) for <sup>15</sup>N. Replicate measurements of internal laboratory standards (albumen) indicate measurement errors of  $\pm 0.1\%$  and  $\pm 0.3\%$  for stable-carbon and stable-nitrogen isotope measurements, respectively.

### 2.3. PCB 153 analysis

Due to the need for larger sample size and the more labor-intensive nature of contaminant analysis, a smaller number of samples were analyzed for organochlorine contaminants. A total of 132 samples were analyzed, including six zooplankton species (numerous whole individuals per sample; *Calanus hyperboreus*,  $n = 20$ ; *Euchaeta glacialis*,  $n = 3$ ; *Metridia longa*,  $n = 3$ ; *Mysis oculata*,  $n = 7$ ; *Themisto libellula*,  $n = 4$ ; *Sagitta* sp.,  $n = 6$ ), one benthic amphipod (numerous whole individuals per sample; *A. nugax*,  $n = 4$ ), one fish species (muscle sub-sample of individual whole animals; *B. saida*,  $n = 8$ ), one marine mammal species (blubber; males only; *P. hispida*,  $n = 15$ ), and seven species of seabird (livers; *A. alle*,  $n = 7$ ; *Uria lomvia*,  $n = 9$ ; *Cephus grylle*,  $n = 9$ ; *Rissa tridactyla*,  $n = 10$ ; *Pagophila eburnea*,  $n = 5$ ; *Larus hyperboreus*,  $n =$

10; *Fulmaris glacialis*,  $n = 10$ ). Details about extraction and analysis methods can be found in Fisk et al. (2001).

### 2.4. Statistical analyses

Because our analysis was aimed at providing an overview of trophic relationships among food web components that encompassed as much natural variation as possible, we pooled samples among stations, collection periods, and sampling depths. We consider these effects on stable isotope values in consumer tissues elsewhere (Hobson et al., unpublished data). For the purposes of developing a robust isotopic model for the North Water, we considered the pooling approach to be optimal.

## 3. Results

### 3.1. <sup>15</sup>N trophic model

Mean stable-nitrogen isotope measurements varied considerably among taxa (5.1–21.1‰) and followed a general enrichment with trophic level (Table 1, Fig. 1). The most depleted  $\delta^{15}\text{N}$  values were measured for ice algae and POM, and the most enriched for seabirds and marine mammals. This difference allowed us to depict trophic level of several organisms relative to the calanoid copepod, *C. hyperboreus*, which we assumed occupied trophic level (TL) 2 (i.e. a primary herbivore). Assuming additionally that, other than for seabirds, isotopic enrichment was constant among trophic levels and of the order of 3.8‰ (Hobson and Welch, 1992a), we calculated the relative trophic level of consumers according to

$$\text{TL} = 2 + (\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{C.\text{hyperboreus}})/3.8.$$

Captive-rearing studies on birds suggest that the diet-tissue isotopic fractionation factor of +2.4‰ is appropriate for these taxa. Following the derivation outlined in Fisk et al. (2001) with a slightly modified  $\delta^{15}\text{N}$  value for *C. hyperboreus* based on larger sample sizes, our trophic-level calculation for birds becomes

$$\text{TL}_{\text{bird}} = 3 + (\delta^{15}\text{N}_{\text{bird}} - 10.3)/3.8.$$

Table 1

Stable-nitrogen and stable-carbon isotope values (mean  $\pm$  SE) of food-web components of the North Water and corresponding derived relative trophic level (TL). Habitat and feeding mode<sup>a</sup> are listed for invertebrates

Taxonomic group or species	<i>n</i> <sup>b</sup>	$\delta^{15}\text{N}$ (‰)	Derived TL	$\delta^{13}\text{C}$ (‰)
POM	38	6.8 $\pm$ 0.3		-22.3 $\pm$ 0.2
Ice algae	8	5.1 $\pm$ 0.3		-17.7 $\pm$ 0.2
<b>Invertebrates<sup>a</sup></b>				
Phylum Cnidaria				
Class Hydrozoa				
<i>A. digitale</i> (PL, PR)	10	9.0 $\pm$ 0.3	2.3	-20.5 $\pm$ 0.1
Class Anthozoa				
Order Actinaria (SES, PR)	3	13.1 $\pm$ 0.6	3.4	-18.3 $\pm$ 0.5
Phylum Ctenophora				
Class Tentaculata				
<i>Mertensia</i> sp. (PL, PR)	9	8.9 $\pm$ 0.5	2.3	-19.0 $\pm$ 0.5
Ctenophores (unidentified) (PL, PR)	2	9.7 $\pm$ 0.9	2.5	-21.6 $\pm$ 1.6
Phylum Mollusca				
Class Bivalvia				
<i>Astarte</i> sp. (EB, SPF)	3	9.1 $\pm$ 0.7	2.3	-16.7 $\pm$ 0.5
<i>Astarte elliptica</i> (EB, SPF)	1	8.5	2.2	-16.6
<i>Astarte montagui</i> (EB, SPF)	4	11.8 $\pm$ 0.2	3.0	-18.2 $\pm$ 0.4
<i>Macoma</i> sp. (EB, SPF)	3	7.1 $\pm$ 0.1	1.8	-17.6 $\pm$ 0.1
<i>Yoldia thraciaeformis</i> (EB, SPF)	4	7.9 $\pm$ 0.2	2.0	-17.8 $\pm$ 0.7
<i>Lepeta caeca</i> (SB, GR)	1	7.2	1.8	-19.4
Class Gastropoda				
<i>Clione</i> sp. (PL, PR)	37	9.6 $\pm$ 0.2	2.5	-22.4 $\pm$ 0.2
<i>Colus</i> sp. A (SB, SC-OM)	1	11.6	3.0	-16.3
<i>Colus</i> sp. B (SB, SC-OM)	1	12.7	3.3	-16.8
Phylum Annelida				
Class Polychaeta				
<i>Lumbrineris</i> sp. (EB-SB, PR-SC)	2	14.1 $\pm$ 0.5	3.6	-18.0 $\pm$ 0.7
<i>Phyllodoce mucosa</i> (EB-SB, PR-SC)	2	12.3 $\pm$ 0.4	3.2	-17.8 $\pm$ 0.5
Phylum Sipuncula				
<i>Phascolosoma eremeta</i> (EB-SB, DF)	2	12.3 $\pm$ 0.1	3.1	-16.8 $\pm$ 0.3
Phylum Arthropoda				
Subphylum Crustacea				
Class Maxillopoda				
Subclass Copepoda				
<i>Calanus glacialis</i> (PL, OM- SFF)	2	9.1 $\pm$ 0.4	2.3	-20.6 $\pm$ 0.8
<i>Calanus hyperboreus</i> (PL, SFF-FF?)	80	7.9 $\pm$ 0.1	2.0	-21.1 $\pm$ 0.1
<i>Chiridius</i> sp. (PL, PR)	2	10.3 $\pm$ 0.3	2.6	-20.5 $\pm$ 0.0
<i>E. glacialis</i> (PL, PR)	55	11.8 $\pm$ 0.1	3.0	-21.8 $\pm$ 0.1
<i>M. longa</i> (PL, PR-SFF?)	37	9.6 $\pm$ 0.1	2.5	-21.2 $\pm$ 0.1
Class Malacostraca				
Subclass Eumalacostraca				
<i>Acanthostephea</i> spp. (SPB-SB, PR)	3	10.4 $\pm$ 0.3	2.6	-17.9 $\pm$ 0.2
<i>A. nugax</i> (SPB-SB, SC)	11	13.2 $\pm$ 0.8	3.4	-18.5 $\pm$ 0.4
<i>Atylus carinatus</i> (SB-SPB, OM)	6	9.2 $\pm$ 0.2	2.3	-18.0 $\pm$ 0.2
Euphausiid (unidentified) (PL, FF)	1	11.4	2.9	-22.0
<i>M. oculata</i> (SPB-SB, DF-PR)	162	10.4 $\pm$ 0.1	2.7	-20.3 $\pm$ 0.1
<i>Onisimus</i> sp. (SB-SPB, SC-OM)	1	10.0	2.6	-18.8
<i>Pandalus</i> sp. (SPB-SB, DF-PR)	2	13.3 $\pm$ 0.5	3.4	-16.0 $\pm$ 0.2
<i>Themisto abyssorum</i> (PL, PR)	10	10.2 $\pm$ 0.4	2.6	-21.8 $\pm$ 0.2
<i>T. libellula</i> (PL, PR)	106	9.7 $\pm$ 0.1	2.5	-20.4 $\pm$ 0.1

Table 1 (continued)

