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SPATIAL AND TEMPORAL PATTERNS OF ENERGY FLOW IN A SEASONALLY VARIABLE MARINE ENVIRONMENT

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SPATIAL AND TEMPORAL PATTERNS OF ENERGY FLOW IN A SEASONALLY VARIABLE MARINE ENVIRONMENT

by

Bailey McMeans

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2012

SPATIAL AND TEMPORAL PATTERNS OF ENERGY FLOW IN A SEASONALLY VARIABLE MARINE ENVIRONMENT

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DECLARATION OF CO-AUTHORSHIP/PREVIOUS PUBLICATION

I. Co-Authorship Declaration

I hereby declare that this dissertation contains original material that is the result of joint research. A.T. Fisk contributed to all chapters by providing the opportunities and facilities necessary to complete the research along with intellectual guidance. M.T. Arts also contributed to all chapters by analyzing the fatty acids and by providing detailed comments and helpful direction. In Chapter 2, S. Rush contributed by commenting on the manuscript and providing statistical consultation. In Chapter 3, N. Rooney provided comments and suggestions on the organization of the text. In Chapter 5, M.A. MacNeil provided statistical help and comments on the text. In all cases, the key ideas, data interpretation, and writing of all chapters were performed by the author, Bailey C. McMeans.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-author(s) to include the above material(s) in my thesis.

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II. Declaration of Previous Publication

This dissertation includes 3 original papers that have been previously published or submitted for publication in peer-reviewed journals, as follows:

Dissertation Chapter	Publication title/full citation	Publication status
Chapter 2	McMeans, BC, Arts, MT, Rush, S, Fisk, AT (2012) Seasonal patterns in fatty acids of *Calanus hyperboreus* (Copepoda, Calanoida) from Cumberland Sound, Baffin Island, Nunavut. Marine Biology. DOI 10.1007/s00227-012-1889-6123	published

Chapter 4	McMeans, BC, Arts, MT, Fisk, AT. Similarity between predator and prey fatty acid profiles is tissue dependent in Greenland sharks (*Somniosus microcephalus*): implications for diet reconstruction. Journal of Experimental Marine Biology and Ecology	submitted

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ABSTRACT

Food web theory has uncovered several structures, or patterns of carbon flow, that increase food web persistence. However, empirical studies focused on these structures have been largely restricted to temperate and tropical areas. In the present dissertation, I sampled the food web of Cumberland Sound, Nunavut during summer (August) and winter (April) of 2007-2009 and used stable isotopes (SI: $\delta^{15}N$, $\delta^{13}C$) and fatty acids (FA) to identify whether this arctic food web exhibited the following structures: 1) spatial resource coupling, 2) individual diet specialization and 3) temporal resource coupling. I first identified that the FA profile of a key arctic herbivore (*Calanus hyperboreus*) consistently differed between summer and winter over two years (e.g. higher 18:1n-9 in winters vs. summers), which aided in the interpretation of FAs in upper trophic levels. I then tested for the presence of spatial resource coupling in the summer food web. Based on $\delta^{15}N$-derived trophic positions and $\delta^{13}C$-derived % reliance on phytoplankton (vs. macroalgae), lower trophic levels fed predominantly on one of two resources and upper trophic levels used multiple resources, supporting the existence of spatial resource coupling. Following a preliminary analysis comparing Greenland shark (*Somniosus microcephalus*) and prey FAs, inter-tissue differences in Greenland shark 22:5n-3 among muscle, liver and plasma revealed that some individual sharks fed on consistent resources, but that the extent of individual diet specialization varied over time. Individual Greenland sharks were therefore concluded to feed as generalists, which is consistent with the finding that Cumberland Sound consumers acted as spatial resource couplers. Finally, SIs and FAs revealed that ~50% of Cumberland Sound species switched their diet between summer and winter. A literature review confirmed this temporal resource coupling by consumers on a pan-arctic scale. Overall, structures of an arctic food web agreed with those predicted by recent food web theory, such that spatial and temporal variability in resource abundance and consumer feeding behaviour are likely important for arctic food web persistence. In this context, any result of climate warming that acts to synchronize resource dynamics or remove consumer resource coupling could decrease the persistence of arctic food webs.

DEDICATION

To Kevin, mom, Fran & Don

Thank you for your incredible patience and support. What you give me is more than I will ever be able to repay.

I love you.

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CHAPTER 1

GENERAL INTRODUCTION

BACKGROUND AND RATIONALE

Food web ecology: beginnings and recent advances

Food webs are complex networks of trophic interactions that describe who eats whom in an ecosystem (Pimm 1982). From groundbreaking insights by Elton (1927), that biomass decreased with each successive trophic step, Lindeman (1942), that energy was lost at each consumer-resource interaction, and Hairston et al. (1960), that consumers can regulate community structure, arose a rich area of food web research. Much of this research has focused on integrating food web structure with mechanisms that promote food web persistence, or the continued existence of food webs through time (MacArthur 1955; May 1973; Yodzis 1981; Worm and Duffy 2003). Early food web ecologists revealed that food webs do have 'structure', or, patterns of carbon flow within a food web that arise from consumer feeding interactions, and identified several food web structures that were common across a range of habitats (e.g. Pimm 1982; Briand and Cohen 1984; Cohen and Briand 1984). For example, food chains were consistently found to be short (< 4 trophic levels, Pimm et al. 1991) and omnivory was generally considered rare (Pimm et al. 1991). Most of these patterns, however, were found to be artifacts of the data used to generate them, and food webs were criticized for being overly simplified, highly aggregated and quantified without attention to spatial scale (Winemiller 1990; Polis 1991; Paine 1988).

Following the criticism of early work, ecologists began to collect more biologically meaningful food web data that were less aggregated and that heeded scale and the biology of individual species. This next wave of food web research gave rise to the now widely accepted perception that, within food webs, omnivory is common (Isaacs 1973; Polis 1991; Polis and Strong 1996) and resource use varies with time and space

(Winemiller 1990; Polis et al. 1997; Akin and Winemiller 2006). Polis et al. (1996, pg. 454) summed up their view of the past and future directions of food web ecology as follows:

> *"We could view this [early] body of work as the fruition of the first historical phase in the development of food web ecology. We firmly believe that progress toward the next mature phase of food web studies mandates grappling with the complexities of spatial processes, temporal heterogeneity, and life history strategies. These strands must all be interwoven into a broad conceptual framework to arrive at a deep understanding of food web structure and dynamics."*

Three major advances in food web theory have brought us closer towards this 'broad conceptual framework' by linking observed structures with food web persistence, while explicitly incorporating complexity, spatial processes and individual traits. These recently identified food web structures, found to promote persistence, are: 1) spatial asynchrony in available resources and the coupling of these resources by consumers (Fig. 1.1, also referred to as multi-channel omnivory, Vadeboncoeur et al. 2005; Rooney et al. 2006; McCann and Rooney 2009), 2) individual diet specialization (Fig. 1.2, Bolnick et al. 2003; Bolnick et al. 2011) and 3) the coupling of temporally asynchronous resources by generalist consumers (Fig. 1.3, McCann et al. 2005). Based on theoretical models, the 1st and 2nd structures (spatial resource coupling and individual specialization) increase food web persistence (details provided under 'Food web structures studied' section) and are common in terrestrial and aquatic food webs from tropical and temperate latitudes (Bolnick et al. 2003; Rooney et al. 2006). The 3rd structure, temporal coupling of asynchronous resources, is thought to impart persistence to food webs in a similar manner to spatial coupling (McCann et al. 2005), but few empirical data have been collected to explore its prevalence in food webs.

The three aforementioned structures, and their associated mechanisms that promote persistence, can be viewed as a current 'framework' for food web ecology. Considering the three components of this framework together, it becomes clear that a common thread is variability, which can be defined as: the quality, state, or degree of being variable or changeable, the quality of being uneven and lacking uniformity (http://www.thefreedictionary.com/variability). Spatial and temporal coupling of resources (i.e. structures 1 and 3 above, Figs. 1.1 and 1.3) is contingent upon different resources varying in their availability (McCann et al. 2005; Rooney et al. 2006) and individual specialization (structure 2, Fig. 1.2), which can have large-scale effects on food webs (Bolnick et al. 2011), only arises when individuals vary in their selection of resources. Interestingly, however, there has been little discussion of how temporal environmental variability fits into this current food web framework. Ecologists have long noted that abiotic, environmental factors affect groups of animals (Andrewartha and Birch 1954). Temporal variability in abiotic conditions, and species responses to this variability, have since been incorporated into the theories of competitive coexistence (Chesson and Huntly 1997) and community regulation (Menge and Sutherland 1976). However, it remains unknown: do spatial and temporal coupling and individual specialization arise and promote food web persistence even in environments that experience drastic temporal changes in abiotic conditions and primary production?

In this dissertation, I seek to identify whether the three structures, recently identified by theory and observed in temperate climates (i.e. Fig. 1.1-1.3), arise in a seasonally variable marine environment (Cumberland Sound, Baffin Island, Nunavut). The goal of this dissertation is to incorporate temporal heterogeneity into our understanding of what structures impart persistence to food webs. To do so, observed structures in an arctic marine food web will be compared with those predicted by recent theory (Figs. 1.1-1.3). Results of this dissertation are important for identifying: 1) what mechanisms promote persistence in food webs from temporally variable environments, and 2) on a larger scale, how universally important are these structures to food webs in general? Because polar seas are experiencing altered food web structure as a result of warmer temperatures and less ice cover duration (MacNeil et al. 2010; Wassmann et al. 2011; Weslawski et al. 2011), the answers to these questions are especially pressing.

In the following section, several terms are defined in the context of their use in the present dissertation and brief summaries of the three food web structures studied are provided.

FOOD WEB STRUCTURES STUDIED

Defining terms

Several terms used here do not have equivocal meanings, and require explicit definition based on their use in the context of this dissertation. 'Structure' is defined as a pattern of carbon flow that arises within a food web as a result of feeding interactions among consumers. 'Resource asynchrony' occurs when multiple resources vary out-of-phase with one another, that is, when one is increasing the other is decreasing, or when one is very abundant, the other is more scarce. The ability of consumers to act as 'couplers' of this resource variability, in space or time, refers to the ability of a species to consume or 'couple' an abundant or increasing resource and to abandon or 'decouple' from a declining resource. Finally, 'stability' is a contentious, ambiguous and often poorly defined term in ecology with a myriad of meanings (Grimm and Wissel 1997). However, its widespread use in the ecological literature, and specifically in relation to food web structure and mechanisms of 'stability' (MacArthur 1955; May 1973; Yodzis 1981; Rooney et al. 2006), make it difficult to avoid its use entirely. In the present dissertation, 'stability' is most often avoided for the more explicit term 'persistence', because the goal of the present dissertation was to shed light on some structures of food webs in seasonally variable environments that could promote their persistence (i.e. continued existence). As defined by Grimm and Wissel (1997), 'stability' is a more general 'short form or substitute' for a broad group of 'stability properties' that include constancy (e.g. when changes in population size are bounded), resiliency (i.e. returning to a reference dynamic after a disturbance) and persistence (i.e. continuing to exist through time). Thus, 'stability', when used in the present dissertation, refers to this group of 'stability properties', not to one concept or idea.

Structure 1. Coupling of spatially asynchronous resources

Resources from one location are known to act as subsidies for consumers in different locations (Polis et al. 1997; Polis et al. 1996; Winemiller 1990; Polis and Strong 1996). Rooney et al. (2006) developed this idea further, and found, using mathematical models, that the most stable food web configurations arose when: 1) resources differed in their production and biomass turnover (i.e. when one was 'fast' (phytoplankton) and one 'slow' (detritus)), and 2) when consumers coupled fast-slow 'resource compartments', which arise when lower trophic levels tend to feed predominantly on one basal resource (Rooney et al. 2006). Based on a comparison of 4 aquatic and 4 terrestrial food webs, food webs were in fact structured in a similar manner to theoretical predictions, such that lower trophic levels tended to derive their energy predominantly from one of two basal resources (e.g. phytoplankton and detritus in aquatic systems), generating 'resource compartments', which were then coupled by upper trophic level consumers (by moving across spatial landscapes, feeding on abundant resources in different resource compartments, Fig. 1.1). Such a structure is stabilizing because the asynchrony of resources (i.e. arising from their fast and slow production and biomass turnover) provides a stable food base for consumers (Rooney et al. 2006). Also, the ability of consumers to move to areas with abundant resources and leave areas with scarce or declining resources imparts a flexible nature to food webs, by allowing scarce resources to recover (Rooney et al. 2006). The conclusion that the spatial coupling of asynchronous resources is important for food web persistence has major implications for inferring underlying processes based on observed structures of real food webs. However, it remains unknown if such structures exist in temporally variable, highly seasonal environments.

Structure 2. Individual specialization

Based on the above work, generalists are important for coupling resource compartments in food webs (Rooney et al. 2006). However, an increasing body of literature has revealed that populations of generalists (i.e. those that consume a wide range of resources) are commonly composed of 'individual specialists' that specialize on a subset of the populations' total resources (Fig. 1.2, e.g. Svanbäck and Bolnick 2005; Bolnick et al. 2007; Araújo et al. 2011; Bolnick et al. 2011; Matich et al. 2011). Because higher phenotypic variability can lead to a larger range of resources used by the population, populations composed of individual specialists can have wider niches and interact with more species than populations composed of individual generalists (Bolnick et al. 2011). In this way, high individual specialization within a predator population should increase connectivity at the food web level and decrease the strength of any one predator-prey link (because only a subset of the population participates in any one interaction with another species). Because weak trophic interactions are important for food web persistence (McCann et al. 1998), high individual specialization in a predator population would be expected to increase food web persistence (Bolnick et al. 2011). However, a predator population with high individual specialization would also be less likely to couple resources in space (Bolnick et al. 2011; Matich et al. 2011). Thus, any consideration of what structures exist in food webs to promote their persistence should also consider the extent of diet variability at the level of individuals. It is currently unknown if consumers inhabiting seasonally variable environments, like arctic seas, which would be predicted to feed as generalists (MacArthur 1955), exhibit individual specialization.

Structure 3. Coupling of temporally asynchronous resources

Spatial and temporal processes are intricately linked (Polis et al. 1996). Similar to the mechanisms described above for space, resources are known to vary in time, and consumers are considered able to respond to this variability by switching their diet to exploit abundant prey (Polis et al. 1996; McCann et al. 2005). Several detailed studies have categorized how food web properties vary with time (Winemiller 1990; Johnson et al. 2009), but few studies have attempted to identify whether temporal structures arise and act to promote persistence in a similar manner to those recently identified in space (i.e. Fig. 1.1, Rooney et al. 2006). Extrapolating from spatial food web theory (Rooney et al. 2006), these stabilizing structures in the temporal dimension are: 1) multiple resources are present and vary asynchronously through time (i.e. as one resource is declining, another becomes abundant) and 2) consumers should respond to such variability by switching their diet in time to exploit abundant and abandon declining resources (Fig. 1.3, McCann et al. 2005). Temporal resource asynchrony would provide a consistent resource base to consumers during both productive and non productive times. The ability of consumers to switch their diet to exploit abundant resources would allow them to maintain biomass, and food webs to maintain diversity, even during non productive times (Polis et al. 1996; McCann et al. 2005). However, very few empirical data exist to determine if temporally asynchronous resources are in fact coupled by consumers in real food webs, although this structure could be equally as important for food web persistence as spatial resource coupling (McCann et al. 2005; Polis et al. 1996).

THE ARCTIC AS A MODEL SYSTEM

Arctic seas are among the most temporally variable environments on earth, experiencing seasonal changes in light, temperature, ice cover, and salinity, as well as random perturbations from storms and floods (Walsh 2008). Primary production occurs only during a short 1-3 month window in the summer (Walsh 2008), and some arctic marine ecosystems experience no primary production during upwards of 90% of the year (Weslawski et al. 1991). This long separation between periods of primary production is what sets arctic ecosystems apart from northern marine ecosystems, where, although seasonality occurs, the duration separating productive periods is much shorter (Weslawski et al. 1991). Thus, arctic animals must be adapted not only to cold temperatures, but to drastic temporal variability in resources (Clarke 1983). The arctic is therefore a fruitful location to investigate how high temporal environmental variability affects the feeding behaviour of individuals, energy flow among species and the existence of spatial and temporal coupling by consumers.

