

Food web structure of a coastal Arctic marine ecosystem and implications for stability

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ABSTRACT: There is little doubt that Arctic ecosystems will continue to face unprecedented change in the coming decades. The identification of food web structures that confer stability to these systems is, therefore, a priority. Here, we use stable isotopes and fatty acids to resolve the food web structure of a seasonally ice-covered fjord (Cumberland Sound, Baffin Island, Canada) sampled in late summer. We show that the food web is structured such that upper trophic levels couple separate energy channels (based on phytoplankton or macroalgae), a previously documented food web structure that has been linked with stability in temperate ecosystems, but never established in a seasonally dynamic, ice-covered ecosystem. Herbivorous zooplankton (e.g. *Calanus hyperboreus*) relied exclusively on phytoplankton, whereas herbivorous benthos used either phytodetritus (e.g. *Hiatella arctica*) or macroalgae (e.g. *Tectura testudinalis*), supporting the existence of separate energy channels. Upper trophic level fishes and marine mammals relied more heavily on phytoplankton- than macroalgal-derived carbon (58 to 100% reliance on phytoplankton), but 6 out of 8 species sampled derived energy from both carbon sources. Since benthic invertebrate predators used both phytodetrital- and macroalgal-based resources, the coupling of separate energy channels was also iterated within the benthos. The temporally pulsed nature of phytoplankton production, characteristic of Arctic seas, indicates that Arctic consumers also act as couplers of resources in time because phytoplankton- and detrital-based carbon would likely reach upper trophic levels earlier and later in the season, respectively. Potential changes in the relative production of macroalgae and phytoplankton under climate change scenarios could impact the stability-promoting food web structure reported here.

KEY WORDS: Resource coupling · Ecological patterns · Arctic marine ecology · Food web · Stable isotopes · Fatty acids · Macroalgae · Climate warming

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INTRODUCTION

Over the next few decades, Arctic marine ecosystems will continue to face increased stress from a multitude of climate change scenarios (Wassmann et al. 2011). The predicted effects of these stressors range in scale from changes in the physiology of individual animals (e.g. decreased health) to overarching ecosystem-level effects (e.g. due to decreased ice cover), and have the potential to affect the structure,

functioning and stability (in terms of variability, resilience and persistence) of Arctic food webs. It is, therefore, essential for ecologists to identify the food web structures that confer stability to these imperiled ecosystems.

The mechanisms governing the stability of food webs has been of interest to ecologists for decades (MacArthur 1955), and structures linked to increased food web stability are known to arise within the complex feeding interactions that make up food webs

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(e.g. Polis et al. 1996). More recent work combining food web theory with empirical observations has revealed that a seemingly common structure, the coupling of different energy channels in space by mobile, upper trophic level predators, imparts stability to food webs (Rooney et al. 2006). These energy channels are based on different basal resources and arise because lower trophic levels often derive energy predominantly from singular carbon sources (e.g. phytoplankton or detritus). Upper trophic level organisms act to couple different energy channels as they move through spatial environments, consuming multiple prey types (McCann & Rooney 2009). Together, these factors impart a 'hump-shape' structure to food webs when graphed on axes of percent reliance on 1 of 2 carbon sources versus trophic position (Fig. 1; Rooney et al. 2006), which is hypothesized to be iterative across spatial scales and within and between ecosystems (McCann & Rooney 2009). Importantly, biomass turnover rates of taxonomic groups and the strength of interactions between consumers and resources are markedly different between the energy channels, resulting in weak and strong energy channels. Strong energy channels are those characterized by high production rates and strong trophic interactions, whereas weak energy channels are based on a resource with low production and constituted by weak trophic interactions (Rooney et al. 2006). The coupling behavior of mobile top predators has the potential to generate asynchronous dynamics of prey species between energy channels, producing a less variable resource base for predators. The weak channel also competes with the

strong channel, muting some of the energy flow that would go through the strong channel in the absence of the weak channel. This muting also enhances stability. Thus far, coupling of energy channels by upper trophic levels has been identified in terrestrial, marine and freshwater food webs from latitudes with temperate climates (Rooney et al. 2006, Dolson et al. 2009), but it is unknown if food webs from latitudes that experience high seasonal variability, and which are driven by brief but large pulses of primary production (Renaud et al. 2011), exhibit such structure.

Climate warming effects are hypothesized to alter the relative contribution of various primary producers to overall food web production in the Arctic (Wassmann et al. 2011, Weslawski et al. 2011). Pelagic primary production in Arctic seas currently takes place during a 1 to 4 mo window, when intense ice algae and phytoplankton blooms fuel pelagic energy channels (Søreide et al. 2006) and, when not completely grazed, sink to provide labile phytodetritus that is rapidly exploited by benthos (Lovvorn et al. 2005). Contrary to the situation in temperate seas, Arctic consumers must contend with >10 mo, in some areas, of sea-ice and snow-cover that markedly reduces or entirely halts primary production (Weslawski et al. 1991). Based on the large magnitude and efficient transfer of energy from phytoplankton to upper trophic levels during productive periods (Falk-Petersen et al. 2007), one may expect that summer Arctic food webs may deviate from theoretical predictions (Fig. 1; Rooney et al. 2006), and instead be driven predominantly by only one carbon source, i.e. phytoplankton. An additional primary production source in some coastal Arctic Seas, however, is macroalgae, although few studies have assessed whether Arctic consumers rely heavily on macroalgal carbon (Dunton & Schell 1987, Hobson et al. 1995). Given the differential biomass turnover rate of macroalgae compared to phytoplankton, macroalgae could provide the basis for an important weak energy channel that could supplement the strong energy channel based on phytoplankton. Such a structure, if apparent, could be important for the stability of coastal Arctic food webs. More broadly, identifying whether or not the coupling of different energy channels by upper trophic levels occurs in Arctic food webs would lend insight into the ubiquity of such structures among ecosystems.