Taxonomic group or species	<i>n</i> <sup>b</sup>	δ <sup>15</sup> N (‰)	Derived TL	δ <sup>13</sup> C (‰)
Phylum Chaetognatha				
<i>Sagitta</i> sp. (PL, PR)	76	10.4±0.1	2.7	-21.4±0.1
Phylum Echinodermata				
Class Crinoidea				
<i>H. glacialis</i> (SBS, SPF)	4	11.7±0.3	3.0	-18.1±0.6
Class Asteroidea				
<i>Ctenodiscus crispatus</i> (SB-EB, DF)	10	12.7±0.4	3.3	-15.1±0.5
Class Ophiuroidea				
<i>Gorgonocephalus arcticus</i> (SBS, SPF-DF)	7	12.2±0.3	3.1	-17.6±1.4
<i>Ophiophthalmus</i> sp. (SB, DF)	10	13.6±0.2	3.5	-10.2±0.4
<i>O. sarsi</i> (SB, DF-OM)	38	9.7±0.3	2.5	-11.3±0.5
Class Echinoida				
<i>Strongylocentrotus pallidus</i> (SB, DF-OM)	3	8.3±0.5	2.1	-15.7±1.6
Phylum Chordata				
Subphylum Tunicata				
Class Appendicularia				
<i>Oikopleura</i> sp. (PL, FF)	4	9.4±0.7	2.4	-22.5±0.8
Mixed zooplankton (1–2 mm)	13	8.5±0.1	2.2	-21.2±0.2
<b>Fish</b>				
<i>B. saida</i> (adult)	8	14.0±0.2	3.6	-19.3±0.1
<i>Boreogadus saida</i> (larvae)	3	10.7±0.8	2.7	-20.0±0.5
<i>Raja radiata</i>	3	14.8±0.2	3.8	-17.9±0.2
Liparid	2	10.6±1.0	2.7	-20.1±1.3
Lumpfish	2	13.7±0.01	3.5	-19.0±0.1
Wolffish (larvae)	1	13.1	3.4	-20.4
<b>Seabirds</b>				
<i>A. alle</i>	122	11.3±0.3	3.2	-18.7±0.2
<i>U. lomvia</i>	62	14.1±0.1	4.0	-19.9±0.04
<i>C. grylle</i>	30	13.7±0.2	3.9	-19.3±0.1
<i>R. tridactyla</i>	26	13.7±0.2	3.9	-19.3±0.1
<i>P. eburnea</i>	5	14.1±0.3	4.0	-19.3±0.1
<i>L. hyperboreus</i>	10	16.2±0.3	4.6	-18.8±0.3
<i>Fulmarus glacialis</i>	24	14.1±0.1	4.0	-19.6±0.1
<b>Marine mammals<sup>c</sup></b>				
<i>Odobenus rosmarus</i> *	6	12.5±0.3	3.2	-17.8±0.1
<i>Balaena mysticetus</i> *	3	13.2±0.7	3.4	-18.2±0.3
<i>Erignathus barbatus</i> *	5	16.8±0.1	4.3	-16.6±0.3
<i>P. hispida</i> (Thule)	100	17.0±0.1	4.4	-19.4±0.1
<i>P. hispida</i> (Grise Fiord)	97	17.5±0.2	4.6	-18.3±0.1
<i>D. leucas</i> (Baffin)	30	16.0±0.2	4.1	-17.7±0.2
<i>D. leucas</i> (Greenland)	40	16.9±0.2	4.4	-17.6±0.1
<i>M. monoceros</i> (Greenland)	89	16.0±0.1	4.1	-18.2±0.03
<i>Ursus maritimus</i> *	3	21.1±0.3	5.5	-18.0±0.3

<sup>a</sup>Habitat: PL, plankton; SPB, supra-benthic; SB, surface benthic; EB, endobenthic; SBS, surface benthic sessile. Feeding mode: FF, filter-feeder; SFF, selective filter-feeder; SPF, suspension-feeder; PR, predator; SC, scavenger; OM, omnivore; DF, detritus-feeder; GR, grazer.

<sup>b</sup>*n* refers to the number of grouped samples involving several individuals.

<sup>c</sup>Asterisk refers to those samples collected outside the North Water (see text).

Our model for the overall food web and that for seabirds provided a very reasonable assessment of organism TL with *C. hyperboreus* at TL 2, the

planktivorous dovekie at TL 3.3, arctic cod at TL 3.6, ringed seal at TL 4.5, and polar bear at TL 5.5 (Table 1). We depicted relative trophic level among

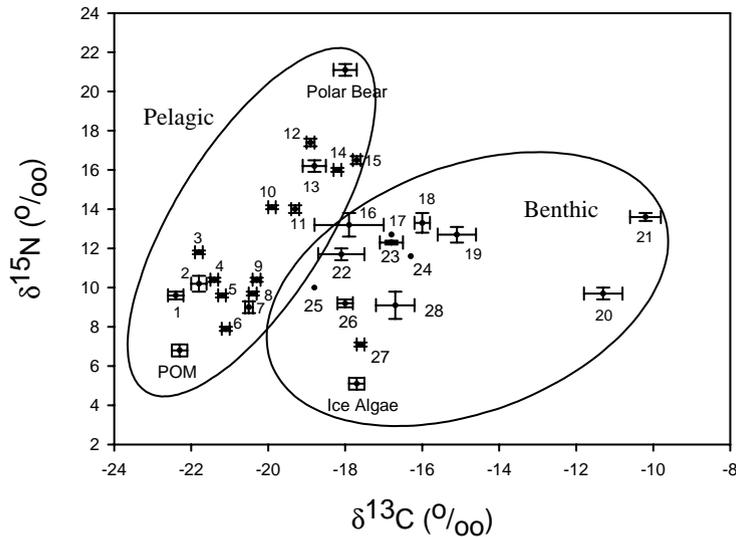


Fig. 1. Stable-carbon and stable-nitrogen isotope values (mean  $\pm$  SE) of pelagic and benthic components of the North Water food web. For clarity, not all samples measured are depicted. See Table 1 for values: 1, *Clione* sp.; 2, *Themisto abyssorum*; 3, *E. glacialis*; 4, *Sagitta* sp.; 5, *M. longa*; 6, *C. hyperboreus*; 7, *A. digitale*; 8, *T. libellula*; 9, *M. oculata*; 10, *U. lomvia*; 11, *B. saida*; 12, *P. hispida* (combined); 13, *L. hyperboreus*; 14, *M. monoceros*; 15, *D. leucas* (combined); 16, Polychaeta (combined); 17, *Colus* sp., B; 18, *Pandalus* sp.; 19, *Ctenodiscus crispatus*; 20, *O. sarsi*; 21, *Ophiophthalmus* sp.; 22, *H. glacialis*; 23, *Phascolosoma eremeta*; 24, *Colus* sp., A; 25, *Onisimus*; 26, *Atylus carinatus*; 27, *Macoma* sp.; and 28, *Astarte* sp.

seabirds (Fig. 2) and marine mammals (Fig. 3) and indicated the positions these consumers would occupy if their diet consisted entirely of *C. hyperboreus*, *T. libellula*, Arctic cod or, in the case of polar bears, ringed seals. Relative trophic level differed among seabirds (ANOVA  $F = 10.9$ ,  $df = 6273$ ,  $p < 0.001$ ), with three distinct groups apparent (Fig. 2). Glaucous gull (*L. hyperboreus*) had a higher trophic level than all other species (Tukey's Test,  $p < 0.05$ ). Among marine mammals, trophic position also differed among species and populations ( $F = 5.1$ ;  $df = 8, 308$ ;  $p < 0.05$ ), with polar bear occupying a higher trophic position than all other species ( $p < 0.05$ ).

### 3.2. Stable-carbon isotopes

Stable-carbon isotope values varied greatly among food web components (Table 1, range in means  $-22.5\%$  to  $-10.2\%$ ). As sources of primary productivity, POM and ice algae were distinct with POM more depleted in  $^{13}\text{C}$  ( $t = 17.95$ ,  $p < 0.001$ ). Benthic organisms such as mollusks and echinoderms were enriched in  $^{13}\text{C}$  compared with pelagic

organisms, resulting in two distinct isotopic groups (Fig. 1). Among pelagic species used in Fig. 1,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values were correlated ( $r^2 = 0.79$ ,  $p < 0.01$ ), indicating a trophic enrichment effect in  $^{13}\text{C}$ . No such relationship was clear among benthic species that showed a broad range in  $\delta^{13}\text{C}$  values.

Within taxonomic groups,  $\delta^{13}\text{C}$  values also showed considerable variation. Notably, among crustaceans, Pandalid shrimp were highly enriched in  $^{13}\text{C}$  ( $-16.0\%$ ). Echinoderms were generally enriched in  $^{13}\text{C}$ , but *Ophiophthalmus* and *Ophiura sarsi* were the two most enriched samples measured ( $-10.2\%$  and  $-11.3\%$ , respectively) and contrasted with the relatively lower  $\delta^{13}\text{C}$  values of *Gorgonocephalus arcticus* and *Heliometra glacialis* ( $-17.6\%$  and  $-18.1\%$ , respectively). Among fish, larvae were among the most depleted samples, and *Raja* spp. was notably enriched at  $-17.9\%$ . Seabirds showed variation in  $\delta^{13}\text{C}$  values (ANOVA  $F = 6.35$ ,  $df = 6, 272$ ,  $p < 0.001$ ) with both dovekie and glaucous gull, occupying the lowest and highest seabird trophic level, respectively, having more enriched values than other species (Tukey,  $p < 0.007$ ). Marine mammals were generally associated with the pelagic

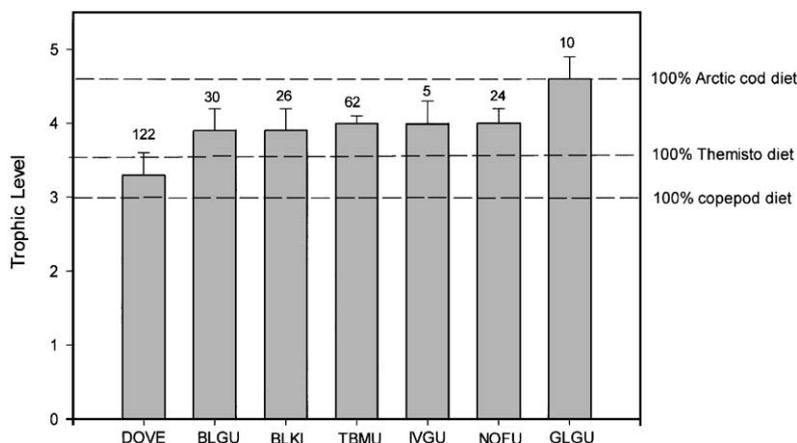


Fig. 2. Relative trophic positions of marine birds collected in the North Water, May–July 1998. Dashed lines indicate expected position of seabirds with exclusive diets of the prey types listed on the right: DOVE, dovekie; BLGU, black guillemot; BLKI, black-legged kittiwake; TBMU, thick-billed murre; IVGU, ivory gull; NOFU, Northern Fulmar; GLGU, glaucous gull.