Previous work has stressed the importance of phytoplankton as a resource for both benthic and pelagic consumers in the arctic during the summer (Renaud et al. 2011; Forest et al. 2008). However, the importance of other autochthonous energy sources, like benthic macroalgae, has been largely ignored in arctic seas (but see Dunton and Schell 1987). It is therefore unclear how species exposed to two carbon sources (e.g. phytoplankton and benthic macroalgae): a) selectively feed in one or both of these energy channels or b) partition resources within these channels.

Because the arctic tends to have lower diversity than temperate or tropical systems (Hillebrand 2004), one might expect lower inter- and higher intra-specific competition in upper trophic level species; the 'recipe' for individual specialization (Svanbäck and Bolnick 2005). On the other hand, organisms inhabiting variable ecosystems that experience resource limitation would be expected to feed as generalists (MacArthur and Pianka 1966). Several marine consumer populations from temperate latitudes exhibit individual diet specializations (Estes et al. 2003; Matich et al. 2011). No study to date, however, has explored the existence of individual specialization in an arctic marine predator.

High seasonality is a major characteristic of arctic oceans, but sea ice cover makes sampling arctic marine organisms during winter difficult. As a result, unlike more temperate areas (Akin and Winemiller 2006), few studies have quantified differences in structure of entire food webs between times of open water (i.e. summer, abundant phytoplankton) and ice cover (i.e. winter, no primary production) (e.g. Søreide et al. 2006 studied summer-winter diet of pelagic food web; Renaud et al. 2011 studied seasonal changes in benthic food web). It therefore remains largely unstudied how entire arctic food webs respond to the absence of primary production.

DISSERTATION OBJECTIVE

The objective of this dissertation is to unite our current understanding of energy flow in a highly seasonal system with the framework generated from recent food web theory by:

1) Assessing patterns of energy flow in space and time among arctic consumers
2) Comparing observed patterns to those predicted from theory (Figs. 1.1-1.3)

The null and alternate hypotheses for this objective are:

Ho: patterns in a highly seasonal system = predicted patterns

Ha: patterns in a highly seasonal system ≠ predicted patterns

In this dissertation, I make use of the principle that 'pattern is generated by process' (pg. 682, Paine 1980). Specifically, based on observed patterns in resource use among arctic consumers, and how these patterns compare with and deviate from theoretical predictions, I hope to shed light on what mechanisms underlie structure and impart persistence to arctic food webs.

METHODS

Chemical tracers, including stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) and fatty acids, are useful tools for investigating changes in food web structure because they provide information about how organisms acquire essential biomolecules (e.g.

protein, fatty acids) necessary for energy and survival. These biomolecules are incorporated into the tissues of a predator over time, and therefore provide an integrated view of an organisms diet that is more dynamic in nature than the more static view provided by stomach contents (Peterson and Fry 1987; Olive et al. 2003). Additionally, because different tissues have different turnover times, analyzing chemical tracers of multiple tissues can be used to identify long-term (slow turnover, e.g. muscle, MacNeil et al. 2006) and recent (fast turnover, e.g. blood plasma, Käkelä et al. 2009) diet.

Values of $\delta^{13}C$ often differ between certain primary producers in marine environments, like phytoplankton and ice algae (Hobson and Welch 1992). Because $\delta^{13}C$ increases only moderately between a food source and a consumer's tissues (i.e. 0-1‰, Post 2002), it can be used to identify a consumer's reliance on two isotopically distinct resources (France 1995). The mechanism driving different $\delta^{13}C$ values between basal resources in different ecosystems is fairly well known, and arises due to differences in the fractionation during uptake of CO_2 from the atmosphere (land plants) or dissolved CO_2 from the water (aquatic plants). C3 plants are the most selective against ^{13}C and subsequently are isotopically lighter than less selective C4 plants (Peterson and Fry 1987). Because dissolved CO_2 in the oceans is heavier than atmospheric CO_2 (due to an equilibrium reaction between CO_2 and HCO_{3-}), phytoplankton have higher ^{13}C than terrestrial C3 plants and typically have $\delta^{13}C$ values between -23 and -20‰ (terrestrial C3 plants $\delta^{13}C \approx -28‰$) (Peterson and Fry 1987). Within aquatic ecosystems, $\delta^{13}C$ further discriminates between primary producers, because phytoplankton tends to be isotopically lighter than benthic algae (Hobson and Welch 1992), likely due to the effect of a benthic boundary layer on the latter, which limits CO_2 availability (France 1995). The mechanisms driving enrichment of ^{13}C between a consumer's tissues and its food source is less well understood, but is likely attributed to respiration of isotopically light CO_2, or excretion of isotoically light waste products that contain carbon (e.g. urea in sharks) (Peterson and Fry 1987).

Values of $\delta^{15}N$ are used to assign trophic positions to consumers because they typically increase by 3-4‰ between a food source and a consumer's tissues (Post 2002). The calculation of trophic position based on $\delta^{15}N$ is somewhat contentious because it is based on several assumptions. Firstly, trophic position calculations require $\delta^{15}N$ values from a system-specific baseline organism that is assumed to represent a time-integrated signature of the primary producer (Vander Zanden and Rasmussen 1999). Filter-feeding primary consumers are useful for this purpose because they are slow growing, assumed to incorporate short term fluctuations in $\delta^{15}N$, and therefore provide a time-averaged baseline value for a given ecosystem (Vander Zanden and Rasmussen 1999).

Perhaps the largest and most contentious issue surrounding $\delta^{15}N$-based trophic positions, however, is the uncertainty surrounding diet-tissue discrimination factors (Caut et al. 2009). For example, these $\Delta^{15}N$ can be taxa- and tissue-specific, such that applying a value derived from a literature review (Post 2002) may be inappropriate (Caut et al. 2009). Values of $\Delta^{15}N$ can also vary with the $\delta^{15}N$ of the food (Caut et al. 2009; Dennis et al. 2010), with starvation (Olive et al. 2003) and with growth (Hesslein et al. 1993). The latter two issues are relatively well understood, and the concern is that two animals eating the same food could differ in their $\delta^{15}N$ due to differences in growth rates (because fast growing animals tend to have much lower $\Delta^{15}N$). On the other hand, starving animals tend to have higher $\delta^{15}N$ and $\Delta^{15}N$ than actively feeding animals because starving animals obtain a smaller amount of ^{14}N from the diet to balance that lost via excretion (Olive et al. 2003). Despite the uncertainties with fractionation values, stable isotopes are still an incredibly useful tool, allowing researchers to track sources of carbon up the food chain (Fry and Sherr 1984). Thus, with caution, combined analysis of $\delta^{15}N$ and $\delta^{13}C$ allows researchers to study both vertical (trophic positions) and horizontal (carbon sources) aspects of food web structure (e.g. Fry 1988; Hobson et al. 2002).

The other dietary tracers used in this dissertation are fatty acids, which serve many functions in eukaryotes, including energy storage, cell membranes structure, immune responses, and hormone signaling. Similar to stable isotopes, fatty acids reflect a long-term, incorporated view of an animals' diet (Iverson 2009). Some fatty acids are essential for proper functioning of animals, including arachidonic acid (ARA, 20:4n-6), eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3) (Arts et al. 2001; Kainz et al. 2004; Parrish 2009). Only algae and bacteria are capable of synthesizing the precursors of these essential fatty acids (linoleic acid (LIN), 18:2n-6, alpha-linoleic acid (ALA), 18:3n-3, Arts et al. 2001). Most marine fishes are thought to have limited ability to elongate ARA, EPA and DHA from LIN and ALA in amounts sufficient to meet their needs (Mourente and Tocher 1993). These fatty acids must therefore be obtained in the diet by marine consumers, and are useful as dietary indicators (Dalsgaard et al. 2003). Other fatty acids are useful for distinguishing between basal resources. For example, diatoms tend to be high in 16:1n-7 and bacteria are high in branched and odd-chain length FA (e.g. 15:0) (Søreide et al. 2008).

One major consideration with the interpretation of fatty acids as dietary indicators is that animals will modify dietary fatty acids to meet their specific needs (e.g. through chain elongation or shortening) (Cooper et al. 2006). However, it is widely accepted that the fatty acid profile of a consumer is greatly affected by the fatty acid profile of its diet (Iverson 2009) and fatty acids have been successfully applied to delineate the diet of marine consumers including zooplankton (Søreide et al. 2008), fish (Budge et al. 2002) and sharks (Schaufler et al. 2005).

All samples for stable isotopes presented in this dissertation were stored at -20°C until analysis and treated with the same pre-analysis protocol (i.e. lipid extraction in 2:1 chloroform: methanol) as previously described (McMeans et al. 2009). Only samples with high $CaCO_3$, like amphipods (e.g. *Gammarus oceanicus*) and snails (*Littorina* spp.), were acid washed prior to stable isotope analysis (using 1M HCl) (for details, see Chapter 3). Stable isotopes were analyzed on a continuous-flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Electron) at the Great Lakes Institute for Environmental Research, Windsor, Ontario. Fatty acid samples were stored at -80°C until analysis and were all separated using a Hewlett Packard 6890 GC coupled to a Flame Ionization Detector at the National Water Research Institute, Burlington, Ontario (see Chapter 2 for detailed analytical methods).

STUDY SYSTEM

Sampling for this dissertation was conducted in Cumberland Sound, located on the east coast of Baffin Island, Nunavut, Canada. This is an appropriate test system for the research presented in this dissertation for several reasons. First, results should be comparable to several previous arctic studies because fjords are a common feature of arctic regions (Hop et al. 2002; Svendsen et al. 2002; Hop et al. 2006; Wlodarska-Kowalczuk et al. 2009). Summer water column primary production at sampling areas in Cumberland Sound (e.g. range July - August 2008 = 2.7-518.4 mg C $m^{-2}day^{-1}$, J. Brush et al., unpublished data) is similar to other locations in the Canadian arctic (Klein et al. 2002). Further, common arctic fauna inhabit Cumberland Sound, from zooplankton like *Calanus hyperboreus,* to fishes like arctic charr (*Salvelinus alpinus*) and pinnipeds like the ringed seal (*Pusa hispida*). The ability to compare results from Cumberland Sound to other areas is important because much arctic marine research to date has been fragmented and regional and there is a call for researchers to draw similarities among arctic locations (Carmack and Wassmann 2006). The goal of a 'pan-arctic' view is the ability of researchers to make generalizations about how certain areas can be expected to change with climate warming (Carmack and Wassmann 2006). This dissertation should contribute to that goal because, in Chapter 6, data were compiled from throughout the arctic to assess the prevalence of biomass changes and diet switches between summer and winter.

Second, the eastern coast of Baffin Island is already experiencing changes associated with climate warming (Kahru et al. 2011) and there is an immediate need to structure food webs and identify how consumers are using resources during both productive and unproductive months. The final reason Cumberland Sound is an appropriate study system is logistical, but still important to the goal of this dissertation. A winter turbot (*Reinhardtius hippoglossoides*) fishery exists in Cumberland Sound that allowed access to winter communities without the use of an ice-breaker ship, which are the most frequently used method to sample offshore arctic environments (e.g. Hobson et al. 2002). As a result, knowledge regarding inshore, coastal arctic food webs, especially in winter, is extremely limited. The ability to sample in generally the same location (within 30 km of land) during summer and winter provided a unique data set with which to explore a similar community in both summer and winter.

The areas sampled in Cumberland Sound were located directly below the arctic-circle, but experience arctic conditions, and much colder temperatures than similar latitudes in the Norwegian Sea, for example, due to the influence of the Gulf Stream on the latter. Cumberland Sound is influenced by both Arctic (i.e. Baffin Island Current) and Atlantic (i.e. Greenland Current) water masses (Aitken and Gilbert 1989). Subsequently, the fauna of Cumberland Sound is of both Arctic and Atlantic origin (Aitken and Gilbert 1989). Cumberland Sound is covered by sea ice cover from approximately November until June or July. Temperatures in surface summer waters are generally at least 3°C (Mathias and Keast 1996), but can decrease below -1.8°C in winter (Simonsen and Treble 2003). Summer in this part of the world occurs in July and August, when waters are ice-free and pelagic primary productivity is at its peak (Grainger 1971; Hsiao 1988, 1992). Winter occurs in December-March, when water column primary production (Hsiao 1988) and phytoplankton cell biomass (Hsiao 1992) are low or absent.

Five sampling trips were conducted: three during summer (August 21-27, 2007 and August 10-15, 2008, August 10-17, 2009) and two during winter (April 10-11, 2008 and April 4-8, 2009). Sampling was conducted during August and early April to capture resource use by consumers (inferred through stable isotopes and fatty acids) during summer and winter, respectively. Sampling for this dissertation was conducted within or up to 30 km outside the mouth of Pangnirtung fjord, the location of the Inuit settlement of Pangnirtung. In summer, Pangnirtung fjord experiences freshwater inflow from River Duval, as well as from melting permafrost and glaciers upland, although the quantity of freshwater entering Pangnirtung fjord has not been quantified. Pangnirtung fjord experiences large tides, up to 7m, and wide (up to 600m) intertidal flats consisting of sand, gravel, boulders and large growths of the brown macroalgae *Fucus* characterize the shores of Pangnirtung fjord (Aitken et al. 1988).

PREDICTIONS AND HYPOTHESES

Regarding the null and alternate hypotheses for this dissertation (Ho: patterns in a highly seasonal system = predicted patterns, Ha: patterns in a highly seasonal system ≠ predicted patterns), I expect that patterns in a highly seasonal system will deviate from those predicted by recent theory (see Figs. 1.1-1.3 for 'predicted patterns'). The rationale for this prediction is detailed in the following outline of each data chapter.

*Chapter2**:** Seasonal Patterns in Fatty Acids of* Calanus hyperboreus *(Copepoda, Calanoida) from Cumberland Sound, Baffin Island, Nunavut (Marine Biology (2012) DOI 10.1007/s00227-012-1889-6)*

I first explore seasonal variability (i.e. summer vs. winter) in fatty acids of an important arctic organism, the herbivorous copepod *Calanus hyperboreus,* over two consecutive years. *C. hyperboreus* forms a crucial link between phytoplankton and upper trophic levels and is directly eaten by many species (zooplankton to baleen whales) (Falk-Petersen et al. 2007). Thus, prior to exploring the feeding behaviour of upper trophic level consumers, it was prudent to first explore how fatty acids varied in this key arctic consumer, both with season and between years. In this chapter, I will explore which fatty acids are altered by *C. hyperboreus* between summer and winter. This work will provide important information about the consistency of fatty acids made available to upper trophic levels over two years, and whether the seasonal pattern in fatty acids of a key arctic herbivore is similar between two years with different times of ice break up (ice broke up earlier in 2007 than in 2008).

Chapter 3: Coupling of macroalgal and phytoplankton energy pathways by consumers inhabiting a seasonally ice-covered fjord (anticipated submission date April 24, 2012)

Next, I ask the question: do arctic marine consumers sampled during the productive period couple two disparate resources in space, as predicted by recent food web theory (Fig. 1.1, Rooney et al. 2006). Specifically, I explore the importance of phytoplankton vs. macroalgae to invertebrates, teleosts, elasmobranchs and pinnipeds sampled during summer (August) in Cumberland Sound using stable isotopes and fatty acids. The hypotheses for this chapter are:

Ho: Lower trophic levels will restrict their feeding to either phytoplankton or macroalgae, and upper trophic levels will consume prey from both resource compartments, evidenced by intermediate values of δ^{13}C-derived % reliance on pelagic carbon and fatty acids (i.e. predicted pattern = observed pattern)

Ha: Lower and upper trophic levels will have similar values of δ^{13}C-derived % reliance on pelagic carbon and fatty acids, indicating little spatial resource coupling (i.e. predicted pattern ≠ observed pattern)

The theoretical prediction is that lower trophic level consumers will partition resources in space (i.e. feed predominantly on either phytoplankton or macroalgae) and that upper trophic levels will couple these resources by feeding in both resource compartments (Fig. 1.1). Due to the dominance of phytoplankton in arctic food webs (e.g. Renaud et al. 2011), I expect that the structure of an arctic food web will deviate from this prediction, and that both lower and upper trophic level consumers will depend on carbon that originated from phytoplankton (i.e. low coupling in space, Fig. 1.1.). This result would support the alternate hypothesis of this dissertation that observed patterns in an arctic food web deviate from those predicted by recent theory.