In the present study, we used stable nitrogen ($\delta^{15}\text{N}$), carbon isotopes ($\delta^{13}\text{C}$) and fatty acids to delineate the structure of a coastal, Arctic food web and to answer the following 2 questions: (1) is a coastal Arctic food web structured such that lower trophic levels

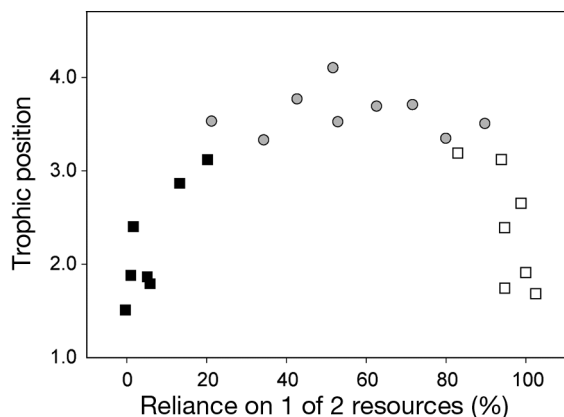


Fig. 1. Conceptual model showing hypothesized food web structure arising from lower trophic levels (black and white symbols) feeding predominantly within 1 of 2 energy channels and upper trophic levels (grey symbols) acting as resource couplers by using prey from both energy channels

use distinct energy channels, based on phytoplankton and macroalgae, which are coupled by upper trophic levels? (2) If so, what is the relative contribution of different resources to upper trophic levels?

MATERIALS AND METHODS

Study site and species sampling

Sampling was conducted within or just outside the mouth of Pangnirtung fjord in Cumberland Sound, Baffin Island (see Fig. S1 in the Supplement for a map of sampling locations; available at www.int-res.com/articles/suppl/m482p017_supp.pdf). Pangnirtung fjord is characterized by wide (up to 600 m) intertidal flats, expansive growths of rockweed *Fucus distichus*, a maximum depth of 150 m and ice cover from November until June or July (see Fig. S2 in the Supplement for photographs). Parts of Cumberland Sound, including the southern portion of Pangnirtung fjord sampled here, are immediately below the Arctic Circle (by ~30 km), but we retain the convention of previous authors by defining Cumberland Sound as part of the Canadian Arctic (e.g. Lee 1973). Cumberland Sound waters experience colder temperatures and a longer duration of ice-cover than similar latitudes in Europe due to the influence of the Gulf Stream on the latter. Both Arctic (i.e. Baffin Island Current) and Atlantic (i.e. Greenland Current) water masses (Aitken & Gilbert 1989) influence Cumberland Sound. The fauna is subsequently of both Arctic and Atlantic Ocean origin (Aitken & Gilbert 1989), which is characteristic of other Arctic fjords (e.g. Kongsfjorden, Svalbard; Hop et al. 2006). Throughout the Canadian Arctic, marine benthic algae are predominantly of Atlantic origin (Lee 1973). Carmack & Wassmann (2006) classify Cumberland Sound, and the remainder of Canadian Archipelago shorelines, as 'outflow shelves' in their review of pan-Arctic shelf types.

Particulate organic matter (POM), rockweed and 21 benthic and pelagic invertebrate and vertebrate species were sampled for stable isotopes and/or fatty acids during summer in August 2007, 2008 and 2009 and classified into functional groups (see Table 1 for species sampling year and functional group classifications) based on previously reported habitat and diet attributes (Table S1 in the Supplement). The following species were sampled only for stable isotopes: POM, jellyfish *Agnatha digitale*, periwinkle *Littorina* sp., arrow worm *Sagitta* sp. and herring *Clupea harengus*. Similar sized individuals of each species

were collected, with the exception of adult sculpin *Myoxocephalus scorpius*, of which small (<24 cm) and large (>24 cm) size classes were sampled and treated separately due to size-related diet variability in this species (Cardinale 2000).

POM was sampled via a 10 µm plankton net (Wildlife Supply Company®) from 50 m to the surface and rockweed was sampled either by hand or by Ponar grab sampler. Each rockweed sample consisted of the distal tip of one leaf from one plant. Benthos were sampled via dip net, except for scallops *Chlamys islandica* which were collected in water 30 to 40 m deep using a dredge. Zooplankton were captured by towing a plankton net (243 µm mesh; Wildlife Supply Company®) at the surface and by performing vertical hauls down to ~50 m. Pelagic fish were sampled via dip nets and gill nets and sculpin were captured using baited fishing line. The remaining fishes were collected using bottom long lines (50 hooks, ~200 m long). Marine mammals were captured during Inuit subsistence hunting.

We sampled representative species for each functional group listed in Table 1. Abundance and biomass data do not exist for Cumberland Sound species, but we collected the most commonly observed species during our sampling efforts. The species sampled included those unique to sub-Arctic and Arctic Seas (e.g. copepod *Calanus hyperboreus*; ringed seal *Pusa hispida*). Species that enter Cumberland Sound from Atlantic waters (herring and capelin *Mallotus villosus*) or from the surrounding rivers (arctic char *Salvelinus alpinus*) were also sampled because they are members of the summer food web. The obvious species missing from our study is polar cod *Boreogadus saida* which were not present in our samples.

Multiple individuals (2 to 10) of each zooplankter, polychaete worm and amphipod *Gammarus oceanicus* were pooled for stable isotope and fatty acids samples to obtain sufficient material for analysis. Similar tissues were sampled for both stable isotopes and fatty acids, except that dorsal muscle and blubber (inner layer) were sampled from marine mammals for these analyses, respectively. All samples were placed into cryovials and immediately frozen at -20°C (stable isotopes) and at -80°C (fatty acids), and kept at these temperatures, until analysis.

Stable isotope and fatty acid analysis

Lipid extracted samples were analyzed for stable isotopes as previously described in McMeans et al.