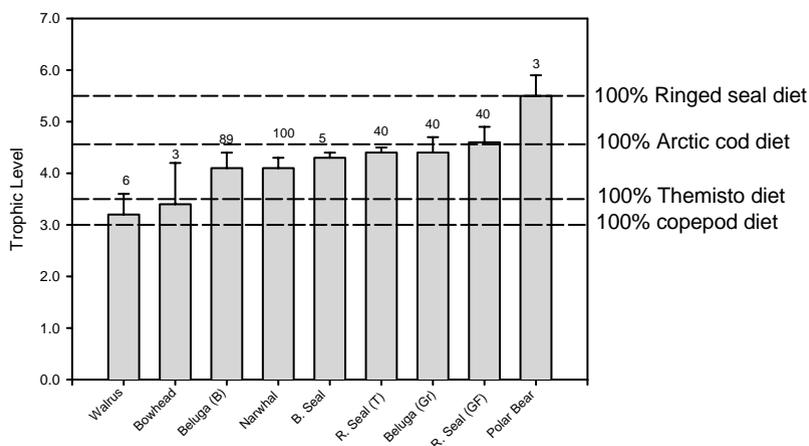


Fig. 3. Relative trophic positions of marine mammals collected in the North Water and adjacent regions as indicated in Table 1: T, Thule; GF, Grise Fiord; B, Baffin; Gr, Greenland.

isotope trajectory of Fig. 1, but bearded seal (*Erignathus barbatus*) was a notable exception with a mean  $\delta^{13}\text{C}$  value of  $-16.6\text{‰}$  indicative of a link to the benthic food web.

### 3.3. PCB 153– $\delta^{15}\text{N}$ relationships

PCB 153 was quantified in all samples. Recovery of internal standards ranged from 60% to 120%; all samples were corrected for percent recovery. Due to high variability in lipid content between sample

types, all concentrations were lipid-corrected prior to developing relationships with  $\delta^{15}\text{N}$  values. Only data for male ringed seals were used in  $\delta^{15}\text{N}$  relationships because the birth and feeding of young provides an additional mechanism to eliminate PCB 153 and other POPs in female *P. hispida* (Cameron et al., 1997). A positive linear relationship ( $r^2 = 0.65$ ,  $p < 0.001$ , linear regression,  $F\text{-value} = 241$ ,  $df = 1131$ ) was found between log of PCB 153 concentration and  $\delta^{15}\text{N}$  value (Fig. 4).

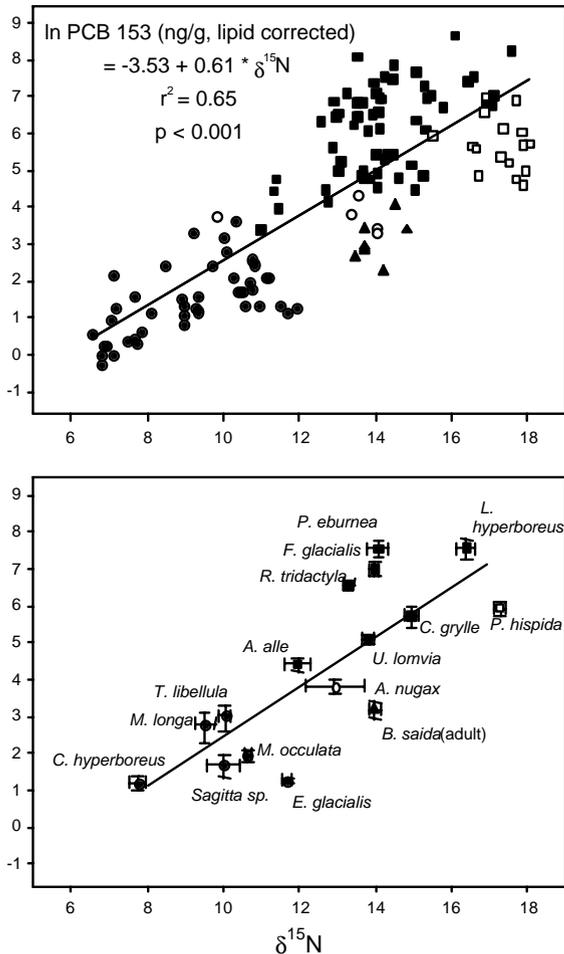


Fig. 4. Relationship between PCB 153 concentrations (lipid basis) and  $\delta^{15}\text{N}$  (‰) in the North Water food web: ●, pelagic zooplankton; ○, benthic amphipods; ▲, arctic cod; □, ringed seals; and ■, seabirds. The top graph contains all data points; the bottom, mean values for each species. Data for PCB 153 concentrations in *P. hispida* are for blubber; in seabird, for liver.  $\delta^{15}\text{N}$  in *P. hispida* and seabirds is muscle. Note that sample sizes are typically smaller than those used in Table 1; mean isotope values will not necessarily agree precisely.

## 4. Discussion

### 4.1. Patterns in $^{15}\text{N}$ and the trophic model

Our isotopic investigation of the North Water marine food web has revealed a general pattern of enrichment in  $^{15}\text{N}$  with trophic level. This pattern is similar to that found by Hobson and Welch (1992a)

for the adjacent Lancaster Sound region and also for the Northeast Water Polynya (Hobson et al., 1995), providing further evidence of the utility of this approach for trophic modeling in marine systems (Michener and Schell, 1994). We used a single trophic enrichment factor of 3.8 for nitrogen throughout the food web and also made the assumption that *C. hyperboreus* occupied TL 2. These are undoubtedly oversimplifications of what must be a more complex isotopic system, with trophic enrichment factors probably changing among groups of organisms (Michener and Schell, 1994). For interpretation of contaminant data, there is the additional complication of contaminant load and  $\delta^{15}\text{N}$  values representing different time periods. Nonetheless, such a model provided a remarkably convincing depiction of trophic relationships among and within taxa. The general placement of herbivorous copepods at TL 2, Arctic cod at TL 3.6, seals at TL 4.5, and polar bears at TL 5.5 indicates a reasonably robust model based on known diet.

### 4.2. Carbon-13 implications for tracing sources of primary productivity

Previous studies of high Arctic marine food webs have demonstrated that POM often may be less enriched in  $^{13}\text{C}$  compared with ice algae (Hobson and Welch, 1992a; Hobson et al., 1995), a result likely associated with a general phenomenon of differential diffusion of dissolved  $\text{CO}_2$  or  $\text{HCO}_3^-$  through boundary layers around plant cells (Smith and Walker, 1980; France, 1995a, b). We found a similar result for the North Water food web with POM averaging 4.6‰ lighter than ice algae. Potentially, such an isotopic difference could be used to trace relative contributions of these two sources of primary productivity to grazers and higher-level consumers. Seasonal enrichment or depletion of  $^{13}\text{C}$  in zooplankton may reflect inputs of ice algae and POM in diets, respectively. However, our analyses were conducted on bulk ice-algae samples; further research is required to determine if isotopic differences are maintained at the species level. Among other factors, carbon isotopic fractionation between inorganic substrates and algal cells is sensitive to cell size (Fry and Sherr,

1984; Goericke et al., 1994) and we expect  $\delta^{13}\text{C}$  values to differ among algal species.

Whether due to greater inputs of enriched ice algae vs. ungrazed POM to the benthos, to the general phenomenon of thicker boundary layers about plant cells influencing carbon fixation in slower moving waters (Hecky and Hesslein, 1995; France and Holmquist, 1997), or to factors related to bacterial or meiofaunal processes in the benthic substrate (McConnaughey and McRoy, 1979; Dunton et al., 1989), we found that benthic organisms were considerably enriched in  $^{13}\text{C}$  compared to pelagic species. This phenomenon appears to be widespread and has been documented in both marine and freshwater systems (France, 1995a, b). It provides a convenient tool to document pelagic vs. benthic feeding preferences in higher trophic-level organisms whose diets and area of foraging are poorly known (see below).

#### 4.3. Insights to individual species feeding ecology

*Invertebrates to fish.* Among the copepods sampled,  $\delta^{15}\text{N}$  values ranged from 7.9‰ (or TL 2.0) for the herbivorous copepod *C. hyperboreus* to 11.8‰ (or TL 3.0) for the carnivorous copepod *E. glacialis*. These two copepods thus provided us with a herbivory–carnivory scale on which to base our results. *C. hyperboreus* is believed to be a primary herbivore (Bradstreet and Cross, 1982), gorging on phytoplankton during the summer spring bloom when it accumulates lipid reserves for overwintering and enters diapause at depth in the fall, living on stored lipids. Although *Chiridius glacialis* is also considered an herbivorous species, its life cycle strategy differs markedly from that of the winter spawning *C. hyperboreus*. *C. glacialis* females feed on ice algae early in spring to fuel reproduction (Conover and Huntley, 1991; Tourangeau and Runge, 1991). Grazing on unpigmented microzooplankton has been suggested for the species in the Northeast Water Polynya (Hirche and Kwasniewski, 1997, see also Ohman and Runge, 1994). At TL 2.3, our results concur with the hypothesis of *C. glacialis* having an omnivorous diet dominated by herbivory.

The trophic ecology of *M. longa* is the least well known of all the dominant Arctic copepods.

*M. longa* can feed on phytoplankton but prefer animal prey (Conover et al., 1991). Its relatively high  $\delta^{15}\text{N}$  value (TL 2.5) supports an omnivorous diet dominated by carnivory.

*C. glacialis* and *E. glacialis* are both carnivorous predators. The lower TL value of *C. glacialis* compared to *E. glacialis* can be explained by its smaller size (cephalothorax length of 3 mm vs. 8 mm) and the smaller prey items it consumes. *E. glacialis* is the largest and most voracious copepod of the Arctic plankton. Copepods of the genus *Euchaeta* are known to feed on other large copepods (Øresland, 1995) and fish larvae (Yen, 1987). *E. glacialis* occupied the highest trophic level (TL 3.0) of all planktonic animals, surpassing Arctic cod larvae (TL 2.7) and the small planktivorous seabird *A. alle* (TL 2.9).