*Chapter 4: Similarity between predator and prey fatty acid profiles is tissue dependent in Greenland sharks (*Somniosus microcephalus*) (Submitted to the Journal of Experimental Marine Biology and Ecology, February 1, 2012, manuscript number: JEMBE-D-12-00056)*

Because I plan to use fatty acids of multiple tissues with different turnover times to investigate individual-level feeding behaviour of Greenland sharks, I first need to assess: 1) the extent that Greenland sharks modify fatty acids from those obtained in diet and 2) which shark tissues provided the most accurate view of diet. To answer these question, in Chapter 4, I compare Greenland shark muscle, liver and blood plasma fatty acids to values for dominant prey (based on stomach contents). I predict that shark liver will be the most modified by the shark and differ the most from prey fatty acids due to the many functions of liver in shark fatty acid metabolism (e.g. energy storage and generation, ketone body biosynthesis, buoyancy, Ballantyne 1997).

*Chapter 5:Iindividual specialization in Greenland sharks (*Somniosus microcephalus*)*

After exploring whether arctic consumers couple resources in space at the population level (Chapter 3), I next apply the methodology established in Chapter 4 to explore the diet of an upper trophic level consumer, the Greenland shark, in more detail at the individual level. Whatever the resource use pattern identified in Chapter 3, it is now important to establish whether individual-level resource use reflects this pattern observed at the population level (i.e. whether consumers are individual specialists or individual generalists) and whether this feeding behaviour remains constant through time. In Chapter 5, I use the range of 22:5n-3 proportions among each Greenland shark's muscle, liver and plasma to infer whether a shark has been feeding on consistent (i.e. similar fatty acid values among tissues) or different diet items over time (i.e. different values among tissues). I use a linear mixed-effects models to calculate the variability within individuals (WIC, within-individual component) and between individuals (BIC, between-individual component) and the total variability exhibited by the population (TNW, total niche width), which is equal to WIC + BIC (Fig. 1.2). High individual specialization would be indicated by low WIC relative to TNW (Fig. 1.2), whereas low individual specialization would be indicated by WIC that is a large proportion of the TNW (Bolnick et al. 2003). I test the following hypotheses in Chapter 5:

Ho: Values of muscle, plasma and liver fatty acids are similar within individuals (i.e. high individual specialization) and do not vary with time

Ha1: Values of muscle, plasma and liver fatty acids are different within individuals (i.e. no individual specialization) and do not vary with time

Ha2: The similarity between muscle, plasma and liver fatty acids within individuals varies with time (i.e. the extent of individual specialization varies with time)

No abundance data exist for Greenland sharks or their prey in Cumberland Sound, so it is difficult to speculate regarding the extent of intra-specific competition in this population. However, because the Greenland shark is the only shark and large predator of both fish and marine mammals in Cumberland Sound, one would expect lower inter- and higher intra-specific competition; the diversifying 'recipe' for individual specialization (Svanbäck and Bolnick 2005). Thus, the theoretical prediction is high individual specialization that is constant (does not vary with time, Fig. 1.2, Ho). However, Greenland sharks are considered generalists based on a wide range of prey consumed (MacNeil et al. 2012), although they are likely capable of focusing on a subset of resources when they are abundant. I therefore expect that if individual resource specialization is identified, that its extent will not remain constant through time (i.e.Ha2, Fig. 1.2). Low and or variable individual specialization would support the alternate hypothesis of this dissertation that observed patterns in an arctic food web deviate from predicted patterns (i.e. Fig. 1.2).

Chapter 6: Temporal resource asynchrony and seasonal diet switching in arctic food webs: comparing empirical patterns with theoretical predictions

After exploring spatial coupling of resources during one season (summer, Chapter 3), and exploring the diet of a top trophic level consumer at the individual level (during summer and winter of two years, Chapter 5), I now explore patterns in overall food web structure over multiple seasons. Stable isotope and fatty acid data sampled from Cumberland Sound consumers during summer and winter, combined with a literature review, will be used to explore seasonal changes in: 1) basal resource availability, 2) changes in consumer biomass and 3) seasonal diet switching by consumers. On the one hand, the ability of consumers to switch their diet with season seems obvious and expected (Weslawski et al. 1991). However, several studies report that biological activity during arctic winter is much higher than previously thought, and that many species adopt a 'business as usual strategy', feeding as opportunistic generalists all year (Werner and Auel 2005; Legezynska et al. 2012). Further, marine food webs in general (Isaacs 1973) and polar food webs specifically (Norkko et al. 2007; Renaud et al. 2011) have been viewed as 'unstructured' due to the high prevalence of omnivory and detritivory, which could lead one to expect a general lack of structure. Although many studies have performed detailed studies of arctic food web structure (e.g. Hobson et al. 2002; Søreide et al. 2008; Dunton et al. 2012), this is the first attempt that I am aware to unite observed structures in arctic food webs with recent structures that are considered important for persistence. To do so, I will test the following hypothesis (Fig. 1.3):

Ho: observed pattern agrees with theoretical prediction

Ha: observed pattern deviates from theoretical prediction)

If consumers switch their diet by exploiting abundant and abandoning declining resources between summer and winter, as inferred from changes in their stable isotopes and fatty acids between season (i.e. between summer and winter), this would support the null hypothesis (Fig. 1.3, Ho). Alternatively, a lack of seasonal pattern (e.g. similar stable isotopes or fatty acids of consumers between season) would indicate that the observed pattern deviates from the predicted pattern, which supports the alternate hypothesis (Fig. 1.3, Ha). Based on the known prevalence of omnivory and opportunistic feeding by arctic consumers (e.g. Dunton et al. 2012; Renaud et al. 2011; Feder et al. 2011), with the exception of herbivorous copepods (Chapter 2, Falk-Petersen et al. 2009), I expect that consumers will not switch their diet in response to temporal resource variability and will feed as opportunists all year (i.e. Ha), which would support the alternate hypothesis of this dissertation that patterns in arctic food webs deviate from theoretical predictions.

Uniting observed patterns with predictions from recent theory (i.e. Figs. 1.1-1.3) will increase understanding, not just of variable environments, but of the mechanisms that govern food web structure in general.

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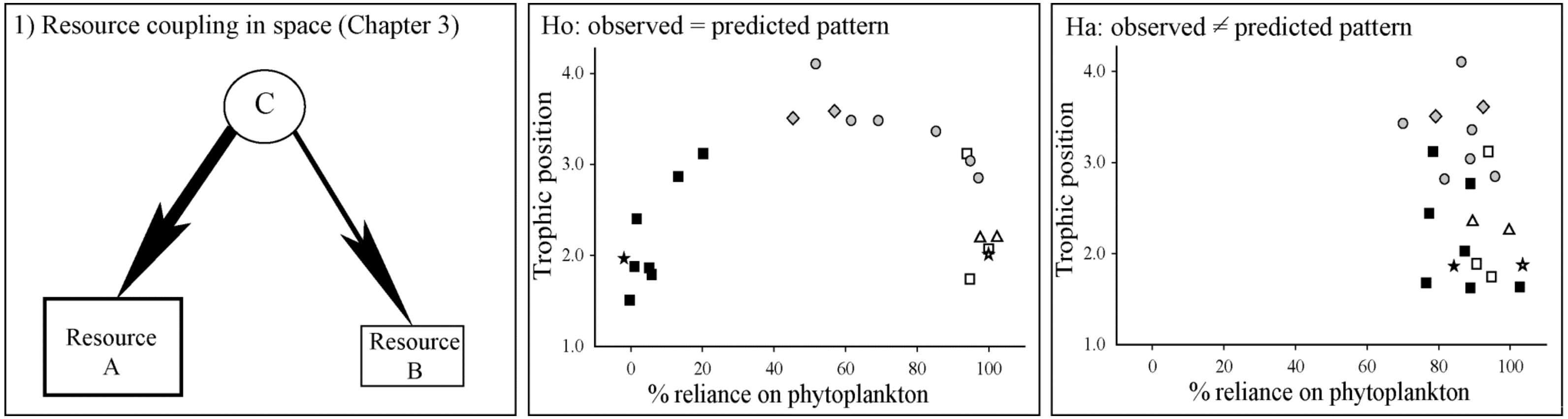
Fig. 1.1 The first structure investigated in the present dissertation is spatial coupling of asynchronous resources. The conceptual model for this structure (left panel) shows the coupling of two asynchronous resources in space (A and B) by a hypothetical consumer (C). The null hypothesis (Ho, middle panel) is that lower trophic levels will restrict their feeding to one of two 'resource compartments' (e.g. phytoplankton and macroalgae), and upper trophic levels will couple these resource compartments. One possible alternate hypothesis (Ha, right panel) is that lower and upper trophic level consumers will feed predominantly on carbon originating from phytoplankton, such that no resource compartments at lower trophic levels and/or coupling by upper trophic levels is apparent.



1) Resource coupling in space (Chapter 3)

Ho: observed = predicted pattern

Ha: observed ≠ predicted pattern

Fig. 1.2. The second food web structure investigated in this dissertation is the extent of individual diet specialization (IS) (in Greenland sharks, *Somniosus microcephalus*). The conceptual model (left panel, redrawn from Bolnick et al. 2003, Amer. Nat. 161(1), 1-28) shows a population of consumers whose total niche width (TNW) is explained by high IS, i.e. high between-individual variation (BIC) and low within-individual variation (WIC). The null hypothesis (Ho, middle panel) is high IS (evidenced by small ranges of fatty acid values in each shark) that does not change with time. The alternate hypothesis (Ha, right panel) is that the extent of IS will change with time (season), evidenced by wide ranges of fatty acids in a given shark in some seasons (i.e. low IS) and small ranges (i.e. high IS) in sharks sampled during other seasons.

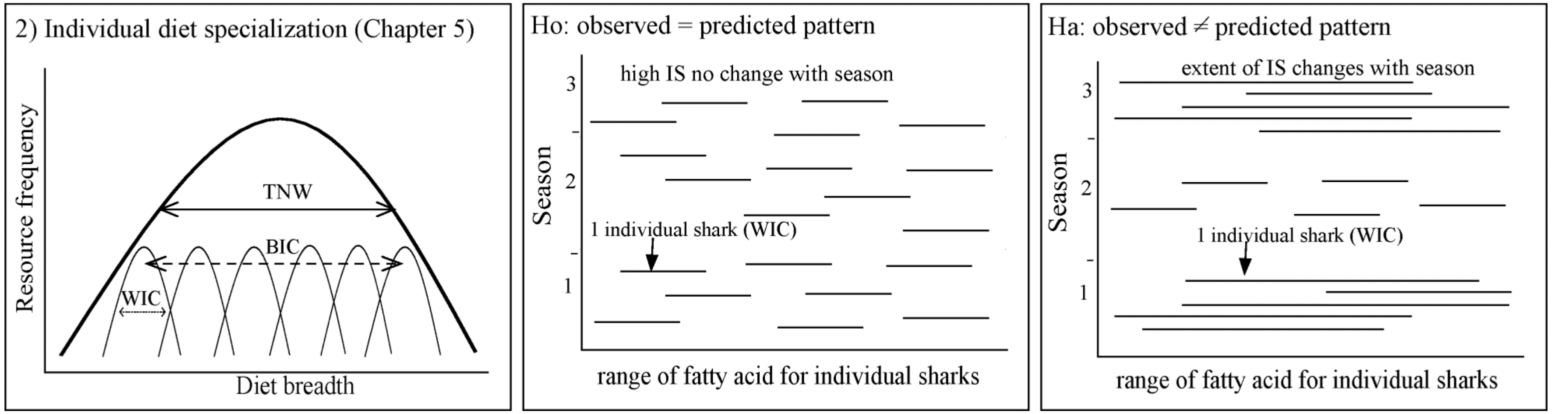
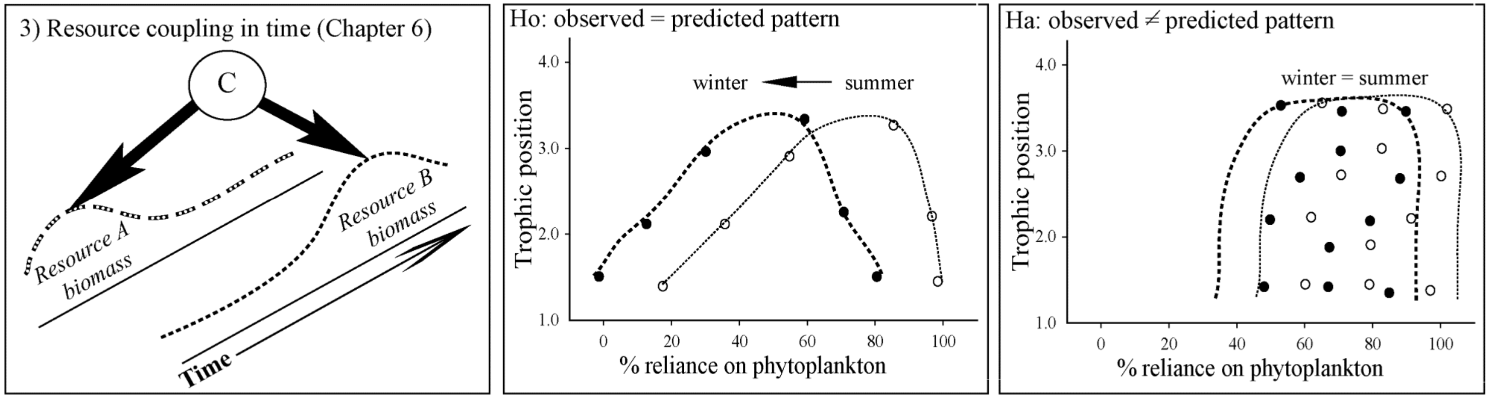


Fig. 1.3. The third food web structure investigated in the present dissertation is temporal coupling of asynchronous resources. The conceptual model (left panel) shows a hypothetical consumer (C) coupling two temporally asynchronous resources (A and B). The null hypothesis (Ho, middle panel) is that consumers will switch their diet with season to exploit resources as they vary through time (here, a switch from high reliance on phytoplankton in summer to greater reliance on alternate carbon sources, e.g. detritus, in winter). The alternate hypothesis (Ha, right panel) is that consumers will feed on similar prey all year and will not switch their diet.



CHAPTER 2

SEASONAL PATTERNS IN FATTY ACIDS OF CALANUS HYPERBOREUS (COPEPODA, CALANOIDA) FROM CUMBERLAND SOUND, BAFFIN ISLAND, NUNAVUT

McMeans, BC, Arts, MT, Rush, S, Fisk, AT (2012) Seasonal patterns in fatty acids of *Calanus hyperboreus* (Copepoda, Calanoida) from Cumberland Sound, Baffin Island, Nunavut. Marine Biology DOI 10.1007/s00227-012-1889-6123

INTRODUCTION

Polar oceans are characterized by pronounced seasonal variability in temperature, light and salinity (Clarke 1983). This inconstancy in physico-chemical conditions drives strong seasonal variability in available food resources, which, in turn, constitutes one of the biggest challenges faced by polar organisms (Clarke 1983). *Calanus hyperboreus* (Krøyer, 1838) is a predominantly herbivorous marine copepod (Falk-Petersen et al. 1987; Stevens et al. 2004b) that inhabits seasonally ice-covered waters in the Atlantic Arctic and sub-Arctic (Conover 1988). The ephemeral nature of phytoplankton availability in Arctic systems coupled with low water temperatures (low basal metabolic rates) promote most arctic copepods to accumulate higher amounts of lipids than temperate or tropical copepods (Lee and Hirota 1973).