Table 1. Species sampled from Cumberland Sound during summer (August). Year of sampling, tissue analyzed and associated codes for Fig. 2 are provided. Benthic herbivores are either filter-feeders (FF) or grazers (G). Values of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ (both ‰), trophic positions (TP) and percent reliance on phytoplankton versus macroalgae (α) are mean \pm SD (species without SD had $n = 1$)

Functional group	Species	Common name	Fig. 2	Date	Tissue	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	TP	α		
Primary producers	Particulate organic matter	POM	na	2008	Whole	-22.1	8.24				
	<i>Fucus distichus</i>	Rockweed	na	2008 2009	Leaf	-14.9 \pm 1.17 -15.13 \pm 1.80	6.40 \pm 1.08 7.49 \pm 1.29				
Zooplankton	Herbivores	<i>Calanus hyperboreus</i>	1 ^a	2008	Whole	-20.37 \pm 0.14	9.88 \pm 0.53	2.0 \pm 0.2	98 \pm 3		
	Omnivores	<i>Mysis oculata</i> ^b	Mysid	2	2009	Whole	-20.84 \pm 0.49	9.90 \pm 0.34	2.0 \pm 0.1	96 \pm 6	
		<i>Aglantha digitale</i>	Jellyfish	3	2009	Whole	-20.79 \pm 0.10	9.02 \pm 0.13	1.7 \pm 0.1	95 \pm 2	
		<i>Myoxocephalus scorpius</i> (larvae)	Larval sculpin	4	2008	Whole	-20.46 \pm 0.26	10.12 \pm 0.39	2.1 \pm 0.1	99 \pm 1	
		<i>Stichaeus punctatus</i> (larvae)	Larval arctic shanny	5	2009	Whole	-20.54 \pm 0.44	10.54 \pm 0.27	2.2 \pm 0.1	95 \pm 7	
		<i>Sagitta</i> sp.	Arrow worm	6	2009	Whole	-21.09 \pm 0.22	10.63 \pm 0.34	2.2 \pm 0.1	100 \pm 1	
Benthos	Herbivores	<i>Chlamys islandica</i> (FF)	7 ^a	2008	Muscle	-19.25 \pm 0.47	14.1 \pm 0.01	3.2 \pm 0.1	94 \pm 9		
	Carnivores	<i>Hiatella arctica</i> (FF)	Scallop	7 ^a	2008	Muscle	-18.63 \pm 0.65	9.65 \pm 0.16	1.9 \pm 0.1	59 \pm 15	
		<i>Gammarus oceanicus</i> (G)	Clam	8	2009	Muscle	-18.79 \pm 0.20	8.89 \pm 0.38	1.7 \pm 0.1	53 \pm 3	
		<i>Littorina</i> sp. (G)	Amphipod	9	2008	Mantle	-19.52 \pm 0.23	8.14 \pm 0.43	1.5 \pm 0.1	71 \pm 5	
		<i>Tectura testudinalis</i> (G)	Periwinkle	10	2008	Whole	-18.55 \pm 0.29	9.48 \pm 0.71	1.9 \pm 0.2	57 \pm 5	
		<i>Buccinum cyaneum</i>	Limpet	11	2009	Whole	-16.13 \pm 0.62	9.39 \pm 0.50	1.8 \pm 0.1	5 \pm 8	
		Nudibranch ^c	Whelk	12	2008	Foot	-15.96 \pm 0.46	9.87 \pm 0.19	2.0 \pm 0.1	4 \pm 5	
		Carnivores	<i>Polychaete</i> ^d	Nudibranch	13	2008	Foot	-17.27 \pm 0.63	12.92 \pm 0.58	2.9 \pm 0.2	46 \pm 12
			<i>Somniosus microcephalus</i>	Greenland shark	21	2008	Whole	-16.81 \pm 0.23	13.54 \pm 0.18	3.1 \pm 0.1	39 \pm 6
	Fishes & marine mammals	<i>Amblyraja hyperborea</i>	Polychaete	14	2008	Whole	-16.18 \pm 0.80	11.21 \pm 0.93	2.4 \pm 0.3	13 \pm 11	
		<i>Clupea harengus</i>	Greenland shark	21	2008	Muscle	-17.74 \pm 0.67	17.07 \pm 0.68	4.6 \pm 0.3	86 \pm 14	
		<i>Mallotus villosus</i>	Arctic skate	18	2007	Muscle	-18.37	16.79	3.9	100	
		<i>Salvelinus alpinus</i>	Herring	15	2007	Muscle	-19.85	13.4	2.9	100	
		<i>Myoxocephalus scorpius</i> (<24 cm)	Capelin	16	2008	Muscle	-19.37 \pm 0.15	13.51 \pm 0.29	3.1 \pm 0.1	96 \pm 3	
<i>Phoca groenlandica</i>		Arctic char	17	2008	Muscle	-18.61 \pm 0.23	14.51 \pm 0.64	3.4 \pm 0.2	85 \pm 8		
<i>Pusa hispida</i>		Shorthorn	19	2008	Muscle	-17.99 \pm 0.58	15.07 \pm 0.39	3.5 \pm 0.1	74 \pm 12		
		Sculpin	20	2008	Muscle	-16.79 \pm 1.07	17.17 \pm 1.14	4.1 \pm 0.3	58 \pm 18		
		Harp seal	22	2008	Muscle	-17.95 \pm 0.13	14.66 \pm 0.55	3.9 \pm 0.3	80 \pm 6		
		Ring seal	23	2008	Muscle			4.1 \pm 0.3	91 \pm 10		

^aMean of 2008 and 2009 shown in Fig. 2

^bBenthic-associated but captured in zooplankton nets

^cUnknown species

^dUnknown species but predatory based on large jaws

(2009). Acid washing was performed for amphipod and periwinkle (details provided in the Supplement). Stable isotopes are expressed as delta δ values where $\delta X = 1000[(R_{\text{sample}} \times R_{\text{standard}}^{-1}) - 1]$, $X = {}^{15}\text{N}$ or ${}^{13}\text{C}$ and R = the ratio of ${}^{15}\text{N}:$ ${}^{14}\text{N}$ or ${}^{13}\text{C}:$ ${}^{12}\text{C}$. Replicate analyses of NIST (National Institute of Standards and Technology) standard bovine muscle (NIST 8414, $N = 159$) and internal lab standard (tilapia muscle, $N = 159$) yielded a precision (i.e. 1 SD) of 0.13 and 0.20‰ for $\delta^{15}\text{N}$ and 0.07 and 0.08‰ for $\delta^{13}\text{C}$, respectively.

Fatty acid methyl esters were generated from the total lipid extract (see McMeans et al. 2012 for detailed analytical methods) and separated on a Hewlett Packard 6890 gas chromatograph (GC) (splitless injection, column = Supelco [SP-2560 column]). Fatty acids were identified using a 37 component fatty acid standard (Supelco 47885-U) and are reported as proportions (i.e. % of total identified fatty acids).