Stable-nitrogen isotope values for macrozooplanktonic animals ranged from 8.9‰ (or TL 2.3) for the medusae *A. digitale* to 13.2‰ (or TL 3.4) for the carrion-feeding lysianassid amphipod *A. nugax*. While the high trophic position of the copepod-eating arrow worm *Sagitta* sp. and larval Arctic cod are coherent with their known carnivorous diet (Drolet et al., 1991; Øresland, 1995; Michaud et al., 1996), other known carnivores have relatively low  $\delta^{15}\text{N}$  values. For example, the gelatinous predators *Aglantha digitale* and *Mertensia ovum* both feed on copepods in Arctic waters (Siferd and Conover, 1992; Pagès et al., 1996) and have relatively low inferred trophic levels (2.3) compared to other animals having similar diets. Unfortunately, few comparative isotopic data exist for arctic gelatinous predators and further study is required to investigate this apparent discrepancy.

As with most predators, the diet of carnivorous zooplankton such as the amphipods *T. libellula* and *Onisimus* sp. varies with size, including larger and more frequent animal prey as the animal grows (Grainger and Hsiao, 1990; Scott et al., 1999). For example, juvenile *T. libellula* feed on algal matter (Grainger and Hsiao, 1990) whereas copepods largely dominate the diet of adults (Wing, 1976; Fortier et al., 2001). The relatively low inferred TL signal of these amphipods compared to that of other predators of copepods such as *E. glacialis* (TL 3.0) likely reflects the dominance in the analysis of young omnivorous animals, which are more

vulnerable to capture by the plankton net than large carnivorous adults. Similarly, Arctic cod adults, which feed on large *Calanus* copepods and amphipods of the genus *Gammarus*, *Onisimus*, and *Themisto* (Bradstreet and Cross, 1982), showed enriched isotopic values (TL3.6) compared to larvae (TL 2.7) that prey on copepod nauplii and small copepodites (Drolet et al., 1991; Michaud et al., 1996).

The results reported here for copepods, Arctic cod and amphipods clearly indicate that important specific and/or ontogenetic differences in stable isotope values can be masked by pooling species and/or developmental stages in the analysis (e.g., as in Schell et al. 1998). Although time consuming, more detailed species- and stage-specific analyses of zooplankton are methodologically feasible as shown in the present study and could greatly improve our understanding of trophodynamics in the arctic marine food web.

We considered the results of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analyses in association with known or assumed habitat preferences and feeding mode of invertebrates. Consistent with pelagic habits, almost all planktonic species displayed the lowest  $\delta^{13}\text{C}$  values and were within the range of  $-20\%$  to  $-22\%$ . Benthic and epibenthic species were more enriched in  $^{13}\text{C}$ ; the two species of mobile brittlestars had the highest  $\delta^{13}\text{C}$  values recorded ( $-10.2\%$  and  $-11.3\%$ ). Benthic invertebrate species generally showed a higher range of  $\delta^{15}\text{N}$  values compared with pelagic species. Those species with a more endobenthic lifestyle tended to have either low (7.1–9.1%) or high (11.8–14.1%)  $\delta^{15}\text{N}$  values. Suprabenthic species, (those living in association with the sediment surface but venturing frequently in the water column) formed two groups, one with intermediate  $\delta^{15}\text{N}$  values of 9.2–10.4% and the other with high values (13.2–13.3%). Omnivores and detritivores tended to have the highest  $\delta^{13}\text{C}$  values and a wide range of  $\delta^{15}\text{N}$  values or trophic positions, whereas filter-feeders and nearly half the predators had lower  $\delta^{13}\text{C}$  values and more average  $\delta^{15}\text{N}$  values. Scavengers and the other half of the predators had average to high  $\delta^{15}\text{N}$  values. The extreme  $^{13}\text{C}$  enrichment seen in omnivores and detritivores likely reflects their use of cycled as well as ungrazed carbon available in the benthos. By

measuring both isotopes for benthic species we were able to delineate trophic and habitat effects and identify trophic clusters that suggest similar feeding patterns among taxa. Further research into evaluating relative sources of nutrient inputs to the benthos will need to consider the elemental turnover rates of carbon and nitrogen in benthic consumers in order to design an appropriate seasonal sampling design (e.g., Fry and Arnold, 1982).

#### 4.3.1. Seabirds

Seabirds in the North Water appear to fall into three distinct trophic levels on the basis of their stable isotope values. Glaucous gulls (*L. hyperboreus*) occupied the highest trophic level. Thick-billed murres (*U. lomvia*), black guillemots (*C. grylle*), black-legged kittiwakes (*R. tridactyla*), ivory gulls (*P. eburnea*), and northern fulmars (*Fulmarus glacialis*) occupied an intermediate trophic position that did not differ statistically from one another, while the dovekie occupied the lowest trophic level. For each of these species, the stable isotope values are lower than expected on the basis of what has been reported in previous studies of stomach contents (as summarized in Bradstreet and Brown, 1985). The lower trophic levels found here suggest that seabirds in this area relied more on lower trophic organisms than in other areas of the Arctic. It is also possible that the importance of lower trophic organisms has been underestimated in studies relying on conventional dietary methods (Hobson, 1993).

At the highest seabird trophic level, glaucous gulls scavenge on seals, take Arctic cod, and also adults and young of other seabirds, especially during the breeding season (Gaston and Nettleship, 1981; Stempniewicz, 1983; N. Karnovsky, unpublished results). However, like most gulls, this species has a broad diet that is expected to change within and between populations (Schmutz and Hobson, 1998). The TL of 4.6 inferred in this study was for birds taken in June when their isotope values will reflect primarily a pre-breeding diet with little incorporation of seabird prey.

The intermediate trophic level inferred for thick-billed murres, black guillemots, black-legged kittiwakes, ivory gulls, and northern fulmars was, for

the most part, consistent with their known diets of the pelagic amphipod, *T. libellula*, and Arctic cod (N. Karnovsky, unpublished data). Diet assessments of thick-billed murres collected at Coburg Island, Bylot Island and Prince Leopold Island colonies, as well as along the Pond Inlet ice edges and Barrow Strait area, contained primarily Arctic cod; *T. libellula* was secondary in terms of total prey biomass (Birkhead and Nettleship, 1981; Gaston and Nettleship, 1981; Bradstreet and Cross, 1982; Bradstreet and Brown, 1985). In the nearby Lancaster Sound and Barrow Strait area, black guillemots feed on both invertebrates and Arctic cod, with cod accounting for the majority of the biomass of adult diets (Bradstreet, 1976, 1980; Bradstreet and Brown, 1985). Likewise, black-legged kittiwakes are known to feed on Arctic cod (Welch and Crawford, 1993). However, stable isotope analysis of black-legged kittiwakes from Browne island showed that there may be a separation between chick and adult diets, with adult birds consuming *T. libellula* while they feed their chicks more cod (Hobson, 1993).

Northern fulmars have been observed to feed on seal carcasses, cod and squid and, along ice edges and upwelling sites, to take copepods and other zooplankton (Salmonsén, 1950; Bradstreet and Cross, 1982; Hobson and Welch, 1992b; Welch and Crawford, 1993). Similarly, ivory gulls have been observed scavenging offal of beluga whales, narwhals, seals, and walruses (*Odobenus rosmarus*; Renaud and McLaren, 1982) and in some areas have been noted to take the amphipod, *A. glacialis* (Divoky, 1976). On the basis of the scavenging activity observed in other areas, both northern fulmars and ivory gulls in this study have unexpectedly low trophic levels, perhaps indicating that they scavenge less in the North Water than elsewhere or that previous reports of scavenging have exaggerated its long-term nutritional importance.

In the North Water during spring and summer dovekeys apparently rely primarily on the copepods *Calanus glacialis* and *C. hyperboreus* (Bradstreet, 1982; N. Karnovsky, unpublished). Later in the breeding season, these birds shift to feeding at a higher trophic level on *T. libellula* and Arctic cod (Bradstreet, 1982; N. Karnovsky, unpublished).

Birds collected in this study were taken primarily during the copepod feeding stage of the early part of the breeding season; the stable isotope results generally support this notion.

Our results indicate that invertebrates play a critical role in arctic seabird diets. Based on the stable isotope analysis, seabirds appear to occupy a lower trophic level in the North Water than elsewhere in the Arctic. Alternatively, previous studies based on conventional approaches elsewhere in the Arctic may have overestimated trophic level since invertebrates may not preserve well in stomachs (Hobson, 1993; Hobson et al., 1995). The central position of cod in the transfer of energy to seabirds in other areas of the Arctic may be replaced by invertebrates in the North Water. Properly placing seabirds in energy and contaminant flow analyses is critical, as both the dovekie and thick-billed murre are important components of the diets of people in the communities adjacent to the North Water (Evans and Kampp, 1991; Boertman and Mosbech, 1998).

#### 4.3.2. Marine mammals

Polar bears occupied the highest trophic level in the North Water. The major prey items of polar bears are ringed and bearded seals (Stirling and Archibald, 1977; Smith, 1980), although polar bears have also been known to prey on walrus (Kiliaan and Stirling, 1978; Calvert and Stirling, 1990), belugas (Lowry et al., 1987; Rugh and Sheldon, 1993), and narwhals (Smith and Sjare, 1990), as well as birds in the summer (Stempniewicz, 1993; Donaldson et al., 1995). Polar bears are thought to feed almost exclusively on ringed seals in the eastern Canadian High Arctic (Stirling and Archibald, 1977; Smith, 1980). Similarly, our isotopic model suggests that polar bears in the area may feed exclusively on ringed seals (Fig. 3). Even though polar bear tissues were obtained from animals in Lancaster Sound,  $\delta^{15}\text{N}$  tissue values for ringed seals in the North Water are similar to those for ringed seals in Lancaster Sound (Hobson and Welch, 1992a). Thus,  $\delta^{15}\text{N}$  tissue values for polar bears in these two areas would likely be similar as well.