Lipids are stored by arctic *Calanus* spp. predominantly as wax esters (Kattner and Hagen 2009), which consist of a fatty acid esterified to a fatty alcohol, and can account for > 91% of total lipids in *C. hyperboreus* (Lee 1974). Certain PUFA like eicosapentaenoic acid (EPA, 20:5n-3), arachidonic acid (ARA, 20:4n-6) and docosohexaenoic acid (DHA, 22:6n-3) are required for somatic growth and membrane functioning of animals and invertebrates (Parrish 2009). However, it is generally accepted that these 'essential' fatty acids cannot be synthesized from their fatty acid precursors (i.e. alpha-linoleic acid (ALA, 18:3n-3) and linoleic acid (LIN, 18:2n-6) by animals in amounts sufficient to meet their needs, and must therefore be acquired in the diet (Parrish 2009). Aquatic algae are the major source of pre-formed, long-chain (≥ 20 carbons) n-3 and n-6 PUFA (Arts et al. 2001; Gladyshev et al. 2009). Thus, as a main grazer of primary production in marine Arctic ecosystems, *C. hyperboreus* serves as both a source of energy and essential fatty acids for higher trophic levels (Søreide et al. 2008; Kattner and Hagen 2009). Knowledge concerning food quality obtained by *C. hyperboreus* during summer, with regard to essential fatty acid acquisition, is therefore important for identifying potential risks to *C. hyperboreus* populations, and, by extension, to the fish, birds and mammals that ultimately depend on the fatty acids that *C. hyperboreus* harvests from the oceans.

C. hyperboreus feeds only during the productive spring and summer months when phytoplankton are available, and synthesizes and stores large amounts of the long chain MUFAs 20:1n-9 and 22:1n-11 in their wax esters (Albers et al. 1996; Graeve et al. 2005). *C. hyperboreus* enters diapause over the unproductive winter, during which time the copepods do not feed and rely entirely on store lipids to mature and reproduce (Conover and Siferd 1993; Falk-Petersen et al. 2009). Presumably, *C. hyperboreus* relies on both dietary PUFA and biosynthesized MUFA to survive the winter and successfully reproduce (Sargent and Falk-Petersen 1988). However, very few studies to date have explored how *C. hyperboreus* alters specific fatty acids between productive summer and unproductive winter months in ice-covered seas (but see Lee 1974; Søreide et al. 2008). Seasonal fatty acid data are especially needed for the Canadian arctic because these areas are experiencing decreases in both the extent and duration of ice-cover, and consequently, earlier timing of maximum annual phytoplankton biomass (Kahru et al. 2011), which could affect *Calanus* populations (Søreide et al. 2010). To the best of our knowledge, however, no such data exist.

Quantifying dynamics in fatty acids over multiple seasons across consecutive years could provide important information on the seasonal lipid strategy of *C.*

hyperboreus, including identifying which lipids are likely important for their survival. These findings could become important for monitoring how longer open-water periods and earlier phytoplankton growth influence the quality and quantity of lipids accumulated by *C. hyperboreus* annually. Further, it is imperative to identify how *C. hyperboreus* fatty acid profiles change over time (i.e. with seasons and years), because this information contributes important baseline data for future studies focused on the feeding ecology of higher trophic level organisms (Brett et al. 2009). Here we quantify fatty acid profiles of *C. hyperboreus* from Cumberland Sound, Baffin Island, Canada during summer (i.e. August, open-water) and winter (i.e. April, ice-cover) over two successive years. We suggest that such information can eventually be used to better assess and monitor the cumulative effects of annual variability in physical forcing variables (temperature, light, nutrients) on copepods and their consumers in the context of climate change.

MATERIALS AND METHODS

Study site

Copepod sampling was conducted as part of a larger study in Cumberland Sound, and occurred within 30 km southwest (65°55'02"N, 66°27'30"W) and 30 km northwest (66°12'41"N, 66°35'35" W) of the mouth of Pangnirtung Fjord (66°4'43"N, 65°57'45" W, Fig. 2.1). The southeast coast of Baffin Island is influenced by both Arctic (Baffin Island Current) and Atlantic water masses (Greenland Current; Dunbar 1951), and consequently, the fauna of Cumberland Sound is of both Arctic and Atlantic origin (Aitken and Gilbert 1989). Cumberland Sound is typically ice-covered from November until approximately June. Temperatures in Cumberland Sound typically exceed 3°C in surface waters during summer (Mathias and Keast 1996) but decline to -1.8°C in winter, when the entire water column can reach temperatures near 0°C (Simonsen and Treble 2003). Details on the progression of summer phytoplankton growth do not exist for Cumberland Sound, but in Frobisher Bay, a fjord also on the southeast coast of Baffin Island and ~3 degrees south of Cumberland Sound, primary productivity is typically highest in July and August, with sharp declines in September (Grainger 1971).

Ice-coverage and chlorophyll a

Satellite data were accessed through the National Oceanographic Atmospheric Administration's Environmental Research Division's Data Access Program to determine the approximate dates of ice break-up (dataset title: Ice Coverage, Aqua AMSR-E, Global (1 Day Composite), Cavalieri et al. 2004, updated daily) and maximum surface chlorophyll *a* (dataset title: Chlorophyll-a, Aqua MODIS, NPP, Global, Science Quality (8 Day Composite), O'Reilly et al. 2000) in Cumberland Sound during the summers of 2007 and 2008 (Fig. 2.2). Satellite ice coverage data are daily averages and chlorophyll *a* data are 8 d averages.

Copepod sampling

Calanus hyperboreus were collected during four sampling trips: during open-water in August 21-27, 2007 and August 10-15, 2008 and during ice-cover in April 10-11, 2008 and April 4-8, 2009. Previous researchers working in southeastern Baffin Island waters (i.e. Frobisher Bay) have referred to winter as occurring in December-March, spring from April-June and summer from July-August (Hsiao 1988, 1992). These designations are somewhat arbitrary but are useful for referring to the general onset of ice algae (late spring) and phytoplankton production (summer) in this part of the world, with winter referring to a time of low water column primary production (Hsiao 1988) and phytoplankton cell biomass (Hsiao 1992). Considering a turnover time of 11 d for fatty acids in *C. hyperboreus* (Graeve et al. 2005), April samples reflect activity occurring in late March, and these samples will hereafter be referred to as 'winter.' August samples reflect activity in mid-early August and will hereafter be referred to as 'summer.' The rationale chosen sampling times was to capture the signature of *C. hyperboreus* after they incorporated the signature of summer phytoplankton growth and after the winter low primary production period.

All *C. hyperboreus* were collected using a 243-μm plankton net (Wildlife Supply Company®, Buffalo, New York) by performing both surface horizontal tows and vertical hauls in the summer, and vertical hauls through holes cut in the sea ice during winter. The maximum depth of sampling sites was ~400 m, and vertical hauls were conducted down to near-bottom depth. For all samples, the contents of each plankton tow were first rinsed into buckets filled with seawater. The samples were then poured through a 2-mm sieve fitted on top of a 0.5-mm sieve (both Fieldmaster®). Individuals were gently removed from the sieves using tweezers. Approximately 10 *C. hyperboreus* were pooled for each fatty acid sample, placed in cryogenic vials immediately frozen at -80°C in liquid nitrogen, and kept at -80°C until analysis. *Calanus hyperboreus* samples consisted of adult females (AF), and stage IV and V copepodites based on prosome length (Hirche et al. 1994) measured on type specimens. One exception is the two samples from April 2009 that consisted entirely of AF.

Fatty acid analysis

*C. hyperboreus s*amples were freeze dried (48 h) and weighed to the nearest microgram (Sartorious ME5 microbalance). Lipids were extracted from each sample (dry weight of samples: range =12.11-44.33 mg, mean ±SD =34.79±9.02 mg) by homogenizing in 2 mL of 2:1 (v/v) chloroform:methanol (C:M) (Folch et al. 1957). The lipid extract was adjusted to 8 mL with 2:1 C:M, 1.6 mL of a 0.9% NaCl in water solution was added, the phases were mixed and centrifuged (2000 rpm at 4°C) and the upper aqueous layer was removed. The solvent layer was evaporated under nitrogen gas, re-dissolved in 2 mL of 2:1 C:M and percent total lipid (on a dry weight tissue basis) was determined gravimetrically. Fatty acid methyl esters were generated by adding sulphuric acid in methanol (1:100 mixture) to the vials, flushing the headspace with nitrogen and incubating (16 h) at 50ºC in a water bath. After the samples cooled, potassium hydrogen carbonate, isohexane:diethyl ether (1:1) and butylated hydroxy toluene (0.01%) were added, and the vials were vortexed and centrifuged. The upper organic layer was transferred to another centrifuge tube; isohexane:diethyl ether (1:1) was added to the original tube which was then shaken, vortexed, and centrifuged. FAME were evaporated under nitrogen, dissolved in hexane, transferred to amber glass GC vials and separated using a Hewlett Packard 6890 GC (splitless injection, column = Supelco (SP-2560 column) 100 m X 0.25 mm ID X 0.20 µm thick film). Fatty acids were identified using a 37-component fatty acid standard (Supelco 47885-U) added with methyl stearidonate (Fluka, 43959), 13-eicosenoic acid methyl ester (Sigma E3512), 9-eicosenoic acid methyl ester (Indofine Chemical, 20-2001-1), 16-docosatetraenoic acid methyl ester (Sigma D3534) and 19-docosapentaenoic acid methyl ester (Supelco, 47563-U). Identification of 11-docosenoic acid methyl was accomplished via a Triple Quadrupole GC/MS (Agilent

7890A with Agilent 7000 mass detector) and confirmed by comparing the mass spectrum to the American Oil Chemists’ Society Lipid Library (http://lipidlibrary.aocs.org/index.html). In the present study, "∑SAFA" is used to indicate the sum of all fatty acids with zero double bonds, "∑MUFA" indicates the sum of all fatty acids with one double bond, and "∑PUFA" indicates the sum of all fatty acids with ≥ 2 double bonds.

Data Analysis

C. hyperboreus fatty acids were expressed as both μg fatty acid mg dry tissue^{-1} (abbreviated here as μg mg^{-1}) and relative proportions (individual fatty acid ∑ fatty acids^{-1}, expressed as a %). Statistical analyses were performed primarily on proportional data, with the exception of analysis of variance (ANOVA) and Tukey's post hoc tests performed on total fatty acids (∑μg fatty acids mg^{-1}) and unsaturation index (∑(μg fatty acid mg $^{-1}$*number of double bonds)). 'Summary' fatty acid proportions (i.e. ∑n-3 and ∑n-6 PUFAs, ∑SAFA, ∑MUFA and ∑PUFA) and % lipid were also compared among sampling dates via ANOVA and Tukey's post hoc tests. Principal component analysis (PCA) was used to investigate seasonal patterns in individual *C. hyperboreus* fatty acids. Data were standardized to a mean of zero and unit variance prior to their inclusion in the PCAs, and fatty acids that had unscaled weights (i.e. scaling=0) ≥ 0.3 (which corresponded to correlations/loadings >0.5) were considered influential to that principal component (McGarigal and Cushman 2000). The sample scores extracted for principal components 1 (PC1) and 2 (PC2) were compared among sampling dates using ANOVA and post hoc tests. The 'mixed' samples containing multiple stages (AF, CV, CVI) and the AF samples from April 2009 were coded differently in the ANOVAs. Ten separate

ANOVAs were performed, and *P* values were corrected accordingly using a sequential Bonferroni procedure (Holm 1979). Statistical analyses were performed in R (R Development Core Team 2010) and the package 'vegan' was used for PCA (Oksanen et al. 2010).

RESULTS

Ice break-up occurred in late May of 2007 and in early August of 2008, and sampling was therefore conducted closer to the time of ice break-up in 2008 (Fig. 2.2). Maximum surface chlorophyll *a* based on satellite data was reported on June 30 of 2007 and August 24 of 2008 (Fig. 2.2, O'Reilly et al. 2000). Ice began to reform in late November of 2007 and in early November of 2008 (Fig. 2.2, Cavalieri et al. 2004, updated daily).

Summer samples were dominated by high EPA, 16:1n-7, 22:1n-11, 20:1n-9, DHA and 16:0, whereas winter samples were dominated by high 16:1n-7, 20:1n-9, EPA, 22:1n-11, DHA and 18:1n-9, when expressed as both relative proportions (Table 2.1) and µg mg^{-1} (Table 2.2). Summer *C. hyperboreus* had significantly higher ∑n-3s ($F_{4,14}$=21.64, *P* <0.01), ∑n-6s ($F_{4,14}$=276.25, *P* <0.005), ∑PUFAs ($F_{4,14}$=41.94, *P* <0.006), and unsaturation index ($F_{4,14}$=26.30, *P* <0.007), and significantly lower ∑MUFAs ($F_{4,14}$=25.54, *P* <0.008) than winter samples (Fig. 2.2). Total fatty acids (∑µg mg^{-1}, Table 2.2) were higher in summer than winter samples ($F_{4,14}$=18.13, *P* <0.01), although the difference between summer and winter 2008 was not significant (*P*>0.01). Percent (%) lipid was also higher in summer samples (Table 2.1), but only differed significantly between summer 2008 and winter 2009 ($F_{4,14}$=4.21, *P* <0.03). ∑SAFA did not differ among sampling dates (*P* >0.05). Winter AF samples had a lower unsaturation index and lower total fatty acids than winter mixed samples (Table2), but these differences were not significant (*P* >0.05).

The first three principal components extracted by the PCA of *C. hyperboreus* fatty acid proportions explained 70.3% of the variance in the data (Table 2.3). PC1 separated summer (positive scores) from winter *C. hyperboreus* (negative scores), due to positive loadings of LIN, 18:4n-3 and EPA in summer, and negative loadings of 16:1n-7, 20:1n-9 and 22:1n-9 in winter (Fig. 2.3). Sample scores extracted for PC1 were significantly higher in summer vs. winter copepods ($F_{4,14}$=35.20, *P* <0.006), and did not differ between the winter mixed and AF samples (*P* >0.05). PC 2 was characterized by negative loadings of 16:0 and positive loadings of ALA, 18:4n-3 and 22:1n-11 (Table 2.3), but PC2 scores did not differ among sampling dates (*P* >0.01). 18:1n-7, ARA and DHA did not load significantly on the first two PC axes extracted, reflecting their similar proportions among samples (Table 2.1). Average proportions of 18:1n-9 were higher in winter samples, although this fatty acid did not load significantly on the first two PC axes (Table 2.3).

Non-metric multidimensional scaling performed on the *C. hyperboreus* fatty acid proportions (Euclidean distances, dimensions = 2, stress = 0.06, results not shown) produced a similar ordination to the PCA, lending confidence to the above results. Furthermore, the $\mu g\ mg^{-1}$ data generally supported results of the PCA and ANOVAs performed on proportions, because summer samples tended to have higher PUFA, including LIN, 18:4n-3 and EPA, and because 18:1n-7 was similar among sampling dates (Table 2.2). Similar to proportional data, winter samples (excluding AF) were also higher in $\mu g\ mg^{-1}$ of 18:1n-9 (Table 2.2), but were not consistently higher in $\mu g\ mg^{-1}$ of 16:1n-7, 20:1n-9 and 22:1n-9 vs. summer *C. hyperboreus* (Table 2.2). Finally, there were slightly lower µg mg^{-1} values of ARA and DHA in winter vs. summer samples (Table 2.2), whereas proportions were similar among sampling dates (Table 2.1).

DISCUSSION

Between-season variability in fatty acid proportions (i.e. winter vs. summer) was greater than within-season variability (e.g. summer vs. summer) because the first PC axis completely separated summer from winter *C. hyperboreus.* The separation of summer samples on PC1 due to high proportions of LIN, 18:4n-3 and EPA, as well as high ∑n-3, ∑n-6, ∑PUFA and unsaturation index, is consistent with phytoplankton consumption, and agrees with previous reports (Lee 1974; Søreide et al. 2008) that summer *C. hyperboreus* have higher EPA and 18 PUFAs relative to winter samples. Fatty acid data for phytoplankton and other potential food sources (e.g. bacteria) are needed to differentiate the contribution of specific taxa to the diet of summer *C. hyperboreus*. However, phytoplankton were available in Cumberland Sound during our field operations based on chlorophyll *a* (integrated over 0-40m) measured at the *C. hyperboreus* sampling locations (67.6 mg m^{-2} on August 14, 2007, B. McMeans, unpublished data; 53.4 mg m^{-2} on July 31, 2008, J. Brush, unpublished data), supporting the contention that summer fatty acid profiles reflected consumption of phytoplankton.