Data analyses

Applying stable isotopes to accurately estimate trophic positions (TP) and carbon sources (α , in the present study, relative reliance on phytoplankton versus macroalgae) requires identifying appropriate baselines (Post 2002). Values of $\delta^{13}\text{C}$ are often higher in macroalgae versus phytoplankton and have been used as baselines in isotope mixing models (Fredriksen 2003, Nilsen et al. 2008). However, obtaining a phytoplankton sample free of other carbon sources and detritus is difficult (Iken et al. 2010) and using POM or offshore phytoplankton values as baselines in mixing models can result in over-estimation of consumer reliance on macroalgae (Miller & Page 2012). Primary consumers, on the other hand, are temporarily and spatially less variable in their $\delta^{13}\text{C}$ than primary producers (Vander Zanden et al. 1998, Iken et al. 2010) and should also be good integrators of spatial and among-species isotopic variability within available phytoplankton and macroalgae. We, therefore, used the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of a primary consumer (i.e. assumed to occupy $\text{TP} = 2$) of phytoplankton (copepod *Calanus hyperboreus*; Stevens et al. 2004, Søreide et al. 2008) and macroalgae (limpet *Tectura testudinalis*; Fredriksen 2003) as baselines for calculations of TP and α . Since outputs from 1- and 2-source TP models (see Post 2002) were similar, the following 1-source TP model was applied for all individuals:

$$\text{TP}_{\text{consumer}} = \text{TP}_{\text{baseline}} + \frac{\delta^{15}\text{N}_{\text{consumer}} - \delta^{15}\text{N}_{\text{baseline}}}{\Delta^{15}\text{N}} \quad (1)$$

Copepod mean $\delta^{15}\text{N}$ (from the same year as the given consumer was sampled) was used as the $\delta^{15}\text{N}_{\text{baseline}}$ and 3.4‰ was used as the diet-tissue discrimination factor (i.e. $\Delta^{15}\text{N}$; Post 2002). Calculating Greenland shark *Somniosus microcephalus* TP can be problematic due to, for example, uncertainty over $\Delta^{15}\text{N}$ (Hussey et al. 2012). The Greenland shark's TP was, therefore, calculated using: (1) 2.3‰ for the $\Delta^{15}\text{N}$ (derived for large sharks; Hussey et al. 2010), and (2) the mean $\delta^{15}\text{N}$ of capelin as the $\delta^{15}\text{N}_{\text{baseline}}$ (capelin $\text{TP} = 3.1$, Table 1). Percent reliance on phytoplankton versus macroalgae (α) was calculated for each individual using a 2-source mixing equation (Post 2002) modified to incorporate enrichment of consumer ${}^{13}\text{C}$ at each trophic step (i.e. $\Delta^{13}\text{C}$) above the primary consumer baselines as follows:

$$\alpha = \frac{\delta^{13}\text{C}_{\text{consumer}} - [\Delta^{13}\text{C} \times (\text{TP}_{\text{consumer}} - \text{TP}_{\text{baseline}})] - \delta^{13}\text{C}_{\text{limpet}}}{\delta^{13}\text{C}_{\text{copepod}} - \delta^{13}\text{C}_{\text{limpet}}} \times 100 \quad (2)$$

$\Delta^{13}\text{C}$ was set at 0.8‰ (Dunton & Schell 1987, Fredriksen 2003), $\text{TP}_{\text{baseline}}$ is 2 and $\text{TP}_{\text{consumer}}$ is the result of the 1-source TP model for each individual (Eq. 1). By using primary consumers, instead of primary producers, as baselines for isotope models, we assumed that the stable isotope signatures of copepod and limpet represented an integrated signature of available phytoplankton and macroalgae in the area. Since all of our sampling was conducted within Pagnirtung fjord (with the exception of arctic skate and herring, Fig. S1), we consider this an acceptable assumption for elucidating the structure of this coastal food web.

The data were first assessed for normality (q-q plots) and homoscedacity (Levene's tests). Since rockweed, copepod and scallop were sampled during multiple years for stable isotopes (2008 and 2009, Table 1), 2-way ANOVAs (factors = year and species) were used to identify inter-annual differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for copepod and scallop. Separate Welch's t tests were used for this purpose in rockweed due to higher stable isotope variability in this versus other sampled species (Table 1). ANOVA and Tukey's post hoc tests were used to compare $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and TPs among functional groups (i.e. zooplankton versus benthos versus fish and marine mammals) and $\delta^{13}\text{C}$ -derived values of α (i.e. % reliance on phytoplankton) were compared among these groups via a Kruskal-Wallis non-parametric ANOVA followed by Mann-Whitney tests (with Bonferroni corrections).

Different classes of macroalgae differ in their fatty acid profiles, but in general, macroalgae have lower

C₂₂ polyunsaturated fatty acids (PUFA) relative to phytoplankton (Graeve et al. 2002). The brown macroalgae, Phaeophyta, also have high proportions of n-6 PUFA (Graeve et al. 2002) relative to phytoplankton, which have high 16:1n-7 and n-3 PUFA (Stevens et al. 2004). No biomass data exist for Cumberland Sound macroalgae, but rockweed is clearly abundant on the shores of Pangnirtung fjord (Fig. S2). We, therefore, assume that rockweeds provide the largest source of fresh and detrital macroalgae to consumers. Fatty acid profiles of Cumberland Sound rockweed versus published values for POM from the Canadian Arctic (Table S2 in the Supplement) agreed with previous reports that, in general, brown macroalgae have high proportions of certain fatty acids including 18:2n-6 and 20:4n-6 (Graeve et al. 2002) and phytoplankton have high 16:1n-7, 22:6n-3 and n-3:n-6 (Stevens et al. 2004). To identify similarities in the proportions of these 5 fatty acid trophic markers among Cumberland Sound species, non-metric multidimensional scaling (NMDS, dimensions = 2, Euclidean distances) was performed on: (1) lower trophic levels: rockweed, zooplankton, benthos and (2) upper trophic levels: fish and marine mammals. All analyses were performed in R (R Development Core Team 2010) and the significance level was set at 0.01.