Ringed seals are considered to be opportunistic feeders (McLaren, 1958; Johnson et al., 1966; Lowry et al., 1978; Weslawski et al., 1994). Arctic

cod appears to be the major source of food for ringed seals between late autumn to early spring, whereas in summer, pelagic amphipods such as *T. libellula*, euphausiids, mysids, and benthic crustaceans become important (Johnson et al., 1966; Lowry et al., 1980a; Weslawski et al., 1994). The isotopic data reflect an integration of diet during the late spring to early summer period. Our isotopic model suggests that during this period, the diet of ringed seals in both Grise Fiord and Qaanaaq consisted predominantly of Arctic cod (Fig. 3), although lower trophic-level organisms occurred more frequently in the diet of ringed seals from Qaanaaq. Dietary studies have shown that although Arctic cod is the predominant prey type in the diet of ringed seals in Grise Fiord and Qaanaaq in late spring/early summer, polar cod (*Arctogadus glacialis*) is also an important source of prey for ringed seals in these areas, especially in Grise Fiord (e.g., Bradstreet and Finley, 1983; Siegstad et al., 1998; Holst, 2000). At this time, however, no stable isotope values are available for polar cod.

Bearded seals are primarily benthic feeders (Kenyon, 1962; Lowry et al., 1980b), which is consistent with the enrichment of their  $\delta^{13}\text{C}$  tissue value. Bearded seal diet in the eastern Canadian High Arctic consists mainly of fish, including Arctic cod and sculpins, as well as a variety of benthic invertebrates (Finley and Evans, 1983). Similarly, our model suggests a diet consisting predominantly of fish (Fig. 3).

Most walrus migrate to the North Water in the spring and summer, although some are known to overwinter there (Vibe, 1950; Finley and Renaud, 1980). Atlantic walrus take a wide variety of benthic prey, including bivalves such as *Mya truncata* and *Hiattella arctica*, which tend to be the most important prey items, as well as gastropods and polychaetes (Vibe, 1950; Mansfield, 1958; Welch et al., 1992; Fisher and Stewart, 1997). Ringed and bearded seal remains also have been found occasionally in walrus stomachs from the North Water (Vibe, 1950) and other areas in the Canadian Arctic (Mansfield, 1958; Loughrey, 1959). The isotopic data suggest that the diet of walrus in the North Water consists predominantly of bivalves, as reflected in their lower  $\delta^{15}\text{N}$  tissue values compared to other marine mammals.

Even though  $\delta^{15}\text{N}$  tissue values for *M. truncata* and *H. arctica* are unknown, the  $\delta^{15}\text{N}$  tissue values for bivalves of the genus *Astarte*, which have been shown to occur in the walrus diet (Fisher and Stewart, 1997), fall within the isotopic range of possible prey items.

The North Water may be an overwintering site for some belugas and narwhals (Vibe, 1950; Sergeant and Hoek, 1974; Mansfield et al., 1975; Sergeant and Brodie, 1975), as well as for bowhead whales (Richard et al., 1998; Holst and Stirling, 1999). However, most animals migrate to the polynya between late spring and early summer, presumably to feed. Beluga and narwhal occupied similar trophic levels. Their diets are assumed to consist mainly of fish, including Arctic cod and polar cod, as well as squid (Mansfield et al., 1975; Finley and Gibb, 1982; Heide-Jørgensen and Teilmann, 1994; Heide-Jørgensen et al., 1994). Our isotopic model shows a lower trophic position for these species than one consistent with a diet predominated by Arctic cod (Fig. 3), indicating that lower trophic-level prey such as squid or pelagic crustaceans may constitute a large proportion of their diets (e.g., Bradstreet and Cross, 1982).

The bowhead whale is a plankton feeder; our isotope results are consistent with this lower trophic-level position compared to most other marine mammals. Its diet consists primarily of euphausiids and copepods, but epibenthic organisms such as mysids and gammarid amphipods are also eaten regularly (Lowry et al., 1978; Hazard and Lowry, 1984; Carroll et al., 1987; Lowry, 1993). The isotope data suggest a higher trophic level for the bowhead whale than would be expected if the diet consisted exclusively of the copepod *C. hyperboreus* (Fig. 3), which is known to be an important prey item for bowheads in Alaska (Lowry and Frost, 1984). Although there are no published reports of the diet of bowhead whales in the North Water, according to Lowry (1993) the spring diet of bowhead whales taken near Point Barrow, Alaska, consists of 54.2% copepods, 42.4% euphausiids, 2.6% mysids, and 0.8% other invertebrates, whereas the fall diet consists of 96.0% euphausiids, 0.3% mysids, 2.6% gammarid amphipods, and 1.1% other items. Contrary to Antarctica and to other subarctic seas, euphausiids are numerically

insignificant in the eastern Canadian Arctic. *T. libellula* largely dominates pelagic macrozooplankton crustaceans in the area. As non-selective feeders, we suspect that *T. libellula* is a large part of their diet. According to Dunbar (1941, 1957), *T. libellula* forms the most important link in the food chain between copepods and other smaller planktonic forms on the one hand, and the vertebrates on the other, thus playing in the Arctic the trophic role of euphausiids in the Southern Ocean. According to our isotopic model, bowhead whales feeding exclusively on *C. hyperboreus* or *T. libellula* should present a TL of 3.0 and 3.5, respectively. Thus, our value of 3.4 for eastern bowhead whales using the North Water suggests a diet comprised largely of *T. libellula*.

#### 4.4. Contaminants

Data for a large range of PCB congeners and other persistent organic pollutants (POPs, e.g., chlordanes, DDT, etc.) were generated for the North Water food web. For brevity, and because the focus of this paper is stable isotopes, only data for PCB 153 is presented (see Fisk et al. 2001). PCB 153 was chosen because it is considered one of the most recalcitrant and bioaccumulative PCB congeners, usually having among the highest concentrations of any POP measured in Arctic biota (Muir et al., 1988; Henriksen et al., 1996). Because PCB 153 is lipophilic and very slowly biotransformed by any species investigated so far, metabolic differences between groups of animals or species will not confound the PCB 153– $\delta^{15}\text{N}$  relationships. As well, PCB 153 is commonly used as a marker for assessing the bioaccumulation or biomagnification of other POPs (Boon et al., 1994).

The strong positive relationship observed between PCB 153 concentrations (lipid basis) and  $\delta\delta^{15}\text{N}$  confirms the biomagnification of this contaminant through Arctic marine food webs (Muir et al., 1988; Braune and Norstrom, 1989). Assuming that a change in  $\delta^{15}\text{N}$  value of 3.8‰ represents one trophic level, the slope of 0.61 corresponds to a trophic magnification factor of 10.2. Therefore, on average, the lipid-corrected concentration of PCB 153 increases 10.2 fold from one trophic level to the next in the North Water food web. This slope of

0.61 is lower than those reported for  $\Sigma\text{PCB}$  ( $\Sigma\text{PCB}$  represents the concentration of a large number of individual PCB compounds, of which PCB 153 is a major contributor) in a temperate marine food chain (slope=0.88) (Jarman et al., 1996) and for PCB 153 in an Arctic marine food chain (slope=0.81) (Norstrom, 1994). Jarman et al. (1996) used seabird eggs vs. muscle tissue and Norstrom (1994) combined data from a number of different studies using trophic level vs. raw  $\delta^{15}\text{N}$  values that may confound direct comparisons with our study.

Examination of the PCB 153 concentrations shows the utility of examining ecological process with contaminants. Ivory gull, black-legged kittiwake, and northern fulmar all had PCB 153 concentrations which were greater than predicted for their respective  $\delta^{15}\text{N}$  values based on the PCB 153– $\delta^{15}\text{N}$  relationships (Fig. 4). This is likely due to past exposure to high PCB 153 concentrations, either through accumulation from scavenging dead marine mammals or from feeding at winter habitats which are more contaminated. There are no reported half-lives of PCB 153 in seabirds however, the half-life of mirex in herring gulls (*Larus argentatus*) has been reported as 559 days (Clark et al., 1987). Mirex is recalcitrant and has similar physical and chemical properties to PCB 153 therefore half-lives of PCB 153 in seabirds are likely similar to mirex and >1 yr. This is much longer than the turnover rate of  $^{15}\text{N}$  in muscle protein, which represents the integrated diet of seabirds over the past month (Hobson, 1993). In general, kittiwakes apparently do not scavenge marine mammals (Baird, 1994), so that their high PCB 153 concentrations are likely due to accumulation in their winter habitat of the more highly contaminated eastern seaboard of North America (Muir et al., 1990). Northern fulmars migrate and are known to scavenge marine mammals (Finley et al., 1952), but the relative role of each of these variables in their PCB 153 concentrations is not known. However, Ivory gulls do not migrate significantly out of the Arctic (Haney and Macdonald, 1995). High PCB 153 concentrations suggest that scavenging of marine mammal tissue is more predominant in ivory gulls throughout the year than is reflected in current  $\delta^{15}\text{N}$  values. These

results emphasize the need to consider the temporal context of the isotopic vs. contaminants data as well as the fact that  $\delta^{15}\text{N}$  values are based on muscle protein, whereas contaminants often are more directly related to lipids (Jarman et al., 1996).

#### 4.5. *Implications for tracing carbon and energy flux*

One goal of this study was to integrate the use of stable isotope analysis into models of carbon flux to higher trophic-level organisms. Although we will present the details of these analyses elsewhere, we consider here the general approach to the use of stable isotope models in energy- and carbon-flux calculations using seabirds as an example. To our knowledge, stable isotope models have not been used previously in large-scale marine carbon flux models.

The general approach used in studies investigating the role of seabirds in energy and carbon flux in marine systems has been to quantify daily energy requirements of individuals based on field metabolic rates and body size and to integrate those requirements at the population level over time and space (Weins and Scott, 1975). Total integrated energy requirements for breeders, non-breeders, and young of the year are then combined to estimate total energy flux during the breeding season and other times associated with an estimated area of ocean surface to yield energy flux per unit area (Schneider et al. 1987).