The *C. hyperboreus* fatty acid data presented here are, to the best of our knowledge, the first for eastern Canadian waters outside of the NOW (North Water Polyna, Stevens et al. 2004a; Stevens et al. 2004b). Both *C. hyperboreus* from Cumberland Sound and from the NOW during autumn (Stevens et al. 2004b) had 16:1n7, 20:1n-9, 22:1n-11 and EPA in the highest proportions. Summer 2007 Cumberland Sound samples had the most similar proportions of the above fatty acids (although 22:1n-11 was higher) relative to conspecifics from NOW station 54a (Stevens et al. 2004b), where *C. hyperboreus* were concluded to be feeding on ciliates, flagellates and/or dinoflagelles. On the other hand, summer 2008 Cumberland Sound samples were more similar to those from NOW station 68 (Stevens et al. 2004b), where *C. hyperboreus* were feeding on diatoms (Stevens et al. 2004b). It is prudent to note here that comparisons among studies that analyzed different lipid fractions are acceptable because the total fatty acid fraction (as reported here) and wax ester fraction (e.g. Stevens et al. 2004b) have similar proportions of most fatty acids (Graeve et al. 1994). One exception is 16:1n-7, which is lower in total fatty acids vs. wax esters (Graeve et al. 1994), indicating that our 16:1n-7 values are lower than would be expected if the wax ester fraction was analyzed. Zooplankton fatty acids respond rapidly to changes in the composition and/or availability of phytoplankton (Lee et al. 1972; Stevens et al. 2004b), which likely explains the observed differences between summer 2007 and 2008 samples reported here. This explanation is especially likely because we sampled closer to the time of ice break-up in summer 2008 (Fig. 2.2). There is a need for future efforts to better categorize the progression of the phytoplankton bloom in Cumberland Sound, and the associated changes in the fatty acid profile of herbivorous zooplankton.

Similar to results from Cumberland Sound and the NOW, *C. hyperboreus* sampled during June and July in the Fram Strait also had EPA, 16:1n-7, 20:1n-9, 22:1n-11 and DHA in the highest proportions (Kattner et al. 1989). One difference is that 18:4n3 was a major fatty acid in *C. hyperboreus* from the latter study, contributing almost 30% to copepods in areas where *Phaeocystis pouchetii* was abundant (Kattner et al.

1989). This fatty acid only contributed a maximum of 5.4% to Cumberland Sound samples (summer 2007, Table 2.1) and 9.7% to surface NOW *C. hyperboreus* (Stevens et al. 2004b), which supports the suggestion that large scale differences in fatty acids can exist between the Canadian and Norwegian arctic (Sargent and Falk-Petersen 1988). These differences likely reflect different compositions of algal species (Sargent and Falk-Petersen 1988), which warrants further investigation.

Few studies have reported fatty acids for *C. hyperboreus* during winter months, but both Lee (1974) and Søreide et al. (2008) observed that proportions of fatty acids like LIN, 18:4n-3 and EPA decreased and C18 and C22 MUFA increased in *C. hyperboreus*'s wax esters during the winter. It is unknown whether Cumberland Sound *C. hyperboreus* were in diapause at depth or had recently ascended to surface waters when sampled in winter 2008 and 2009. However, lower ∑PUFA, unsaturation index and % lipid of winter vs. summer samples provides evidence that these individuals were not actively feeding on ice algae or phytoplankton when sampled (which both have high PUFA, Søreide et al. 2008). A previous report from the Beaufort Sea showed that *C. hyperboreus* were feeding at a very low rate (0.2 μg C ind^{-1} h^{-1}, perhaps on microzooplankton) in mid-April prior to spring phytoplankton growth (Seuthe et al. 2007). Further, vertical ascent in *C. hyperboreus* is related to the timing of primary productivity (Hirche and Niehoff 1996), and active accumulation of lipid likely does not start until phytoplankton growth begins. Late March and early April are generally a time of low water column chlorophyll *a* and primary productivity in Frobisher Bay, when sea ice is still ~1-1.5m thick (Grainger 1971). Sea ice thickness was ~0.8 m and 1.3 m at our sampling locations in Cumberland Sound during winter 2008 and 2009, respectively (snow thickness ~15-30 cm), and we therefore assume that water column productivity was low, and subsequently that *C. hyperboreus* were not actively feeding. The observed fatty acid profiles of winter samples support this assumption and, therefore, reflect the overwintering strategy of *C. hyperboreus* with regards to lipid metabolism. Additional work is needed in Cumberland Sound to identify the depth of overwintering, the timing of vertical ascent to surface waters, and the commencement of feeding by *C. hyperboreus*.

The comparison between summer and winter fatty acids in the present study supports previous perceptions about lipid dynamics in *C. hyperboreus* during winter months. First, *C. hyperboreus* is known to incorporate and retain dietary PUFA in their phospholipids to maintain membrane function (Scott et al. 2002). For example, proportions of EPA, ARA and DHA in *C. hyperboreus* phospholipids can remain similar all year (Lee 1974). Therefore, observed values of EPA, ARA and DHA in winter *C. hyperboreus* from Cumberland Sound could reflect the portions that were retained in the phospholipids. Previous work in freshwater systems has also shown that zooplankton selectively retain certain essential fatty acids (Kainz et al. 2004), and conserve ARA and EPA during starvation (Schlechtriem et al. 2006).

Second, lower observed proportions and µg mg^{-1} of LIN, 18:4n-3 and EPA in winter samples agrees with reports that *C. hyperboreus* catabolizes a portion of dietary PUFA from their wax esters to meet energetic demands during the winter (Lee 1974), and during other times of little to no feeding (Kattner et al. 1989). The energetic cost of maintaining bodily functions during diapause is thought to be low, with molting and gonad formation the major causes of wax ester depletion during winter in *Calanus* spp. (Hopkins et al. 1984; Sargent and Falk-Petersen 1988). In high Canadian arctic (i.e.

Resolute Bay) *C. hyperboreus*, stage IV is the dominant overwintering stage, stage V molt all winter to adult males and females (some of which will wait to reproduce until the following winter), and egg production and release in adult females (AF) occurs from March to mid-May (Conover and Siferd 1993). Eggs were still observed in the oviducts of AF during both winter 2008 and 2009 sampling operations (i.e. egg release was not complete, B. McMeans, personal observation). Therefore, lower LIN, 18:4n-3 and EPA in winter vs. summer Cumberland Sound *C. hyperboreus* likely reflects the selective catabolization of these PUFA to fuel maturation in stage V copepodites and egg formation in AF.

Our seasonal comparison of fatty acids also provided two findings regarding the potential role of MUFAs during the winter that have not been thoroughly discussed in the literature. First, proportions of 16:1n-7, 18:1n-7, 20:1n-9, 22:1n-9 and 22:1n-11 were not consistently lower in winter vs. summer Cumberland Sound samples, which agrees with previous reports for *C. hyperboreus* from the Norwegian arctic (Søreide et al. 2008). This result is notable because all of these MUFA are found predominantly in storage molecules (wax esters and TAG, Albers et al. 1996), and should have decreased in winter copepods if they serve as energy stores to fuel reproductive process as presumed (e.g. for C20 and C22 MUFA, Sargent and Falk-Petersen 1988). AF from Cumberland Sound did have lower 20:1n-9 and 22:1n-11 than mixed winter samples on a $\mu g\ mg^{-1}$ basis (Table 2.2), supporting this presumption. Further, although C20 and C22 MUFA are not a major component of *Calanus* eggs (Sargent and Falk-Petersen 1988), lipids in AF are at their lowest once egg release is complete (Lee et al. 1972), and proportions of the above MUFA may be expected to decrease further in winter AF to fuel egg release. Analysis of separate stages of *C. hyperboreus* would have provided more insight into the role of these MUFA in specific overwintering and reproductive processes. However, because AF in the present study had already formed eggs (although we cannot assume that egg formation was complete), it appears that MUFA are not the major fuel for overwintering, maturation or egg formation in *C. hyperboreus*.

A second finding from the present study that merits discussion is the higher average proportions of 18:1n-9 in winter *C. hyperboreus* versus summer, although the variability in winter samples was high (Table 2.1). Average μg mg^{-1} values of 18:1n-9 were also higher in winter mixed samples (but not in AF) versus summer (Table 2.2), and previous researchers have also reported high 18:1n-9 in winter *C. hyperboreus* (Søreide et al. 2008; Lee 1974) and *C. finmarchicus* (Stage V and AF, Falk-Petersen et al. 1987). Increasing 18:1n-9 in winter could be accomplished if *C. hyperboreus* were desaturating 18:0 to 18:1n-9 (Kattner and Hagen 1995; Sargent and Falk-Petersen 1988), although the reason *C. hyperboreus* would increase, or at least maintain, proportions of this MUFA from summer to late winter is unknown. Perhaps there is a biochemical role of 18:1n-9 in winter *C. hyperboreus* in addition to serving as an energy source. For example, the retention of ARA and DHA in winter-sampled *C. hyperboreus* from the present study, coupled with the increase in 18:1n-9, provide field evidence to support recent laboratory observations that fishes and mammals alter the combinations of specific MUFA-PUFA pairings in the *sn-1* and *sn-2* positions of phospholipids in response to cold exposure (Arts and Kohler 2009). Additionally, the combination of PUFA with cis Δ9 MUFA in the *sn-1* position of carp liver phospholipids was found to have the greatest effect on membrane physical properties (Fodor et al. 1995). However, further experimental work is required to validate this observation for *C. hyperboreus*.

Implications for monitoring Calanus hyperboreus *populations*

Ice cover duration has decreased in the Canadian arctic (Kahru et al. 2011), and a discussion of the potential effects of changing ice conditions on *C. hyperboreus* populations is warranted. Earlier ice break-up is anticipated to cause a mismatch between the emergence of first-feeding *C. glacialis* naupulii and the timing of algae blooms (Søreide et al. 2010). Changing ice cover duration would likely affect *C. hyperboreus* differently, however, because female *C. hyperboreus* do not need access to food for successful reproduction during the winter (Conover 1967). However, nauplii might rely on ice algae in late winter/early spring for their first feeding (at stage NIII to NVI) (Conover and Siferd 1993). No study has addressed the effect of ice algae duration on *C. hyperboreus* nauplii survival, but it seems reasonable that earlier ice break up could result in a shorter duration for nauplii to exploit ice algae. Of course, earlier ice break-up could also result in earlier phytoplankton productivity, which could provide a food source for first feeding *C. hyperboreus* nauplii.

The effects of earlier ice break-up on *C. hyperboreus* populations are unclear, but *C. hyperboreus* is considered highly adapted to inter-annual variability in resource availability (Falk-Petersen et al. 2009) due to plasticity in the timing of their reproductive cycle (Conover and Siferd 1993). However, the large amounts of lipid accumulated by *Calanus* species is related to the short and variable duration of their food supply in polar seas (Albers et al. 1996). Less ice-cover and longer periods of open-water could therefore influence the quantity of lipids accumulated by *C. hyperboreus* annually. Further, food quality (i.e. PUFA content) can affect the survival of *C. glacialis* naupulii (Daase et al. 2011). Thus, any change in the quantity or quality of lipids associated with changing ice conditions could affect *C. hyperboreus* populations and the amount of lipids made available to upper trophic levels. It is therefore important to monitor how the fatty acid profile of *C. hyperboreus* changes over time.

Data presented here will be useful for monitoring the acquisition of fatty acids by *C. hyperboreus* in the summer, and utilization in the winter. We recommend summer *C. hyperboreus* monitoring to focus on changes in PUFA like ARA, EPA and DHA because *C. hyperboreus* fatty acids vary with phytoplankton availability and composition (Stevens et al. 2004b; Kattner et al. 1989), and should therefore reflect changes in phytoplankton quality. Monitoring of winter *C. hyperboreus* fatty acids would provide insight into changes in lipid strategy (i.e. which fatty acids are catabolized, conserved and/or biosynthesized), and could reflect underlying changes in ability to acquire lipids in the summer. Winter monitoring should focus on PUFA, because they are the major fuel for overwintering and reproduction, based on our results. Additionally, the unsaturation index (Treen et al. 1992) could be useful for monitoring overall changes in the degree of fatty acid unsaturation over time, and should be a highly sensitive indicator of change because it is based on $\mu g\ mg^{-1}$ fatty acid values. Changes in 18:1n9 and long chain MUFA should also be noted because, based on the observation that they are not consistently depleted in winter *C. hyperboreus*, they could be important for winter survival.

In conclusion, *Calanus hyperboreus* from Cumberland Sound exhibited similar seasonal patterns in fatty acids over two years, which provides evidence that specific fatty acids are consistently catabolized (e.g. EPA), conserved (e.g. DHA) and maintained (or increased) (e.g. 18:1n-9) between summer and winter. Our sampling was coarse, at only two times annually, but still revealed that PUFA are selectively catabolized to a greater degree than biosynthesized C20 and C22 MUFA to fuel maturation and egg formation during winter. The observation that *C. hyperboreus* maintains or increases proportions of certain MUFA during the winter (this study; Lee 1974; Søreide et al. 2008) suggests that these fatty acids have some purpose for successful overwintering or reproduction, and indicates that the role of MUFA in winter *C. hyperboreus* should be further explored. The data presented here are novel for this part of the world and are important for monitoring short and long-term changes in *C. hyperboreus*, as well as other zooplankton taxa and their higher trophic level consumers in arctic ecosystems. Additional work combining fatty acids with other dietary metrics (e.g. stable isotopes, sterols) collected over a more frequent (e.g. monthly) and prolonged (i.e. years) time scale, combined with data for the composition, abundance and fatty acids for phytoplankton, would greatly improve our understanding of the mechanisms governing *C. hyperboreus* fatty acids, and how this might relate to changes in environmental conditions.

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Table 2.1. Fatty acid proportions of *Calanus hyperboreus* (fatty acid ∑fatty acids-1, expressed as a %, mean ± SE) sampled during summer (i.e. August) and winter (i.e. April) over two years in Cumberland Sound. Each individual sample (number of samples = “n”) was comprised of ca. 10 individuals of copepodite stages CIV, CV and adult females, except for the samples from winter 2009 marked with '♀' that consisted entirely of adult females.

Date	Summer 2007	Winter 2008	Summer 2008	Winter 2009	Winter 2009 ♀
n	5	2	5	5	2
16:0	5.6 ± 0.3	5 ± 0.2	6.1 ± 0.3	5.9 ± 0.5	4.1 ± 0.3
16:1n-7	16.6 ± 0.6	22.9 ± 0.5	17.3 ± 0.3	17.8 ± 0.3	20.5 ± 0.6
18:1n-9	2.4 ± 0.2	5.9 ± 2.1	3.9 ± 0.1	7.6 ± 1.8	4.8 ± 0.4
18:1n-7	2.3 ± 0.1	1.9 ± 0.3	1.4 ± 0	2.4 ± 0	2.3 ± 0.1
18:2n-6	3.9 ± 0.1	1.1 ± 0.5	3.5 ± 0.1	1.2 ± 0.1	1.6 ± 0.1
20:1n-9	10.5 ± 1.1	17.3 ± 1.3	11.3 ± 0.4	16.1 ± 1.4	15.1 ± 0.3
18:3n-3	1.2 ± 0.3	1.3 ± 0.5	0.9 ± 0.3	0.8 ± 0.3	0.3 ± 0
18:4n-3	5.4 ± 0.6	1.2 ± 0.2	1.5 ± 0.1	1.2 ± 0.2	1.7 ± 0.2
22:1n-11	14.5 ± 1.5	12.1 ± 0	8.7 ± 0.5	9.9 ± 0.6	9.8 ± 0.5
22:1n-9	1.8 ± 0.4	3.3 ± 0.7	1.6 ± 0.1	2.2 ± 0.3	5.2 ± 0.1
20:4n-6	0.2 ± 0	0.1 ± 0	0.2 ± 0	0.2 ± 0	0.3 ± 0
20:5n-3	16.9 ± 1	10.7 ± 0.7	20.8 ± 0.3	12.6 ± 0.5	13.8 ± 0.1
22:5n-3	1 ± 0.1	0.4 ± 0.1	0.7 ± 0	0.5 ± 0	1 ± 0.1
22:6n-3	9.3 ± 0.3	8.4 ± 0.3	8.9 ± 0.4	10.5 ± 0.4	9.4 ± 0
∑n-3	34.1 ± 1.2	22.5 ± 0.4	33.2 ± 0.6	26.1 ± 1	26.4 ± 0.2
∑n-6	4.9 ± 0.1	2.3 ± 0.6	8.6 ± 0.1	2.6 ± 0.1	3.4 ± 0.1
∑SAFA	11.8 ± 1.2	10.6 ± 0.7	13.2 ± 0.7	13.4 ± 1.3	9 ± 0.3
∑MUFA	49.2 ± 2.3	64.7 ± 0.9	44.9 ± 0.7	57.8 ± 0.7	61.1 ± 0
∑PUFA	38.9 ± 1.2	24.8 ± 0.2	41.9 ± 0.5	28.8 ± 1.2	29.8 ± 0.3
% lipid	33.7±2.0	29.3±4.5	36.0±1.3	27.2±1.5	27.4±3.0

Percent (%) lipid: mass of lipid dry weight of sample^{-1}

Table 2.2. Mean ± 1SE µg fatty acid mg^{-1} dry tissue of *Calanus hyperboreus* collected in Cumberland Sound during summer (i.e. August) and winter (i.e. April) of two consecutive years. Individual samples (total number of samples equals 'n') were comprised of ca. 10 individuals of copepodite stages CIV, CV and adult females, except for the samples from winter 2009 marked with '♀', which consisted entirely of adult females.