RESULTS

No differences existed in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between 2008 and 2009 for rockweed (Welch's *t* test, $p > 0.05$), copepod or scallop (2-way ANOVA, $p > 0.05$, Table 1 provides all values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). The among-functional group comparison of $\delta^{15}\text{N}$ and $\delta^{15}\text{N}$ -derived TPs (Table 1) revealed that zooplankton = benthos < fish and marine mammals (Table 2). Values of $\delta^{13}\text{C}$ decreased significantly from benthos > fish and marine mammals > zooplankton, and calculated values of α exhibited the opposite trend, increasing from benthos < fish and marine mammals < zooplankton (Fig. 2, Table 2). Thus, coupling of macroalgae and phytoplankton energy channels by upper trophic levels was apparent because calculated values of α for fish and marine mammals (i.e. 58 to 100) fell in between, although overlapped with, that of benthos (4 to 71) and zooplankton (94 to 100) (Fig. 2). Herbivorous, omnivorous and carnivorous zooplankton relied entirely on pelagic carbon (Fig. 2, $\alpha > 95$), whereas benthos exhibited a wider range of resource use, from heavy reliance on macroalgae in periwinkle ($\alpha = 5 \pm 8$, mean \pm SD) and a carnivorous

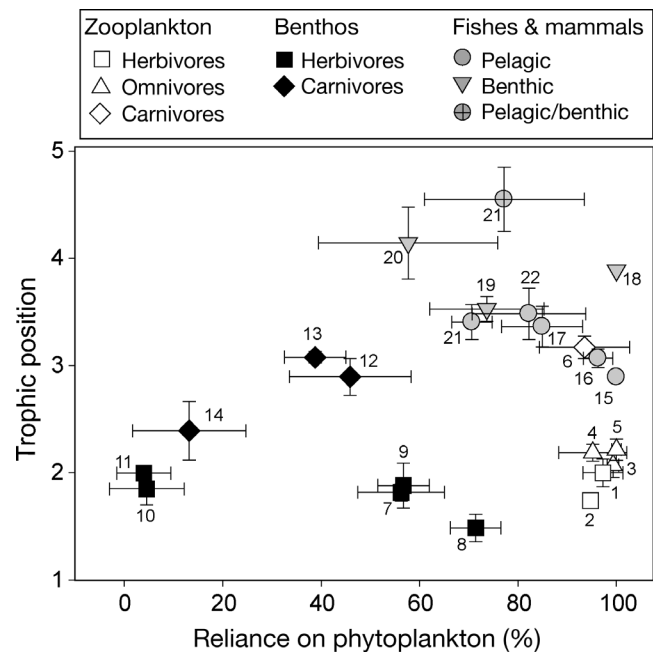


Fig. 2. Percent (%) reliance on phytoplankton (α) and trophic positions of benthos (black symbols), zooplankton (white) and fish and marine mammal consumers (grey) from Cumberland Sound (mean \pm SD, see Table 1 for species codes). Values of α are the results of a 2-source $\delta^{13}\text{C}$ mixing model with primary consumers of phytoplankton and macroalgae as endpoints. Trophic positions were calculated using a one-source, $\delta^{15}\text{N}$ -based model

polychaete (unknown species, $\alpha = 13 \pm 11$), to the use of both macroalgae and phytoplankton by scallop, clam *Hiatella arctica* and amphipods (Fig. 2, $\alpha = 53 \pm 3$ to 71 ± 5). The carnivorous whelk *Buccinum cyanum* and nudibranch (unknown species) appeared to couple the 2 aforementioned groups (Fig. 2, $\alpha = 46 \pm 12$ and 39 ± 6 , respectively).

The NMDS performed on lower trophic level species' fatty acid proportions supported $\delta^{13}\text{C}$ -derived α values because all zooplankton separated away from rockweed due to higher proportions of phytoplankton trophic markers (16:1n-7, 22:6n-3, n-3:n-6), and lower proportions of the macroalgae trophic markers 18:2n-6 and 20:4n-6 (Fig. 3A, fatty acid proportions provided in Table S2). Clam and amphipod (high 16:1n-7) and scallop (from both 2008 and 2009, high 22:6n-3, Fig. 3A) fatty acids supported some phytoplankton consumption, as indicated by α values (53 to 71), although closer proximity to rockweed on the NMDS plot indicates greater reliance on this carbon source by amphipod versus the clam and scallop (Fig. 3A). The remainder of benthos clustered more closely to rockweed due to high proportions of 18:2n-6 and 20:4n-6 (Fig. 3A), supporting consumption of

Table 2. Significant differences in food web metrics among Cumberland Sound functional groups based on 3 ANOVAs and 1 Kruskal-Wallis non-parametric ANOVA. TP: $\delta^{15}\text{N}$ -derived trophic position; α : $\delta^{13}\text{C}$ -derived percent reliance on phytoplankton; df: degrees of freedom

Metric	Functional Group	Test statistic	df	p
Vertical food web structure				
$\delta^{15}\text{N}$	Zooplankton = benthos < fish & mammals	$F = 255.01$	2,150	<0.001
TP	Zooplankton = benthos < fish & mammals	$F = 195.50$	2,150	<0.001
Horizontal food web structure				
$\delta^{13}\text{C}$	Zooplankton < fish & mammals < benthos	$F = 134.57$	2,150	<0.001
α	Zooplankton > fish & mammals > benthos	$\chi^2 = 106.58$	2	<0.001

macroalgae as indicated by α values. High phytoplankton fatty acid trophic markers in copepod (e.g. high 16:1n-7) and macroalgae markers in limpet (e.g. high 20:4n-6) support their respective consumption of these carbon sources and their use as the phytoplankton and macroalgae baselines, respectively, in calculations of α .