In order to convert energy-flux calculations to equivalent amounts of fixed carbon or tonnage of prey species it is necessary to know the diet or trophic level of the consumers and how this may change seasonally and with age or breeding status. This requirement follows from the need to convert energy values to equivalent carbon mass, since different prey organisms have different energy equivalents. More importantly, regardless of differential caloric content of prey types, energy flux through one prey-trophic level is not equivalent to the same energy flux through a higher trophic level due to low conversion efficiencies between trophic levels. Although energy conversion between trophic levels may be as high as 20% (Cushing, 1975; Smith and Eppley, 1982), a value of 10% is typically assumed (Briggs and Chu, 1987; Welch et al. 1992).

Clearly, if trophic-level estimates are not accurate, carbon-flux estimates or derived proportions of fixed carbon consumed by seabirds and other upper trophic-level organisms may be off by as much as an order of magnitude. This effect is particularly true of seabirds and marine mammals whose diets are often poorly known (Hobson et al., 1994). Hobson (1993) demonstrated how chick diet is often of a higher trophic level than adult diet for high Arctic seabirds (see also Hodum and Hobson, 2000). Our isotopic analysis of adult seabird diet in the North Water shows generally a greater consumption of invertebrate prey than was previously assumed, indicating a more efficient transfer of fixed carbon to seabirds. It will be important to utilize derived trophic estimates presented in this paper for several species and groups in order to estimate carbon flux through higher trophic-level organisms.

#### **Acknowledgements**

Funding for this project was provided in part by a Natural Science and Engineering Research Council (NSERC), the Canadian Wildlife Service, the Polar Continental Shelf Project and a National Science Foundation (NSF) Grant to G. Hunt Jr. We thank the many scientists of the International North Water Polynya Study (NOW), who assisted us, especially I. Stirling for invaluable guidance and assistance in the field and laboratory, D. Andriashuk and N. Lunn for excellent assistance with collections, and G. Hunt Jr., and R. Norstrom for their valuable support and assistance. R. Dietz provided beluga, narwhal, and ringed seal tissue from west Greenland, P. Healy prepared samples for stable isotope analysis, and G. Parry ran stable isotope samples at the Department of Soil Science, University of Saskatchewan. M. Loewen and M. Mulvihill extracted and analyzed samples for PCB 153. We also thank the Hunters and Trapper Association of Grise Fiord for permission to collect birds and other samples in their area and G. Gilchrist for assisting with permit applications. This project would not have been possible without the dedicated and skillful assistance of the captains and crew of the Canadian Coast Guard Vessel

*Pierre Radisson*. W. Ambrose and R. Norstrom provided helpful comments on an earlier version of this manuscript. This is a contribution to the International North Water Polynya Study.

## References

- Atwell, L., Hobson, K.A., Welch, H.E., 1998. Biomagnification and bioaccumulation of mercury in an Arctic marine food web: insights from stable-nitrogen isotope analysis. *Canadian Journal of Fisheries and Aquatic Science* 55, 1114–1121.
- Baird, P.H., 1994. Black-legged kittiwake. *The Birds of North America* 92, 1–26.
- Birkhead, T.R., Nettleship, D.N., 1981. Reproductive biology of thick-billed murres *Uria lomvia*: an intercolony comparison. *Auk* 98, 258–269.
- Boertman, D., Mosbech, A., 1998. Distribution of the little Auk (*Alle alle*) breeding colonies in Thule district, northwest Greenland. *Polar Biology* 19, 206–210.
- Boon, J.P., Oostingh, I., van der Meer, J., Hillebrand, M.T.J., 1994. A model for the bioaccumulation of chlorobiphenyl congeners in marine mammals. *European Journal of Pharmacology* 270, 237–251.
- Bradstreet, M.S.W., 1976. Summer feeding ecology of seabirds in Eastern Lancaster Sound, 1976. LGL Ltd., Toronto, Environmental Research Associates. Report for Norlands Petroleum, Calgary, 187pp.
- Bradstreet, M.S.W., 1980. Thick-billed murres and black guillemots in the Barrow Strait area, N.W.T., during spring: diets and food availability along ice edges. *Canadian Journal of Zoology* 58, 2120–2140.
- Bradstreet, M.S.W., 1982. Pelagic feeding ecology of dovekies *Alle alle* in Lancaster Sound and western Baffin Bay. *Arctic* 35, 126–140.
- Bradstreet, M.S.W., Brown, R.G.B., 1985. Feeding ecology of the Atlantic Alcidae. In: Nettleship, D.N., Birkhead, T.R. (Eds.), *The Atlantic Alcidae*. Academic Press, London, pp. 264–318.
- Bradstreet, M.S.W., Cross, W.E., 1982. Trophic relationships at high Arctic ice edges. *Arctic* 35, 1–12.
- Bradstreet, M.S.W., Finley, K.J., 1983. Diet of ringed seals (*Phoca hispida*) in the Canadian High Arctic. Report by LGL Ltd., Toronto, Ontario.
- Braune, B.M., 1994. Trends and effects of environmental contaminants in Arctic seabirds, waterfowl, and other wildlife, II. Contaminants in Arctic seabirds. In: Murray, J.L., Shearer, R.G. (Eds.), *Synopsis of Research Conducted Under the 1993/1994 Northern Contaminants Program*, Environmental Studies, Vol. 72. Indian and Northern Affairs Canada, Ottawa, pp. 312–322.
- Braune, B.M., Norstrom, R.J., 1989. Dynamics of organochlorine compounds in herring gulls, III. Tissue distribution and bioaccumulation in Lake Ontario gulls. *Environmental Toxicology and Chemistry* 8, 957–968.
- Briggs, K.E., Chu, E.W., 1987. Trophic relationships and food requirements of California seabirds: updating models of trophic impact. In: Croxall, J.P. (Ed.), *Seabirds: Feeding Ecology and Role in Marine Ecosystems*. Cambridge University Press, Cambridge, pp. 279–304.
- Broman, D.C., Naf, C., Rolff, C., Zebuhr, Y., Fry, B., Hobbie, J., 1992. Using ratios of stable nitrogen isotopes to estimate bioaccumulation and flux of polychlorinated dibenzo-p-dioxins (PCDDs) and dibenzofurans (PCDFs) in two food chains from the northern Baltic. *Environmental Toxicology and Chemistry* 11, 331–345.
- Calvert, W., Stirling, I., 1990. Interactions between polar bears and overwintering walruses in the central Canadian High Arctic. *International Conference on Bear Research and Management* 8, 351–356.
- Cameron, M.E., Metcalfe, T.L., Metcalfe, C.D., Macdonald, C.R., 1997. Persistent organochlorine compounds in the blubber of ringed seals (*Phoca hispida*) from the Belcher Islands, Northwest Territories, Canada. *Marine Environmental Research* 43, 99–116.
- Carroll, G.M., George, J.C., Lowry, L.F., Coyle, K.O., 1987. Bowhead whale (*Balaena mysticetus*) feeding near Point Barrow, Alaska, during the 1985 spring migration. *Arctic* 40, 105–110.
- Clark, T.P., Norstrom, R.J., Fox, G.A., Won, H.T., 1987. Dynamics of organochlorine compounds in herring gulls (*Larus argentatus*): II. A two-compartment model and data for ten compounds. *Environmental Toxicology and Chemistry* 6, 547–559.
- Conover, R.J., Huntley, M., 1991. Copepods in ice-covered seas—distribution, adaptations to seasonally limited food, metabolism, growth patterns and life strategies in polar seas. *Journal of Marine Systems* 2, 1–41.
- Conover, R.J., Harris, L.R., Bedo, A.W., 1991. Copepods in cold oligotrophic waters—how do they cope? *Bulletin of the Plankton Society of Japan, Special Volume*, pp. 177–198.
- Cushing, D.H., 1975. *Marine Ecology and Fisheries*. Cambridge University Press, Cambridge.
- DeNiro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta* 42, 495–506.
- DeNiro, M.J., Epstein, S., 1981. Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica et Cosmochimica Acta* 45, 341–351.
- Divoky, G.J., 1976. The pelagic feeding habits of ivory and Ross's gulls. *Condor* 78, 85–90.
- Donaldson, G.M., Chapdelaine, G., Andrews, J.D., 1995. Predation of thick-billed murres, *Uria lomvia*, at two breeding colonies by polar bears, *Ursus maritimus*, and walruses, *Odobenus rosmarus*. *Canadian Field-Naturalist* 109, 112–114.
- Drolet, R., Fortier, L., Ponton, D., Gilbert, M., 1991. Production of fish larvae and their prey in subarctic southeastern Hudson Bay. *Marine Ecology Progress Series* 77, 105–118.
- Dunbar, M.J., 1941. Marine macroplankton from the Canadian Eastern Arctic, I. Amphipoda and schizopoda. *Canadian Journal of Research* 20, 33–46.