Date	Summer 2007	Winter 2008	Summer 2008	Winter 2009	Winter 2009 ♀
n	5	2	5	5	2
16:0	9.3±0.8	7.1±1	12.4±0.4	7±0.6	4.4±0.2
16:1n-7	27.7±2	33±4.9	35.2±1.4	21.2±1.4	21.8±3.1
18:1n-9	4±0.4	9±4.5	8±0.3	9.2±2.5	5.2±1
18:1n-7	3.7±0.2	2.8±0.8	2.8±0.1	2.8±0.1	2.5±0.2
18:2n-6	6.6±0.5	1.7±0.9	7.1±0.3	1.4±0.2	1.7±0.2
20:1n-9	17.2±1.4	24.6±2.3	23.1±1.4	19±1.8	16±1.5
18:3n-3	1.8±0.5	2±1.1	2±0.8	0.9±0.4	0.4±0
18:4n-3	9.2±1.4	1.8±0.5	3.2±0.2	1.5±0.2	1.9±0.4
22:1n-11	23.8±2	17.5±2.9	17.9±1.6	11.7±0.9	10.4±0.7
22:1n-9	2.8±0.6	4.6±0.1	3.2±0.3	2.6±0.3	5.5±0.5
20:4n-6	0.4±0.1	0.2±0.1	0.4±0	0.3±0	0.3±0
20:5n-3	28.3±2.7	15.3±1.6	42.4±1.7	15±1.2	14.7±1.8
22:5n-3	1.6±0.1	0.6±0	1.5±0.1	0.6±0.1	1±0.1
22:6n-3	15.4±0.5	12±1.6	18±0.6	12.4±0.5	10±1.1
∑n-3	56.7±4.2	32.3±4.9	67.8±2.9	30.9±2.1	28.1±3.4
∑n-6	8.1±0.5	3.4±1.3	17.5±0.8	3.1±0.3	3.6±0.6
∑SAFA	19.8±2.4	15.4±3.5	26.8±1.2	15.8±1.6	9.6±0.7
∑MUFA	81.2±3.5	93±14.6	91.7±4.3	68.6±3.8	65±7.3
∑PUFA	64.8±4.6	35.8±6.4	85.6±3.6	34.2±2.4	31.7±3.9
UI	385	268	478	239	221
Total FA	165.8±7.9	144.2±24.5	204.1±7.8	118.6±6	106.4±12

Unsaturation index (UI): ∑(µg fatty acid mg^{-1}*number of double bonds)

Table 2.3. Eigenvalues, proportion explained and unscaled weights of each fatty acid variable on the first three principal components (PC) of a PCA performed on *Calanus hyperboreus* fatty acid proportions.

Principal components	PC1	PC2	PC3
Eigenvalue	4.57	2.52	2.06
Cumulative Proportion	0.35	0.55	0.70
Fatty acid			
16:0	0.2	-0.3	0.0
16:1n-7	-0.3	-0.1	0.2
18:1n-7	-0.2	0.2	-0.6
18:1n-9	-0.2	-0.2	-0.2
18:2n-6	0.4	0.2	0.1
20:1n-9	-0.4	0.0	0.1
18:3n-3	0.0	0.4	0.1
18:4n-3	0.3	0.3	-0.3
22:1n-11	0.0	0.6	-0.1
22:1n-9	-0.4	0.2	0.1
20:4n-6	0.2	-0.2	-0.5
20:5n-3	0.4	-0.2	0.2
22:6n-3	-0.1	-0.2	-0.46

Fig. 2.1. *Calanus hyperboreus* sampling locations during summer (open-water, August) 2007 and 2008 and winter (ice-cover, April) 2008 and 2009 in Cumberland Sound, Baffin Island, Nunavut, Canada.

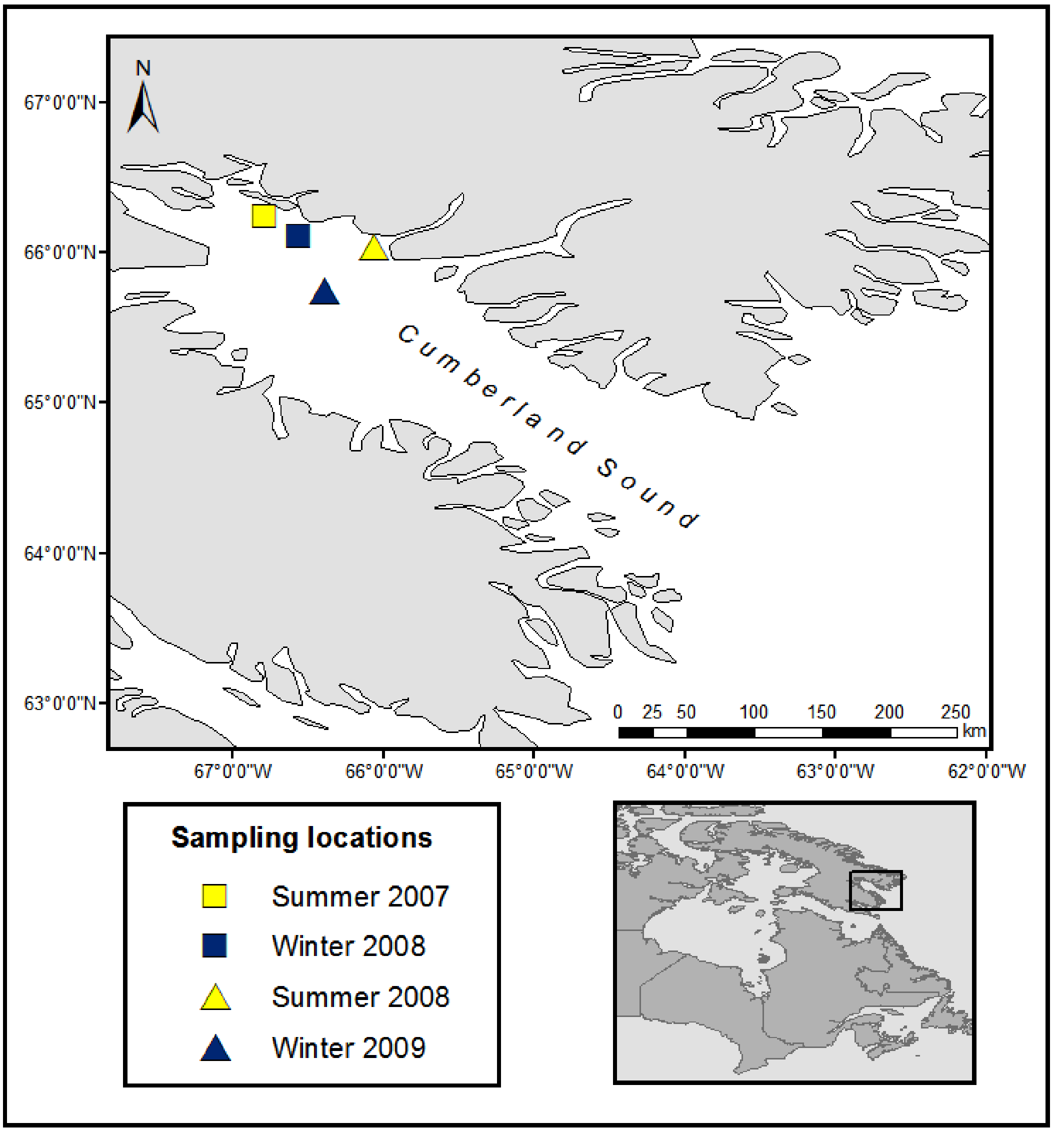


Fig. 2.2. Mean and standard deviation of relative proportions (fatty acid ∑fatty acids^{-1}, expressed as %) of *Calanus hyperboreus* monounsaturated fatty acids (∑MUFA: grey symbols), polyunsaturated fatty acids (∑PUFA: white symbols), and saturated fatty acids (∑SAFA: black symbols) over four sampling events (highlighted) in Cumberland Sound, Baffin Island, Nunavut. Timing of ice-cover and maximum surface chlorophyll *a* in Cumberland Sound obtained from satellite data are shown from May 2007 to April 2009.

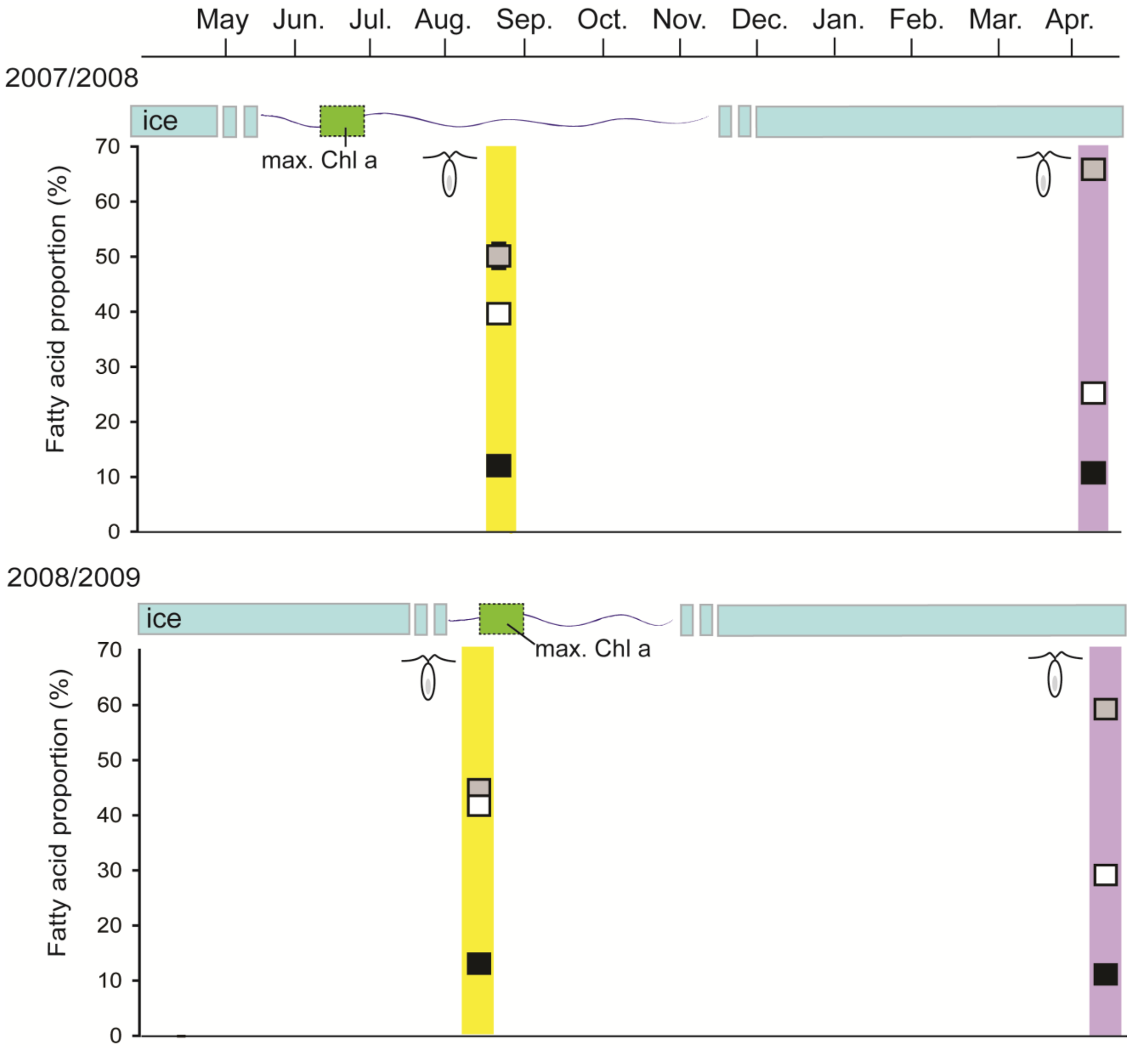
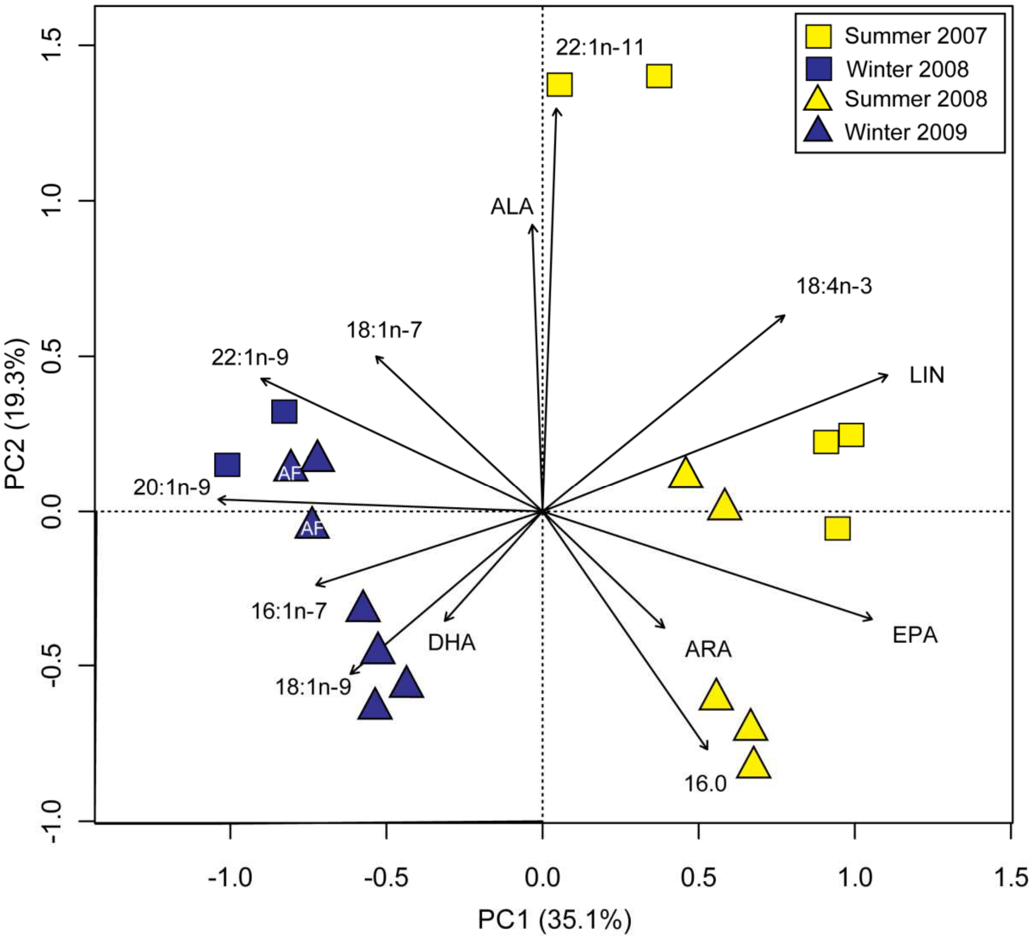


Fig. 2.3. Biplot of the component scores (symbols) and fatty acid variable loadings (vectors) on the first two principal components from a PCA performed on fatty acid proportions (%) in *Calanus hyperboreus*. Both scores and variables are scaled by the square root of the eigenvalues (i.e. scaling = 3). All samples consisted of pooled copepodite stage VI, V and adult females except for two winter 2009 samples that consisted entirely of adult females (marked with 'AF').