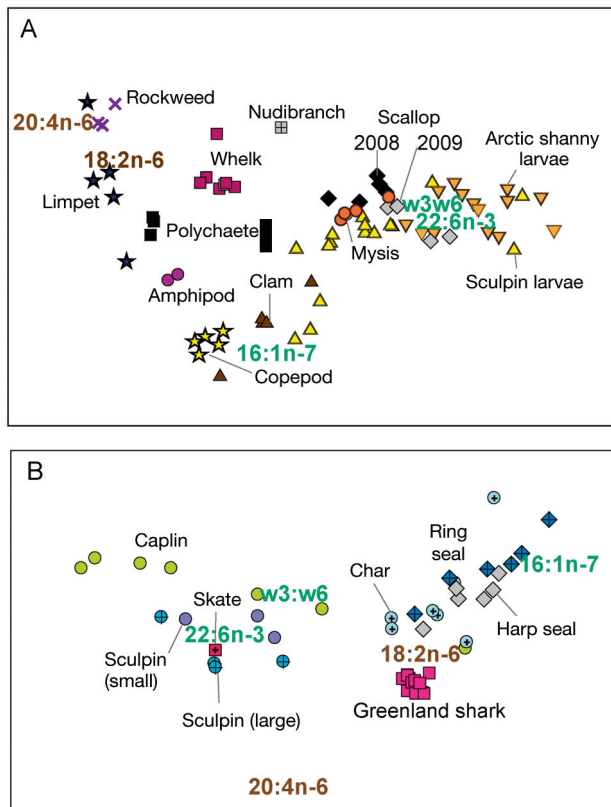


Fig. 3. Results of non-metric multidimensional scaling performed on phytoplankton (green) and macroalgae (brown) fatty acid trophic markers of: (A) rockweed, zooplankton, benthos (dimensions = 2, stress = 0.04), and (B) fishes and marine mammals (dimensions = 2, stress = 0.02, see Table 1 for scientific names). 'Small' and 'large' sculpin were <24 cm and >24 cm, respectively

Fish and marine mammals separated from each other on the NMDS plot of upper trophic levels due to different relative contributions of phytoplankton fatty acids (Fig. 3B), likely due to reliance on phytoplankton as indicated by α values, and species-specific fatty acid requirements. Unlike the other fatty acid trophic markers, mean proportions of 18:2n-6 varied little among fish and marine mammal species (1.1 to 1.8%, Table S2) and, therefore, may not be useful as a trophic marker in upper trophic levels (which agrees with results of Hall et al. 2006). Proportions of 20:4n-6 (Table S2), on the other hand, increased from a mean \pm SD of $0.4 \pm 0.1\%$ in the pelagic capelin ($\alpha = 96 \pm 3$) to $1.5 \pm 0.2\%$ in the benthic-pelagic Greenland shark ($\alpha = 86 \pm 14$) to $4.4 \pm 1.5\%$ in large individuals (i.e. >24 cm) of the benthic sculpin ($\alpha = 58 \pm 18$), which coincides with α values that indicate low, medium and high reliance on macroalgae-derived carbon in these species, respectively. Higher 20:4n-6 in the arctic skate (3.7%) than the pelagic capelin could indicate a greater reliance on macroalgae-derived carbon in arctic skate than indicated by its α value of 100 (Fig. 2). Based on combined stable isotope and fatty acid data, all fish and marine mammal species sampled acted as couplers of phytoplankton- and rockweed-based resources to some extent except for capelin (i.e. $\alpha = 96 \pm 3$, high proportions of phytoplankton fatty acids) and perhaps herring (i.e. $\alpha = 100$, no fatty acid data).

DISCUSSION

Results from the present study indicate that the coastal Cumberland Sound food web is structured such that separate energy channels based on different basal resources (phytoplankton and macroalgae) were coupled by upper trophic levels, which agrees with previously reported food web structures (Rooney et al. 2006, McCann & Rooney 2009) and further indi-

cates that such structures arise even in seasonally variable ecosystems. The almost exclusive use of phytoplankton by zooplankton, and macroalgae by the benthic herbivores, limpet and periwinkle, supported the existence of energy channels in Cumberland Sound. These results are consistent with previous findings that phytoplankton is the dominant energy source to Arctic zooplankton during the summer months (Søreide et al. 2006), and that benthic herbivore grazers exert strong control over, and, therefore, effectively exploit macroalgae (including *Fucus* spp.) in both intertidal and subtidal marine habitats (Poore et al. 2012).

For the fishes and marine mammals, phytoplankton was an important energy source based on high values of α (i.e. $\delta^{13}\text{C}$ -derived % reliance on phytoplankton) and high proportions of phytoplankton fatty acid trophic markers, which supports the notion that production in upper trophic levels is predominantly phytoplankton-driven in many Arctic seas (Hobson et al. 1995, Renaud et al. 2011). However, macroalgae also played a role in fueling the food web because some macroalgae-derived carbon was utilized by almost all fishes and marine mammals sampled (i.e. most species had mean $\alpha < 100$). Values of α also varied within-species based on standard deviations (Table 1), indicating intra- as well as inter-specific variability in the extent of resource coupling. The ability of individuals and species to differentially feed on multiple prey types is advantageous for consumers inhabiting temporally variable ecosystems like the Arctic, and based on recent advances in food web theory (McCann & Rooney 2009), such coupling of different resources is also likely to be important for Arctic food web stability.

Higher $\delta^{13}\text{C}$ in the bivalves (clam and scallop) and amphipod relative to zooplankton suggests that the phytoplankton consumed by these benthos was likely to be in the form of detritus (sedimenting POM typically becomes ^{13}C enriched; Lovvorn et al. 2005). Thus, a consumer in Cumberland Sound that preys on herbivorous zooplankton and amphipods, like Arctic char (Table S1), could obtain carbon that originated from 2 different phytoplankton pools: phytoplankton (consumed by zooplankton) and phytodetritus (consumed by amphipods), as well as from rockweed (consumed by amphipods). Arctic benthos are known to use a wide range of resources, which likely explains their ability to maintain high biomass even in areas of low autochthonous production (Feder et al. 2011). Within the framework of food web theory, however, the ability of benthos to use multiple resources could also function to increase the

number of basal resource types that ultimately support production in upper trophic levels, a potentially important yet unrecognized role in Arctic food webs.

Both stable isotope and fatty acid analysis suggested the existence of distinct energy channels within the benthos, based on macroalgal and phytodetrital carbon, that were coupled by the benthic predators whelk and nudibranch. Our results, therefore, provide empirical evidence to support the suggestion that the coupling of different energy channels is repeated at various scales (McCann & Rooney 2009). Other mobile, benthic omnivores (e.g. crabs and shrimps; Feder et al. 2011) would also be expected to couple distinct energy channels within benthic food webs.