- Dunbar, M.J., 1957. The determinants of production in northern seas: a study of the biology of *Themisto libellula* Mandt. Canadian Journal of Zoology 35, 797–819.
- Dunton, K.H., Saupe, S.M., Golikov, A.N., Schell, D.M., Schonberg, S.V., 1989. Trophic relationships and isotopic gradients among Arctic and subarctic marine fauna. Marine Ecology Progress Series 56, 89–97.
- Evans, P.G.H., Kampp, K., 1991. Recent changes in thick-billed murre populations in west Greenland. In: Studies of high latitude seabirds, 2. Conservation biology of thick-billed murres in the Northwest Atlantic. Occasional Paper Canadian Wildlife Service, Ottawa, Vol. 69, pp. 7–14.
- Falk, K., Hjort, C., Andreasen, C., Christensen, K.D., Elander, M., Ericson, M., Kampp, K., Kristensen, R.M., Mberg, N., Mller, S., Weslawski, J.M., 1997. Seabirds utilizing the Northeast Water Polynya. Journal of Marine Systems 10, 47–65.
- Finley, K.J., Evans, C.R., 1983. Summer diet of the bearded seal (*Erignathus barbatus*) in the Canadian High Arctic. Arctic 36, 82–89.
- Finley, K.J., Gibb, E.J., 1982. Summer diet of the narwhal, *Monodon monoceros*, in Pond Inlet, northern Baffin Island. Canadian Journal of Zoology 57, 1985–1997.
- Finley, K.J., Renaud, W.E., 1980. Marine mammals inhabiting the Baffin Bay North Water in Winter. Arctic 33, 724–738.
- Finley, K.J., Renaud, W.E., Fisher, J., 1952. The Fulmar. Collins, London.
- Fisher, K.I., Stewart, R.E.A., 1997. Summer foods of Atlantic walrus, *Odobenus rosmarus rosmarus*, in northern Foxe Basin, Northwest Territories. Canadian Journal of Zoology 75, 1166–1175.
- Fisk, A.T., Hobson, K.A., Norstrom, R.J., 2001. Influence of chemical and biological factors on trophic transfer of persistent organic pollutants in the Northwest Polynya marine food web. Environmental Science and Technology 35, 732–738.
- Fortier, M., Fortier, L., Hattori, H., Saito, H., Legendre, L., 2001. Visual predators and the diel vertical migration of copepods under Arctic sea ice during the midnight sun. Journal of Plankton Research 23, 1263–1278.
- France, R.L., 1995a. Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Marine Ecology Progress Series 124, 307–312.
- France, R.L., 1995b. Differentiation between littoral and pelagic foodwebs in lakes using stable carbon isotopes. Limnology and Oceanography 40, 1310–1313.
- France, R.L., Holmquist, J.G., 1997.  $\delta^{13}\text{C}$  variability of macroalgae: effects of water motion via baffling by seagrasses and mangroves. Marine Ecology Progress Series 149, 305–308.
- Fry, B., Arnold, C., 1982. Rapid  $^{13}\text{C}/^{12}\text{C}$  turnover during growth of brown shrimp (*Penaeus aztecus*). Oecologia 54, 200–204.
- Fry, B., Sherr, E.B., 1984.  $\delta^{13}\text{C}$  measurements as indicators of carbon flow in marine and freshwater ecosystems. Contributions in Marine Science 27, 13–47.
- Gaston, A.J., Nettleship, D.N., 1981. The thick-billed murres of Prince Leopold Island—a study of the breeding ecology of a colonial high arctic seabird. Canadian Wildlife Service Monograph Series No. 6, 350pp.
- Goericke, R., Montoya, J.P., Fry, B., 1994. Physiology of isotope fractionation in algae and cyanobacteria. In: Lajtha, K., Michener, R.H. (Eds.), Stable Isotopes in Ecology. Blackwell, Oxford, pp. 181–221.
- Grainger, E.H., Hsiao, I.C., 1990. Trophic relationships of the sea ice meiofauna in Frobisher Bay, Arctic Canada. Polar Biology 10, 283–292.
- Haney, J.C., Macdonald, S.D., 1995. Ivory gulls. The Birds of North America 175, 1–23.
- Hazard, K.W., Lowry, L.F., 1984. Benthic prey in a bowhead whale from the northern Bering Sea. Arctic 37, 166–168.
- Hecky, R.E., Hesslein, R.H., 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. Journal of the North American Benthological Society 14, 631–653.
- Heide-Jørgensen, M.P., Teilmann, J., 1994. Growth, reproduction, age structure and feeding habits of white whales (*Delphinapterus leucas*) in West Greenland waters. In: Born, E.W., Dietz, R., Reeves, R.R. (Eds.), Studies of White Whales (*Delphinapterus leucas*) and narwhals (*Monodon monoceros*) in Greenland and adjacent waters; Meddelelser om Grønland, Bioscience 39, 195–212.
- Heide-Jørgensen, M.P., Dietz, R., Leatherwood, S., 1994. A note on the diet of narwhals (*Monodon monoceros*) in Inglefield Bredning (NW Greenland). In: Born, E.W., Dietz, R., Reeves, R.R. (Eds.), Studies of White Whales (*Delphinapterus leucas*) and Narwhals (*Monodon monoceros*) in Greenland and Adjacent Waters; Meddelelser om Grønland, Bioscience 39, 213–216.
- Henriksen, E.O., Gabrielsen, G.W., Skaare, J.U., 1996. Levels and congener pattern of polychlorinated biphenyls in kittiwakes (*Rissa tridactyla*), in relation to mobilization of body-lipids associated with reproduction. Environmental Pollution 92, 27–37.
- Hirche, H.J., Kwasniewski, S., 1997. Distribution, reproduction and development of *Calanus* species in the Northeast Water in relation to environmental conditions. Journal of Marine Systems 10, 299–317.
- Hobson, K.A., 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. Marine Ecology Progress Series 95, 7–18.
- Hobson, K.A., Schell, D.M., 1998. Stable-carbon and nitrogen isotope patterns in baleen from eastern Arctic bowhead whales (*Balaena mysticetus*). Canadian Journal of Fisheries and Aquatic Science 55, 1–7.
- Hobson, K.A., Welch, H.E., 1992a. Determination of trophic relationships within a high Arctic marine food web using stable-isotope analysis. Marine Ecology Progress Series 84, 9–18.
- Hobson, K.A., Welch, H.E., 1992b. Observations of foraging Northern fulmars (*Fulmaris glacialis*) in the Canadian High Arctic. Arctic 45, 150–153.

- Hobson, K.A., Piatt, J.F., Pitocchelli, J., 1994. Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* 63, 786–798.
- Hobson, K.A., Ambrose Jr., W.G., Renaud, P.E., 1995. 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. *Marine Ecology Progress Series* 128, 1–10.
- Hodum, P.J., Hobson, K.A., 2000. Trophic relationships among Antarctic fulmarine petrels: insights into dietary overlap and chick provisioning strategies inferred from stable-isotope ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) analyses. *Marine Ecology Progress Series* 198, 273–281.
- Holst, M., 2000. Ecology of ringed seal in the North Water Polynya. M.Sc. Thesis, University of Alberta, Edmonton, Alberta, 138pp.
- Holst, M., Stirling, I., 1999. A note on sightings of bowhead whales in the North Water Polynya, Northern Baffin Bay, May–June 1998. *Journal of Cetacean Research and Management* 1, 153–156.
- Jarman, W.M., Hobson, K.A., Sydeman, W.J., Bacon, C.E., McLaren, E.B., 1996. The influence of trophic position and feeding location on contaminant levels in the Gulf of the Farallones food web revealed by stable isotope analysis. *Environmental Science and Technology* 30, 654–660.
- Jarman, W.M., Sydeman, W.J., Hobson, K.A., Bergqvist, P.-A., 1997. Relationship of polychlorinated dibenzo-P-dioxins (PCDDs) and polychlorinated dibenzofuran levels to stable nitrogen isotope abundance in marine birds and mammals in coastal California. *Environmental Toxicology and Chemistry* 16, 1010–1013.
- Johnson, M.L., Fiscus, C.H., Ostenson, B.T., Barbour, M.L., 1966. Marine Mammals. In: Wilimovsky, N.J., Wolfe, J.N. (Eds.), *Environment of the Cape Thompson Region, Alaska*. US Atomic Energy Commission, Oak Ridge, TN, pp. 877–924.
- Kelly, J.F., 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78, 1–27.
- Kenyon, K.W., 1962. Notes on phocid seals at Little Diomed Island, Alaska. *Journal of Wildlife Management* 26, 380–387.
- Kiliaan, H.P.L., Stirling, I., 1978. Observations on overwintering walrus in the eastern Canadian High Arctic. *Journal of Mammalogy* 59, 197–200.
- Lawson, J.W., Hobson, K.A., 2000. Diet of harp seals (*Pagophilus groenlandicus*) in nearshore northeast Newfoundland: inferences from stable-carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope analysis. *Marine Mammal Science* 16 (3), 578–591.
- Loughrey, A.G., 1959. Preliminary investigation of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus). *Canadian Wildlife Service Wildlife Management Bulletin No. 14, Series 1*.
- Lowry, L.F., 1993. Foods and feeding ecology. In: Burns, J.J., Montague, J.J., Cowles, C.J. (Eds.), *The Bowhead Whale*. Special Publication Number 2. The Society for Marine Mammalogy, Lawrence, KS, pp. 201–238.
- Lowry, L.F., Frost, K.J., 1984. Foods and feeding of bowhead whales in western and northern Alaska. Scientific Report, Vol. 35, Whales Research Institute, pp. 1–16.
- Lowry, L.F., Frost, K.J., Burns, J.J., 1978. Food of ringed seals and bowhead whales near Point Barrow, Alaska. *Canadian Field Naturalist* 92, 67–70.
- Lowry, L.F., Frost, K.J., Burns, J.J., 1980a. Variability in the diet of ringed seals, (*Phoca hispida*), in Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 37, 2254–2261.
- Lowry, L.F., Frost, K.J., Burns, J.J., 1980b. Feeding of bearded seals in the Bering and Chukchi seas and trophic interaction with Pacific walrus. *Arctic* 33, 330–342.
- Lowry, L.F., Burns, J.J., Nelson, R.R., 1987. Polar bear, *Ursus maritimus*, predation on belugas, *Delphinapterus leucas*, in the Bering and Chukchi seas. *Canadian Field-Naturalist* 101, 141–146.
- Mansfield, A.W., 1958. The biology of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus) in the eastern Canadian Arctic. Fisheries Research Board of Canada Report, Series No. 653.
- Mansfield, A.W., Smith, T.G., Beck, B., 1975. The narwhal, *Monodon monoceros*, in eastern Canadian waters. *Journal of the Fisheries Research Board of Canada* 32, 1041–1046.
- McConnaughey, T., McRoy, C.P., 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. *Marine Biology* 53, 257–262.
- McLaren, I.A., 1958. The Biology of the Ringed Seal (*Phoca hispida* Schreber) in the Eastern Canadian Arctic. Bulletin of the Fisheries Research Board of Canada No. 118.
- Michener, R.H., Schell, D.M., 1994. Stable isotope ratios as tracers in marine and aquatic food webs. In: Lajtha, K., Michener, R.H. (Eds.), *Stable isotopes in ecology and environmental science*. Blackwell Scientific Publications, Oxford, pp. 138–157.
- Michaud, J., Fortier, L., Rowe, P., Ramseier, R., 1996. Feeding success and survivorship of Arctic cod larvae, *Boreogadus saida*, in the Northeast Water Polynya (Greenland Sea). *Fisheries Oceanography* 5, 120–135.
- Muir, D.C.G., Norstrom, R.J., Simon, M., 1988. Organochlorine contaminants in Arctic marine food chains: accumulation of specific polychlorinated biphenyls and chlordane-related compounds. *Environmental Science and Technology* 22, 1071–1079.
- Muir, D.C.G., Ford, C.A., Stewart, R.E.A., Addison, R.F., Zinck, M.E., Beland, P., 1990. Organochlorine contaminants in belugas, *Delphinapterus leucas*, from Canadian waters. *Canadian Bulletin of Fisheries and Aquatic Sciences* 224, 165–190.
- Muir, D.G., Segstro, M.D., Hobson, K.A., Ford, C.A., Stewart, R.E.A., Olpinski, S., 1995. Can seal eating explain elevated levels of PCBs and organochlorine pesticides in walrus blubber from eastern Hudson Bay (Canada)? *Environmental Pollution* 88, 1–14.
- Nettleship, D.N., Evans, P.G.H., 1985. Distribution and status of the Atlantic Alcidae. In: Nettleship, D.N., Birkhead, T.R. (Eds.), *The Atlantic Alcidae*. Academic Press, London, pp. 53–154.