CHAPTER 3

COUPLING OF MACROALGAL AND PHYTOPLANKTON ENERGY PATHWAYS BY CONSUMERS INHABITING A SEASONALLY ICE-COVERED FJORD

INTRODUCTION

Explicitly linking food web structures (i.e. patterns of carbon flow within a food web that arise from feeding interactions among consumers) with mechanisms that increase persistence (i.e. the continued existence of a food web through time) has proven a difficult task (Paine 1988; Levin 1998). Given that anthropogenic activities are known to affect food web structure (Rooney et al. 2008; Wassmann et al. 2011), connecting structures with mechanisms of persistence is of increasing importance. Recent theoretical models have linked a seemingly common food web structure with the ability of food webs to persist through time: the existence of resources that differ in biomass turnover rates and abundance (i.e. that vary asynchronously), which are 'coupled' in space by generalist consumers (i.e. that move across spatial boundaries to feed on multiple resources as they become abundant, Rooney et al. 2006; McCann and Rooney 2009). When present, this 'spatial coupling of asynchronous resources' (see Fig. 1.1. for visual representation of this structure) is associated with several empirical patterns. First, lower trophic levels generally feed within distinct 'resource compartments' by deriving energy predominantly from one of two (or more) available resources (e.g. phytoplankton or detritus). Second, upper trophic level couplers should use carbon sources from multiple resource compartments, across spatial boundaries (McCann and Rooney 2009). Together, these factors impart a 'hump-shape' structure to food webs (Fig. 1.1; Rooney et al. 2006), which appears to be iterative across spatial scales and within and between ecosystems (McCann and Rooney 2009). Soil, freshwater and marine food webs from temperate climates have been shown to exhibit this 'hump-shape' structure (Rooney et al. 2006; Dolson et al. 2009). However, it is unknown if food webs from latitudes that experience high degrees of seasonality and temporal variability, which can be driven primarily by one energy source (phytoplankton, e.g. Renaud et al. 2011), are structured such that spatially asynchronous resource compartments are coupled by upper trophic levels.

Almost all marine ecosystems exhibit temporally varying levels of productivity to some degree, however, arctic and sub arctic seas that are seasonally ice-covered experience a much shorter duration of primary production (e.g. 1-4 months per year) than more temperate locations (e.g. Baltic Sea, 9 months per year; Weslawski et al. 1991). Short, intense phytoplankton blooms during spring and summer fuel pelagic food chains (e.g. phytoplankton-zooplankton-fish-seabirds; Hobson et al. 2002; Falk-Petersen et al. 2007) and sink to provide labile phytodetritus that is rapidly exploited by benthos (Grebmeier and Barry 1991; Iken et al. 2010). An additional, yet understudied, primary production source in arctic seas is benthic macroalgae, which can be locally abundant in some areas (e.g. Beaufort Sea, Dunton and Schell 1987). With the exception of herbivorous calanoid copepods (Falk-Petersen et al. 2009), arctic consumers are widely acknowledged to exploit a variety of resources, including detritus, and to feed omnivorously (Iken et al. 2005; Forest et al. 2008; Renaud et al. 2011), but only one study to date has assessed if consumers in an arctic sea also rely on carbon and nutrients from macroalgae (but see Dunton and Schell 1987). Further, it is unknown if food webs in highly seasonal arctic seas exhibit 'hump-shape' structures similar to food webs from temperate latitudes (Rooney et al. 2006; Dolson et al. 2009), or if the importance of phytoplankton and prevalence of omnivory preclude such structures from arising.

The goal of the present study was to identify if an arctic food web exhibited spatial coupling of asynchronous resources, because this structure has been previously identified as important for food web persistence (based on theoretical food web models) and is common in food webs from temperate latitudes (Rooney et al. 2006; Dolson et al. 2009). The following questions were asked: 1) do zooplankton feed heavily on phytoplankton and benthos heavily on macroalgae, creating two distinct resource compartments within an arctic food web? and 2) how are these distinct resource compartments, if apparent, coupled by upper trophic levels (elasmobranchs, teleosts and marine mammals)? Stable carbon isotopes ($\delta^{13}C$) and fatty acid trophic markers were applied to trace the relative use of basal resources among consumers. The null hypothesis is that lower trophic levels will rely heavily on either phytoplankton or macroalgae and upper trophic levels will use intermediate amounts of carbon from phytoplankton and macroalgae (as assessed through $\delta^{13}C$ values and fatty acids), indicating resource coupling (i.e. predicted pattern = observed pattern). One possible alternate hypothesis is that lower and upper trophic levels will use similar amounts of one carbon source, indicating little spatial resource coupling (i.e. predicted pattern ≠ observed pattern, see Fig. 1.1. for visual representations of hypotheses).

As arctic seas are currently experiencing decreased ice cover duration (Markus et al. 2009) and earlier timing of primary production (Kahru et al. 2011), the possible effects of climate change on the structure of arctic food webs are also considered.

MATERIALS AND METHODS

Study site

Sampling was conducted within Pangnirtung fjord or just outside the mouth of Pangnirtung fjord in Cumberland Sound (see Fig. 2.1 for map of sampling locations). Pangnirtung fjord is characterized by wide (up to 600 m) intertidal flats consisting of sand, gravel and boulders, and large (up to 7 m) tides (Aitken and Gilbert 1989). *Fucus* grows on boulders in the intertidal and subtidal zones of Pangnirtung fjord, and a benthic fauna of polychaetes, mollusks and amphipods exists from ~5-50 m depth (Aitken and Gilbert 1989). Water depth increases towards the middle of Pangnirtung fjord to a maximum of ~150 m. The ichthyofauna during summer include arctic char (*Salvelinus alpinus*), capelin (*Mallotus villosus*) and shorthorn sculpin (*Myoxocephalus scorpius*). Greenland sharks (*Somniosus microcephalus*) also enter Pangnirtung fjord and ringed (*Pusa hispida*) and harp seals (*Phoca groenlandica*) are common. *Fucus* sp. are the dominant genus covering the shores of Pangnirtung fjord (B. McMeans personal observation, Aitken et al. 1988), and was therefore considered to be the most likely source of fresh and detrital macroalgae to consumers within the sampling area.

Sampling of species

A variety of benthic and pelagic invertebrates and vertebrates, as well as POM and the brown macroalga *Fucus distichus* (rockweed), were collected during summer of three sequential years: 11 August-7 September 2007, 30 July-15 August 2008 and 10-19 August 2009 (see Table 3.1 for species sampled). Data presented here were predominantly collected during 2008 (see Table 3.2 for sampling dates), and three species, rockweed, copepod (*Calanus hyperboreus*), and scallop (*Chlamys islandica*), were sampled during both 2008 and 2009 (Table 3.2).

POM was sampled by towing a 10-µm plankton net (Wildlife Supply Company®, Buffalo, New York) from 50 m to the surface and rockweed was sampled either by hand (low tide) or by ponar (high tide). Each rockweed sample consisted of the tip of one leaf (i.e. distal end) from one plant. Benthic and pelagic invertebrates and vertebrates were classified into functional groups based on previously reported habitat (e.g. benthic versus pelagic) and diet attributes (e.g. herbivore versus carnivore, Table 3.1). These classifications reflect the *dominant* habitat and feeding mode of species. For example, arctic char were classified as pelagic because they feed predominantly on the pelagic amphipod *Themisto libellula* (Moore and Moore 1974) and capelin (B.C. McMeans, personal observation) in Cumberland Sound, although they will also consume benthic amphipods like *Gammarus oceanicus* (Moore and Moore 1974). Similar-sized individuals of each species were collected, with the exception of adult sculpin. Due to size-related diet variability in this species (Cardinale 2000), sculpin were separated into 'small' (<24 cm) and 'large' individuals (>24 cm). Herbivorous and carnivorous benthos were sampled using dip nets by wading into water at low tide, except for scallop that were collected in water 30-40 m deep using a dredge. Zooplankton were captured by towing a 243 μm plankton net (Wildlife Supply Company®, Buffalo, New York) behind a boat at the surface and by performing vertical hauls down to ~40 m. Pelagic fish were sampled via dip nets and gill nets and the benthic sculpin were captured using baited fishing line. The remaining benthic and benthic/pelagic fishes were collected using bottom long lines (typically 50 hooks, ~200 m long). Marine mammals were captured during Inuit subsistence hunting. Multiple individuals (2-10) of each zooplankter, polychaete worm and benthic amphipod (scud, *G. oceanicus*) were pooled for stable isotope and fatty acid samples. White muscle of fishes, and muscle and blubber (inner layer) of marine mammals was dissected from the dorsal surface. All samples were placed into cyrovials and immediately frozen at -20°C (stable isotopes) and at -80°C (fatty acids), and kept at these temperatures, until analysis.

Stable isotope analysis

Samples were lipid extracted prior to stable isotope analysis following a modified Folch et al. (1957) method (detailed in McMeans et al. 2009). Based on suggestions by Mateo et al. (2008), acid washing was avoided except for samples with potentially high $CaCO_3$ content (i.e. scud due to exoskeleton and *Littorina* (periwinkle) due to shell). Due to the importance of copepod $\delta^{13}C$ values in determining the proportion of pelagic carbon consumed by species (see data analysis section below), the influence of acid washing on copepods was also explored, which has been performed by previous researchers (e.g. Tamelander et al. 2006). Removal of carbonates was achieved using 1M HCl added to samples drop-by-drop until bubbling ceased (Jacob et al. 2005). After addition of HCl, bubbling only occurred with scud and periwinkle, and $\delta^{13}C$ decreased by 1.50 ±0.32 and 5.36±1.62‰, respectively; the desired effect for carbonate removal. However, $\delta^{15}N$ also decreased following the acid washing procedure (by 1.25±0.67 and 0.33± 0.82‰ for scud and periwinkle, respectively) and we therefore used $\delta^{15}N$ values from non-acid treated samples. When copepods were acid washed, results were consistent with those of Mateo et al. (2008), because acid treated copepods were occasionally enriched in ^{13}C by as much as 0.66‰; an undesirable result. Further, acid washing only altered $\delta^{13}C$ of copepod by mean±SD of 0.01±0.37‰, and the non acid washed stable isotope values were therefore used for copepod.

Following pre-treatment, approximately 0.5 mg of each sample was weighed into tin capsules and run on a continuous-flow isotope ratio mass spectrometer (Delta V Advantage, Thermo Electron) at the Great Lakes Institute for Environmental Research. Stable isotopes are expressed as delta δ values where $\delta X = 1000[R_{sample}\ R_{standard}{}^{-1}) -1]$, and X = ^{15}N or ^{13}C and R = the ratio of ^{15}N:^{14}N or ^{13}C:^{12}C. Replicate analyses of NIST (National Institute of Standards and Technology) standard bovine muscle (NIST 8414, N = 70) and internal lab standard (tilapia muscle, N = 7) yielded a precision (i.e. one standard deviation) of 0.14 and 0.25‰ for $\delta^{15}N$ and 0.07 and 0.10‰ for $\delta^{13}C$, respectively.

Fatty acid analysis

Total lipids were extracted from samples in 2 mL of 2:1 (v/v) chloroform:methanol (Folch et al. 1957). Fatty acid methyl esters were generated (from the total lipid extract) in a sulphuric-methanol solution (1:100 mixture) (see Chapter 2, McMeans et al. 2012 for detailed analytical methods) and separated on a Hewlett Packard 6890 GC (splitless injection, column = Supelco (SP-2560 column). Fatty acids were identified using a 37-component fatty acid standard (Supelco 47885-U).

Data analyses

Values of $\delta^{13}C$ are higher in macroalgae versus phytoplankton and can be applied to trace the use of these resources by consumers (e.g. Fredriksen 2003). However, using POM as the baseline for phytoplankton in mixing models is often not appropriate because of the difficulty in obtaining a sample free of other carbon sources and detritus (Iken et al. 2010). POM samples can therefore provide inaccurate representations of the marine carbon signature and can result in over-estimation of consumer reliance on macroalgae (Miller and Page 2012). Finally, primary consumers are less variable in their $\delta^{13}C$ than primary producers with space and time (Vander Zanden et al. 1998; Iken et al. 2010). Therefore, the $\delta^{13}C$ of a primary consumer of phytoplankton (i.e. copepod, *C. hyperboreus*; Søreide et al. 2008) and benthic macroalgae (limpet, *Tectura testudinalis*;

Fredriksen 2003) were used as baselines for calculations of trophic position (TP) and the proportion of pelagic carbon consumed (α). Both baselines were assigned a trophic position of 2. There was no difference in the outputs from one- and two-source TP calculations (see Post 2002 for implementation of two-source TP model), and the following one source TP model was therefore applied for all individuals:

$$TP_{consumer} = TP_{baseline} + \frac{\delta^{15}N_{consumer} - \delta^{15}N_{baseline}}{\Delta^{15}N} \qquad \text{Eqn. 1}$$

Copepod average δ^{15}N (from the same year as the consumer was sampled, Table 3.2) was used as the $\delta^{15}N_{baseline}$ and 3.4‰ was used as the diet-tissue discrimination factor (i.e. Δ^{15}N; Post 2002). One exception to the above was Greenland sharks. Because TP calculations for sharks can be problematic, due to, for example, uncertainty over Δ^{15}N (Hussey et al. 2012), the Greenland shark's TP was calculated using 2.3‰ for the Δ^{15}N, which was previously derived for large sharks (Hussey et al. 2009), and the mean δ^{15}N of capelin, which have a relative TP of 3 (Sherwood and Rose 2005; McMeans et al. 2010), as the baseline.

The proportion of phytoplankton (vs rockweed) carbon that was incorporated into the tissues of consumers (i.e. α) was calculated using a modified version of the two-source mixing equation (Post 2002; Vander Zanden and Vadeboncoeur 2002) as follows:

$$\alpha = \frac{\delta^{13}C_{consumer} - [\Delta^{13}C \times (TP_{consumer} - TP_{baseline})] - \delta^{13}C_{limpet}}{\delta^{13}C_{Calanus} - \delta^{13}C_{limpet}} \text{ x } 100 \qquad \text{Eqn. 2}$$

The term [Δ^{13}C x ($TP_{consumer}$ - $TP_{baseline}$)] accounts for the enrichment of consumer ^{13}C at each trophic step (i.e. Δ^{13}C) above the primary consumer baseline. The Δ^{13}C was set at 0.8‰ (Dunton and Schell 1987; Fredriksen 2003; Nilsen et al. 2008) and $TP_{consumer}$ is the result of the one source TP model for each individual (Eqn. 1).

Normality was assessed using q-q plots, and homoscedacity via Levene's tests. Two-way ANOVAs (factors=date and species) were used to identify differences in $\delta^{13}C$ and $\delta^{15}N$ between 2008 and 2009 for copepod and scallop. Macroalgae are variable in their stable isotope values, both among individual plants and within different areas of the same plant (Stephenson et al. 1984; Dunton and Schell 1987). Due to high variability of *Fucus* stable isotopes identified in the present study, relative to other species, a separate Welch's *t* test was therefore used to compare their $\delta^{13}C$ and $\delta^{15}N$ between sampling dates. ANOVA followed by Tukey's post hoc tests were used to compare $\delta^{13}C$, $\delta^{15}N$ and TPs among functional groups (i.e. zooplankton, benthos, consumers). Due to departures from normality, a Kruskal-Wallis non-parametric ANOVA followed by Mann-Whitney tests (with Bonferroni corrections) was used to compare $\delta^{13}C$-derived values of α among functional groups.

Fatty acids were first compared between Cumberland Sound rockweed and published values for POM (from the Canadian arctic, Stevens et al. 2004). Consistent with previous work on macroalgae (Bell and Sargent 1985; Graeve et al. 1994; Kharlamenko et al. 1995; St John and Lund 1996), differences were as follows: rockweed had higher 18:2n-6 and 20:4n-6 than POM, whereas POM had higher 16:1n-7, 22:6n-3 and $\omega3:\omega6$ than rockweed (Table 3.3). Non-metric multidimensional scaling (NMDS, dimensions = 2, Euclidean distances) was then performed including these five fatty acids on Cumberland Sound: 1) rockweed, zooplankton, benthos and 2) fish and marine mammal consumers. All analyses were performed in R (R_Development_Core_Team 2010) and the significance level was conservatively set at 0.01.