Ice and pelagic algae can have similar fatty acids (Søreide et al. 2008) and we, therefore, cannot discount the possibility that ice algae, in addition to phytoplankton, also contributed to high levels of n-3 and 16:1n-7 fatty acids observed in the suspension feeding bivalves and amphipods. However, we are confident based on low 20:4n-6 and high 16:1n-7, 22:6n-3 and n-3:n-6 that macroalgae was not the major source of energy to these species. Other potential energy sources not sampled here include allochthonous terrestrial carbon, which can be important to consumers in some Arctic seas (e.g. Beaufort Sea; Dunton et al. 2006). However, the POM sample from Cumberland Sound (-22.13‰) clearly had a marine $\delta^{13}\text{C}$ signature (terrestrial carbon -27 to -31‰ , marine carbon -22 to -25‰ ; Dunton et al. 2006), and the small $\delta^{13}\text{C}$ range separating copepods and bivalves of $\sim 2\text{‰}$ is consistent with tight benthic-pelagic coupling and low reliance on depleted, terrestrial carbon by Cumberland Sound consumers (similar to results from the Chukchi Sea; Dunton et al. 2006).

Both stable isotopes and fatty acids supported reliance on rockweed by limpet and phytoplankton by copepod. Previous studies have also concluded that limpets obtain 100% of their carbon from macroalgae (i.e. *Helcion pellucidum*; Fredriksen 2003) and that the copepod *Calanus hyperboreus* relies heavily on phytoplankton (Søreide et al. 2006). Copepod $\delta^{15}\text{N}$ has also been previously used to baseline TP calculations (Hobson et al. 2002, Hedeholm et al. 2012). The calculated TP of species in the present study, based on copepod $\delta^{15}\text{N}$, and calculated values of α , using copepod and limpet $\delta^{13}\text{C}$ as baselines, agreed with putative diet information (Table S1). For example, capelin are known consumers of zooplankton (Scott & Scott 1988) that feed at TP = 2.8 to 3.1 in Greenland waters (Hedeholm et al. 2012). Calculated TP of 3.1 and 96% reliance on phytoplankton-derived carbon

for capelin from the present study (Table 1), as well as higher proportion of phytoplankton than macroalgal fatty acid trophic markers (e.g. 20:4n-6 = 0.4%), support this previous diet information. Other fishes, such as shorthorn sculpin, are known to consume both pelagic prey, like small herring, as well as benthic-associated invertebrates like *Mysis* (Cardinale 2000), crab and other shorthorn sculpin (B. McMeans unpubl. data), which supports their calculated TP and α of 3.5 and 74% for small sculpin and 4.1 and 58% in large sculpin, respectively. Therefore, the assignment of species to functional groups based on literature data was supported by our stable isotope and fatty acid analysis. Selecting different species within each functional group should not alter our conclusions because previous studies, which include different Arctic zooplankton and benthic species than those sampled here, found that zooplankton rely heavily on phytoplankton production and that benthos use a wider range of carbon sources than zooplankton (Tamelander et al. 2008). Although not sampled in the present study, polar cod are likely to have acted as resource couplers because they are generalist consumers of both pelagic and benthic invertebrates, with diet compositions likely reflecting local prey availability (Renaud et al. 2012). Additional work is required to explore this idea. Further, the range of carbon sources used by benthos sampled in the present study, based on $\delta^{13}\text{C}$ ranging from -15.96 to -19.52‰ ; is within previously reported ranges for benthos from other Arctic fjords, including Kongsfjorden (-16.9 to -19.6‰ , Renaud et al. 2011) and from offshore ecosystems like the Chukchi Sea (-15.89 to -22.15‰ ; Iken et al. 2010). Based on these findings, we hypothesize that the coupling of different energy channels by upper trophic levels is a common feature of Arctic food webs, including coastal fjords and the open ocean, albeit potentially based on different basal resources than analyzed here (e.g. phytoplankton versus detritus or terrestrial carbon instead of macroalgae).

Another potential factor that could affect our results is that mobile, upper trophic levels such as, for example, Greenland sharks, could have been feeding in areas outside of Cumberland Sound. Stable isotope ratios are known to vary over small and large scales in Arctic seas, although $\delta^{13}\text{C}$ is less spatially variable than $\delta^{15}\text{N}$ (Hansen et al. 2012). The fact that limpet $\delta^{13}\text{C}$ in Cumberland Sound was similar to what was found in the Norwegian sea (-16.16‰ ; Fredriksen 2003) and copepod $\delta^{13}\text{C}$ from the present study was in agreement with what has been found for conspecifics from the high Arctic (i.e. -20.4‰ ;

Hobson & Welch 1992), lends confidence to the supposition that feeding in macroalgal and phytoplankton food chains outside of Cumberland Sound would be reflected in consumer stable isotope profiles. Further, fatty acid data are generally more variable among- than within-species, such that geographical variability in prey fatty acids is likely low (Thiemann et al. 2007). We, therefore, assume that the use of macroalgal-based prey in areas outside of Cumberland Sound would be reflected in predator fatty acid profiles.

The pulsed nature of phytoplankton growth, which is a characteristic of Arctic seas (Weslawski et al. 1991), would impart a temporal aspect to the food web structure reported here. In the pelagic energy channel, phytoplankton and secondary zooplankton production is tightly coupled (Rysgaard et al. 1999), indicating a strong phytoplankton-herbivorous zooplankton interaction typical of a strong energy channel (Rooney et al. 2006). Thus, energy (e.g. in the form of lipids) accumulated by herbivorous copepods like *Calanus hyperboreus* and *C. glacialis* is rapidly and efficiently transferred to upper trophic levels early in the productive season (Fig. 4; Falk-Petersen et al. 2007). In contrast, secondary benthic production is not always coupled with phytoplankton production (Link et al. 2011), indicating a weak interaction between producer and benthic consumer. Instead, there appears to be a lag time between food input to the sea floor and increased benthic biomass (Link et al. 2011), which suggests that carbon routed through the benthic channel (as phytodetritus or macroalgae) would not reach upper trophic levels until later in the summer or fall (Fig. 4). One of the major elements through which energy channels coupled in space confer stability to food webs is the top-down induced asynchrony in resource abundance between energy channels (Rooney et al. 2006, McCann & Rooney 2009). Here, we propose that Arctic food webs (and presumably other food webs in highly seasonally environments) can be structured such that consumers couple resources that are also compartmentalized in time (Fig. 4; McCann et al. 2005), and that the mechanism generating asynchrony between benthic and pelagic energy channels is the bottom-up effect of pulsed phytoplankton growth, which is a different (but not mutually exclusive) mechanism to the top-down mechanism proposed by Rooney et al. (2006).