- Norstrom, R.J., 1994. Chlorinated hydrocarbon contaminants in the Arctic marine environment. *Organohalogen Compounds* 20, 541–545.
- Ohman, M.D., Runge, J.A., 1994. Sustained fecundity when phytoplankton resources are in short supply: omnivory by *Calanus finmarchicus* in the Gulf of St. Lawrence. *Limnology and Oceanography* 39, 21–36.
- Øresland, V., 1995. Winter population structure and feeding of the chaetognath *Eukrohnia hamata* and the copepod *Euchaeta antarctica* in Gerlache Strait, Antarctica Peninsula. *Marine Ecology Progress Series* 119, 77–86.
- Pagès, F., Gonzalez, H.E., Gonzalez, S.R., 1996. Diet of the gelatinous zooplankton in Hardangerfjord (Norway) and potential predatory impact by *Aglantha digitale* (Trachymedusae). *Marine Ecology Progress Series* 139, 69–77.
- Renaud, W.E., McLaren, P.L., 1982. Ivory gull distribution and migration. *Arctic* 35, 141–148.
- Richard, P.R., Orr, J.R., Dietz, R., Dueck, L., 1998. Sightings of belugas and other marine mammals in the North Water, late March 1993. *Arctic* 51, 1–4.
- Ringuette, M., Fortier, L., Fortier, M., Runge, J., Belanger, S., Larouche, P., Weslawski, J.M., Kwasniewski, S., 2002. Advanced recruitment and accelerated population development of Arctic calanoid copepods of the North Water. *Deep Sea Research Part II*, this issue (PII: S0967-0645(02)00179-0).
- Rolff, C., Broman, D., Naf, C., Zebuhr, Y., 1993. Potential biomagnification of PCDD/Fs—new possibilities for quantitative assessment using stable isotope trophic position. *Chemosphere* 27, 461–468.
- Rugh, D.J., Shelden, K.E.W., 1993. Polar bears, *Ursus maritimus*, feeding on Beluga Whales, *Delphinapterus leucas*. *Canadian Field-Naturalist* 107, 235–237.
- Salmonsén, F., 1950. The Birds of Greenland. Munksgaard, Copenhagen.
- Salmonsén, F., 1981. Birds. In: Salmonsén, F. (Ed.), The Fauna of Greenland. Glydendal, Copenhagen, pp. 161–360.
- Schell, D.M., Barnett, B.A., Vinette, K., 1998. Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort Seas. *Marine Ecology Progress Series* 162, 11–23.
- Schmutz, J.A., Hobson, K.A., 1998. Geographic, temporal, and age-specific variation in diets of glaucous gulls in western Alaska. *Condor* 100, 119–130.
- Schneider, D.C., Hunt Jr., G.L., Powers, K.D., 1987. Energy flux to pelagic birds: a comparison of Bristol Bay (Bering Sea) and Georges Bank (Northwest Atlantic). In: Croxall, J.P. (Ed.), Seabirds: Feeding Ecology and Role in Marine Ecosystems. Cambridge University Press, Cambridge, pp. 260–277.
- Scott, C.L., Falk-Petersen, S., Sargent, J.R., Hop, H., Jørgen Lonne, O., Poltermann, M., 1999. Lipids and trophic interactions of ice fauna and pelagic zooplankton in the marginal zone of the Barents Sea. *Polar Biology* 21, 65–70.
- Sergeant, D.E., Brodie, P.F., 1975. Identity, abundance and present status of populations of white whales, *Delphinapterus leucas*, in North America. *Journal of the Fisheries Research Board of Canada* 32, 1047–1054.
- Sergeant, D.E., Hoek, W., 1974. Seasonal distribution of bowhead and white whales in the eastern Beaufort Sea. In: Reed, J.C., Sater, J.E. (Eds.), The Coast and Shelf of the Beaufort Sea. The Arctic Institute of North America, Arlington, VA, pp. 705–719.
- Siegstad, H., Neve, P.B., Heide-Jørgensen, M.P., Härkönen, T., 1998. Diet of the ringed seal (*Phoca hispida*) in Greenland. In: Heide-Jørgensen, M.P., Lydersen, C. (Eds.), Ringed Seals in the North Atlantic. NAAMCO Scientific Publications, Vol. 1. The North Atlantic Marine Mammal Commission, Tromsø, pp. 229–241.
- Siferd, T.D., Conover, R.J., 1992. Natural history of ctenophores in the resolute passage area of the Canadian High Arctic with special reference to *Mertensia ovum*. *Marine Ecology Progress Series* 86, 133–144.
- Smith, T.G., 1980. Polar bear predation of ringed seals and bearded seals in the land-fast sea ice habitat. *Canadian Journal of Zoology* 58, 2201–2209.
- Smith, P.E., Eppley, R.W., 1982. Primary production and the anchovy population in the Southern California Bight: comparison of time series. *Limnology and Oceanography* 27, 1–17.
- Smith, T.G., Sjare, B., 1990. Predation of belugas and narwhals by Polar Bears in Nearshore Areas of the Canadian High Arctic. *Arctic* 43, 99–102.
- Smith, F.R., Walker, N.A., 1980. Photosynthesis by aquatic plants: effects of unstirred layers in relation to assimilation of CO<sub>2</sub> and HCO<sup>-</sup> and to carbon isotopic discrimination. *New Phytology* 86, 245–259.
- Stempniewicz, L., 1983. Hunting methods of the glaucous gull and escape maneuvers of its prey, the dovekie. *Journal of Field Ornithology* 54, 329–331.
- Stempniewicz, L., 1993. The polar bear *Ursus maritimus* feeding in a seabird colony in Franz Josef Land. *Polar Research* 12, 33–36.
- Stirling, I., 1980. The biological importance of polynyas in the Canadian Arctic. *Arctic* 33, 303–315.
- Stirling, I., Archibald, W.R., 1977. Aspects of predation of seals by polar bears. *Journal of the Fisheries Research Board of Canada* 34, 1126–1129.
- Stirling, I., Cleator, H., Smith, T.G., 1981. Marine mammals. In: Stirling, I., Cleator, H. (Eds.), Polynyas in the Canadian Arctic. Canadian Wildlife Service Occasional Papers No. 45, pp. 45–58.
- Tourangeau, S., Runge, J.A., 1991. Reproduction of *Calanus glacialis* under ice in spring in southeastern Hudson Bay, Canada. *Marine Biology* 108, 227–233.
- Vibe, C., 1950. The marine mammals and the marine fauna in the Thule district (northwest Greenland) with observations on ice conditions in 1939–41. *Meddelelsmer om Grønland* 150, 1–115.
- Weins, J.A., Scott, J.M., 1975. Model estimation of energy flow in Oregon coastal seabird populations. *Condor* 77, 439–452.
- Welch, H.E., Crawford, R.E., 1993. Occurrence of Arctic cod (*Boreogadus saida*) schools and their vulnerability to predation in the Canadian High Arctic. *Arctic* 46, 331–339.

- Welch, H.E., Bergmann, M.A., Siferd, T.D., Martin, K.A., Curtis, M.F., Crawford, R.E., Conover, R.J., Hop, H., 1992. Energy flow through the marine ecosystem of the Lancaster Sound Region, Arctic Canada. *Arctic* 45, 343–357.
- Weslawski, J.M., Ryg, M., Smith, T.G., Oritsland, N.A., 1994. Diet of ringed seals (*Phoca hispida*) in a Fiord of West Svalbard. *Arctic* 47, 109–114.
- Wing, B.L., 1976. Ecology of *Parathemisto libellula* and *P. pacifica* (Amphipoda: Hyperiidia) in Alaskan coastal waters. Northwest Fisheries Center, National Marine Fisheries Service, Seattle, Washington, Processed rep., 266pp.
- Yen, J., 1987. Predation by a carnivorous marine copepod, *Eucaheta norvegica* Boeck, on eggs and larvae of the North Atlantic cod (*Gadus morhua* L.). *Journal of Experimental Marine Biology and Ecology* 112, 283–296.