Climate warming could negatively impact the food web structure reported here through both bottom-up (i.e. removal of resource heterogeneity) and/or top-down mechanisms (i.e. removal of resource coupling

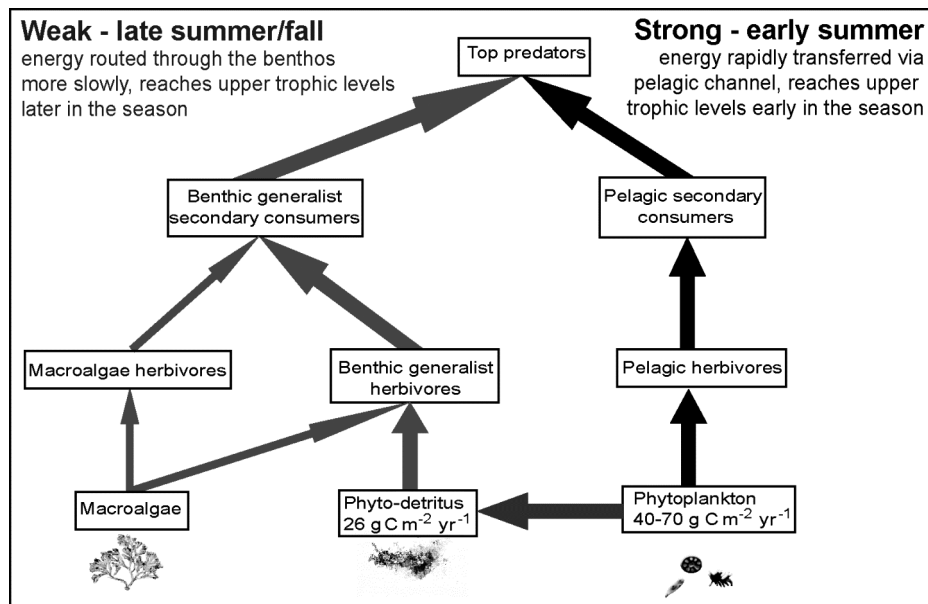


Fig. 4. Conceptual model illustrating the transfer of energy through strong (phytoplankton) and weak (macroalgae and phyto-detritus) energy channels in a hypothetical Arctic marine food web. Estimates of annual phytoplankton productivity and sedimentation of phytoplankton reaching the benthos as phytodetritus are from Frobisher Bay, Baffin Island (Atkinson & Wacasey 1987). Thicker arrows arising from phytoplankton and phytodetritus to consumers reflect the larger amount of energy moving through these channels versus macroalgae, based on previous Arctic ecosystem energy flow models (e.g. integrated over the entire Lancaster Sound area, phytoplankton and macroalgae production was 55 and 1.7 g C m⁻² yr⁻¹, respectively, Welch et al. 1992)

in space or time by upper trophic levels). Resource heterogeneity could decline, for example, through decreased benthic biomass. Declining benthic biomass is predicted to arise under certain climate change scenarios from the effects of decreased benthic-pelagic coupling and increased sedimentation and habitat homogenization (Wassmann et al. 2011, Weslawski et al. 2011). Alternatively, macroalgae biomass could increase with decreased ice cover due to decreased ice scouring (Weslawski et al. 2011), and could become an increasingly important resource for benthos in the face of decreased pelagic-benthic coupling. From a top-down perspective, reductions in sea ice and warmer water temperatures have already resulted in the once benthic-dominated community of the Bering Sea shifting towards dominance by pelagic fish (Grebmeier et al. 2006). Increasing contribution of pelagic consumers to Arctic food webs by newly arriving species like capelin and herring, that rely entirely on pelagic carbon (i.e. through consumption of zooplankton, present study), could serve to decouple Arctic food webs. Anticipating food web level shifts due to climate change is difficult, and the outcome for Cumberland Sound will depend on the relative strength of these mechanisms.

Since not all Arctic areas support macroalgae growth, including the open ocean, and are more influenced by, for example, terrestrial carbon (e.g. Beaufort Sea; Dunton et al. 2006), or ice algae during ice break up (Tamelander et al. 2008), further insight into climate change affects on a pan-Arctic scale would be gained from comparing structures of other Arctic food webs to the results presented here for Cumberland Sound.

In summary, our results show that energy channels based on phytoplankton and macroalgae exist and are coupled by upper trophic levels in a coastal, seasonally ice-covered fjord in late summer. In a broad sense, our study affirms that heterogeneity in basal resources and feeding of upper trophic level consumers (within and between resource channels) are common structures, which exist even in food webs that experience high seasonality. We provide evidence that resource coupling was iterative within the Cumberland Sound food web and suggest that upper trophic level consumers were coupling resources in space as well as time due to the pulsed nature of phytoplankton growth in Arctic seas. Our study provides testable hypotheses that food webs from other Arctic ecosystem types (e.g. open ocean) or during

different times of the year (e.g. during ice break up) will also exhibit distinct energy channels that are coupled by upper trophic levels. These energy channels could be based on different resources than those sampled here, including ice algae or terrestrial carbon. Further work is also required to explore how inter- and intra-specific variability in the extent of resource coupling in predator populations influences food web structure and stability. Results from our study demonstrate that food web theory provides a useful framework with which to interpret the potential effects of environmental change on food web structure and stability. From a food web perspective, our results suggest that it is not changes in biomass or species composition, per se, but the removal of heterogeneity in resource use among, and, perhaps within species that is the biggest threat to the stability of Arctic food webs.

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