Food web components were sampled in August to allow organisms time to incorporate the signature of their summer diet, which should have been occurring since ice break up (mid July 2008 and early June 2009). Few stable isotope or fatty acid turnover studies exist for arctic organisms, although turnover is likely slow due to cold temperatures. However, *C. hyperboreus* has a turnover time of 11 d for fatty acids (Graeve et al. 2005), and *Onisimus litoralis* turned over half of its nitrogen and carbon in 22.4 and 18.7 days, respectively, even at 1°C (Kaufman et al. 2008). Nordström et al. (2009) was able to observe differences in isotopes in invertebrates and juvenile teleosts from month to month during the productive period in the northern Baltic Sea. Even though August is considered mid to late summer in Baffin Island waters (Hsiao 1988), phytoplankton was still present during sampling based on measured values of chlorophyll *a*, which were 67.6 mg m^{-2} on August 14, 2007 (B. McMeans, unpubl. data) and 53.4 mg m^{-2} on July 31, 2008 (J. Brush, University of Waterloo, unpubl. data) (integrated over the upper 40 m). Thus, it seems reasonable that species sampled in August would reflect their summer diet from the previous weeks (invertebrates) or months (fishes, mammals), which for the latter would still be during open water, or at least during ice break up. One definite exception is the Greenland shark, whose muscle stable isotope and fatty acid values likely reflect longer incorporation times due to their large size and presumably slow growth rate (MacNeil et al. 2006; MacNeil et al. 2012). However, their stable isotope and fatty acids values are still informative regarding their relative location within the food web.

RESULTS

No significant inter-annual variability existed in $\delta^{13}C$ or $\delta^{15}N$ for the three species sampled in both 2008 and 2009 (i.e. rockweed, Welch's *t* test, $P>0.01$; copepod or scallop, two-way ANOVA, both $P>0.01$). Values of $\delta^{15}N$ and $\delta^{15}N$-derived TPs were significantly lower in zooplankton and benthos versus fish and marine mammal consumers (Table 3.4). At the species level, calculated TPs for zooplankton and benthos supported their functional group assignments and previous diet information (Table 3.1) and ranged from 1.5 to 2.0 in herbivores, from 2.1 to 2.2 in omnivores and from 2.4 to 3.2 in carnivores (Fig. 3.1, Table 3.2). Calculated TPs also agreed with the known diets of pelagic fish and mammals (2.4 to 3.5), benthic fishes (3.9 to 4.1) and was 4.6 in the benthic/pelagic Greenland shark, which consumes fishes and marine mammals (Table 3.2).

Values of $\delta^{13}C$ decreased significantly from benthos to fish and marine mammal consumers to zooplankton, and calculated values of α exhibited the opposite trend (Table 3.4). Thus, coupling of macroalgae and phytoplankton by upper trophic level consumers was apparent because calculated values of α for fish and marine mammals (i.e. 58-100) fell in between, although overlapped with, that of benthos (4-71) and zooplankton (94-100) (Fig. 3.1). Herbivorous, omnivorous and carnivorous zooplankton relied entirely on pelagic carbon based on calculated values of $\alpha>95$ (Fig. 3.1, Table 3.2). Benthos exhibited a wider range of resource use, from heavy reliance on macroalgal carbon in some herbivorous mollusks (i.e. limpet and periwinkle, $\alpha<5$) and the carnivorous polychaete ($\alpha=11$), to the use of both macroalgae and phytoplankton by the benthic herbivores scallop, clam and *G. oceanicus* ($\alpha=53$ to 71, Table 3.2). The carnivorous whelk (*Buccinum cyaneum*) and nudibranch appeared to couple the two aforementioned groups ($\alpha=46$ and 39, respectively, Fig. 3.1). Most of the energy acquired by fish and marine mammal consumers in Cumberland Sound ultimately arose from phytoplankton production based on α values ranging from 58 to 100 (Fig. 3.1). However, macroalgae did contribute to the energy acquired by several pelagic fish and mammals (e.g. char and harp seal, α=85 and 71, respectively) as well as large individuals of the benthic sculpin (α =58, Table 3.2).

The NMDS performed on rockweed and invertebrate fatty acids supported δ^{13}C-derived values of α because all zooplankton separated away from rockweed due to higher proportions of phytoplankton trophic markers (16:1n-7, DHA and ω3:ω6), and lower proportions of macroalgae markers 18:2n-6 and 20:4n-6 (Fig. 3.2A, Table 3.3). Benthos, on the other hand, clustered more closely to rockweed due to high proportions of 18:2n-6 and 20:4n-6 (Fig. 3.2A). The three herbivorous benthos with intermediate α values also exhibited fatty acid evidence of phytoplankton consumption due to high 16:1n-7 in clam and scud and high 22:6n-3 in scallop (Fig. 3.2A), and their location relative to rockweed on these plots indicates higher reliance on phytoplankton by the bivalves and reliance on both rockweed and phytoplankton by scud. The carnivorous mollusks, whelk and nudibranch, fell in between the rockweed- and phytoplankton- reliant invertebrates on the NMDS plot (Fig. 3.2A), supporting the suggestion by α that they coupled these two resource compartments.

NMDS performed on consumers revealed that pelagic fish and mammals separated from each other due to different relative contributions of phytoplankton trophic markers (Fig. 3.2B, Table 3.3), supporting reliance on phytoplankton as indicated by α values. Unlike the other fatty acid biomarkers, proportions of 18:2n-6 varied little among consumer species (1.1-1.8%, Table 3.3) and may not be useful as a macroalgae biomarker in upper trophic levels (which agrees with results of Hall et al. 2006).

Proportions of 20:4n-6, on the other hand, varied from 0.4% in pelagic fish like capelin to 4.4% in benthic fish like sculpin (Table 3.3), which coincides with lower and higher $\delta^{13}C$ in these fishes, respectively ($\delta^{13}C$ capelin=-19.37 ± 0.15, large sculpin=-16.79 ± 1.07), indicating that 20:4n-6 can trace macroalgae use by upper trophic levels. Further exploration of 20:4n-6 among consumers indicated decreasing proportions from 3.5±1.5% in benthic to 1.5±0.2% in benthic/pelagic to 0.4±0.2% in pelagic consumers. These differences were significant based on a Kruskal-Wallis non-parametric ANOVA (χ^2=39.8, DF=2, P<0.001). Thus, the macroalgae biomarker 20:4n-6 supported values of α in indicating greater reliance on rockweed carbon by benthic fishes like sculpin (α=58-74) than by pelagic fishes like capelin (α=96). One exception is the skate (α=100), which had higher proportions of 20:4n-6 than capelin (Table 3.3), suggesting greater reliance on rockweed-consuming prey by skate than indicated by α values. Based on combined stable isotope and fatty acid data, all fish and marine mammal species sampled acted as couplers of phytoplankton and rockweed to some extent except for herring (*Clupea harengus*) and capelin (both α >95).

DISCUSSION

The exclusive use of phytoplankton by all zooplankton species, and rockweed by several benthos, is consistent with the expectation that lower trophic levels tend to feed within resource compartments (McCann and Rooney 2009). Combined with the observation that most fish and marine mammal consumers relied to some extent on both phytoplankton and rockweed (i.e. all except capelin and herring had α<85), results from Cumberland Sound indicate that, at least when sampled during the productive period, an arctic food webs was structured such that resource compartments based on different basal resources were coupled by upper trophic levels, which reaffirms previously identified food web structures (Post et al. 2000; Rooney et al. 2006; McCann and Rooney 2009). For the top predators in Cumberland Sound, phytoplankton was the dominant energy source based on values of α and fatty acid trophic markers. This is perhaps not surprising considering the importance of fresh phytoplankton and phytodetritus as an energy source to both benthic and pelagic consumers in many arctic seas (e.g. Falk-Petersen et al. 2007; Iken et al. 2010; Renaud et al. 2011). As observed previously in the Beaufort Sea (Dunton and Schell 1987), however, macroalgae was also utilized by several benthic and pelagic species, indicating that the *Fucus* lining the shores of Pangnirtung fjord does play a role in fueling the food web. This structure was, however, highly skewed such that top predators ultimately derived the majority of their energy from phytoplankton.

The phytoplankton and rockweed consumed by benthos were likely in the form of detritus, based on higher δ^{13}C in the bivalves and scud relative to zooplankton (sedimenting POM and detritus becomes isotopically enriched, Lovvorn et al. 2005) and the ~1‰ lower δ^{13}C of limpet versus rockweed (Table 3.2) (rockweed detritus was depleted in ^{13}C versus fresh material, Fig. 6.5). Previous studies have also found that benthos rapidly exploit phytodetritus (Grebmeier and Barry 1991), and that 'aged' macroalgae is more palatable for consumers than fresh macroalgae (Norderhaug et al. 2003). Thus, a consumer in Cumberland Sound that preys on herbivorous zooplankton and amphipods, for example, like arctic char (Moore and Moore 1974), could obtain carbon that originated from two different phytoplankton pools: phytoplankton (consumed by zooplankton) and phytodetritus (consumed by amphipods), as well as from macroalgae (consumed by amphipods). Results from Cumberland Sound support previous conclusions that the benthos use a greater range of resources than zooplankton (Iken et al. 2005; Tamelander et al. 2006), which is important for allowing benthos to maintain greater biomass in areas than would otherwise be possible on autochthonous production alone (Feder et al. 2011). However, based on the present study, the benthos are also important for making arctic food webs more reticulate by increasing the *number* of resources made available to ultimately support production in upper trophic levels.

The reliance by different benthic species on different resources also created a set of distinct resource compartments within the benthos, macroalgae and phytodetritus, that were apparently coupled by the benthic predators whelk and nudibranch. Other highly mobile, benthic omnivores that can move long distances and feed on both benthic and pelagic prey (e.g. crabs and shrimps, Feder et al. 2011) would also be expected to couple distinct resource compartments within the benthic food web. The results reported here are among the first empirical evidence to support the suggestion by McCann and Rooney (2009) that the coupling of different resource compartments is repeated at various scales (i.e. within a trophic level, within an ecosystem, between ecosystems), and provides additional evidence of the importance of the benthos for arctic food web structure.

It is important to consider that the pulsed nature of phytoplankton growth in arctic seas (Weslawski et al. 1991; Forest et al. 2008) would impart a temporal aspect to the food web structure reported here. Early during the productive period, energy derived from phytoplankton would rapidly reach top predators through the pelagic pathway (Fig. 3.3), given the efficient trophic transfer of phytoplankton through food webs (Rooney et al. 2006). During this time there would be relatively little detritus in the water column (e.g. during spring blooms, Søreide et al. 2006). Energy derived ultimately from phytoplankton, but routed through the benthic channel (i.e. via phytodetritus), would reach upper trophic levels later in the season (towards the end of the bloom in late summer or fall, Fig. 3.3). One of the major elements through which asynchronous resources coupled in space confer stability to food webs is the top-down induced asynchrony in resource abundance between resource compartments (Rooney et al. 2006; McCann and Rooney 2009). Based on results of the present study, arctic food webs appear to be structured such that benthic and pelagic resource abundance is asynchronous, but driven by the bottom-up effect of pulsed phytoplankton growth, which is a different (but not exclusive) mechanism to that proposed by Rooney et al. (2006).

The possibility that ice algae, not phytoplankton, sinking to the benthos contributed to high ω3s and 16:1n-7 observed in the suspension feeding bivalves and scud in Cumberland Sound cannot be discounted (because ice and pelagic algae can have similar fatty acids; Søreide et al. 2008). However, based on low 20:4n-6 and high 16:1n-7, 22:6n-3 and ω3:ω6 PUFAs, macroalgae was not the major source of energy to these species. Other potential energy sources not sampled here include terrestrial carbon, which can be very important to consumers in some arctic seas (e.g. Beaufort Sea, Dunton et al. 2006). However, we found no evidence for the use of terrestrial carbon by the species sampled in Cumberland Sound because terrestrial material is depleted in ^{13}C relative to carbon of marine origin (terrestrial -27 to -31‰, marine -22 to -25‰, Dunton et al. 2006). POM samples from Cumberland Sound (-22.13‰), and primary consumers of phytoplankton (e.g. *C. hyperboreus*, -20.37‰) clearly had marine δ^{13}C signatures.

Drawing from recent food web theory (Rooney et al. 2006), any action that increases resource homogenization or decreases resource coupling by upper trophic levels could negatively impact arctic food webs (Rooney et al. 2008; McCann and Rooney 2009). Global climate change is the most likely cause of such changes, which has already resulted in altered timing of primary production and community structure (reviewed by Wassmann et al. 2011). Predicting the consequences of warming temperatures is difficult (Carmack and Wassmann 2006), but plausible changes include: 1) decreased food quantity and quality (e.g. regarding polyunsaturated fatty acid content) reaching the benthos (due to less intense, lower quality phytoplankton production) (Weslawski et al. 2011), and 2) decreased benthic biomass (due to increased habitat homogenization associated with permafrost melt and increased sedimentation) (Weslawski et al. 2011). On the other hand, macroalgae biomass could increase with decreased ice cover due to decreased ice scouring (Weslawski et al. 2011), and could become increasingly important for supporting benthic biomass in the face of decreased pelagic-benthic coupling.

From a top-down perspective, the northward expansion of mobile consumers into the arctic could impact the extent of resource coupling. Reductions in sea ice and warmer temperatures have already resulted in the once benthic-dominated community of the Bering Sea shifting towards dominance by pelagic fish (Hunt et al. 2002, Grebmeier et al. 2006). Increasing contribution of pelagic consumers to arctic food webs, like capelin and herring (i.e. α>95, this study) that have already expanded into Cumberland Sound, could serve to decrease the presence of resource coupling in arctic food webs.

In summary, results from the present study indicate that the food web of an arctic, seasonally ice-covered fjord is structured in a similar manner to that previously reported for other food webs. Specifically, heterogeneity in basal resources and feeding of consumers (within and between resource compartments) were found to exist even in a food web that experiences high seasonality. Previous assertions about arctic food webs (Iken et al. 2005; Renaud et al. 2011) were also supported because phytoplankton and phytodetritus were significant contributors to the food web, and the benthos consumed a range of different resource types. From a food web perspective, it is not changes in biomass or species composition, per se, but the removal of variability in resource use among, and perhaps within, species that is the biggest threat to arctic food web persistence.

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Table 3.1. Functional group membership of species sampled from Cumberland Sound during summer (August) and associated codes for Fig. 1. Benthic herbivores are either filter-feeders (FF) or grazers (G). Major diet items are provided from locations as near to the east coast of Baffin Island as possible.

Functional Group	Species	Fig. 1 code	Diet items
Zooplankton			
herbivores	*Calanus hyperboreus*	1	Phytoplankton[1]
	Mysis oculata[*]	2	phytoplankton, macroalgae[2]
omnivores	*Aglantha digitale*	3	phytoplankton, copepods, detritus[3]
	Myoxocephalus scorpius (larvae)	4	diatoms, *Balanus* naupulii[4]
	Stichaeus punctatus (larvae)	5	bivalve larvae[5]
carnivores	*Sagitta* sp.	6	zooplankton[6]
Benthos			
herbivores	*Chlamys islandica* (FF)	7	phytoplankton, detritus[7]
	Hiatella arctica (FF)	8	phytoplankton, detritus[8]
	Gammarus oceanicus (G)	9	Phytoplankton, macroalgae, detritus[9]
	Littorina (G)	10	algae[10]
	Tectura testudinalis (G)	11	algae[10]
carnivores	*Buccinum cyaneum*	12	polychaetes, bivalves, carrion[11]
	Nudibranch	13	unknown
	Polychaete	14	predatory based on mouth parts (i.e. large fangs)
Fish consumers			
pelagic	*Clupea harengus*	15	zooplankton[12, 13]
	Mallotus villosus	16	zooplankton[13]
	Salvelinus alpinus	17	*Themisto*[14], *M. villosus*[12], *Mysis*[12]
benthic	*Amblyraja hyperborea*	18	*Lebbeus polaris*[12]
	Myoxocephalus scorpius (small, <24cm)	19	Isopods, *Mysis*[12,15]
	Myoxocephalus scorpius (large, >24cm)	20	*C. harengus*[15],crab[12],*M. scorpius*[12]
benthic/pelagic	*Somniosus microcephalus*	21	*P. hispida, R. hippoglossoides, M. scorpius*[12]
Mammal consumers			
pelagic	*Phoca groenlandica*	22	*Themisto, M. villosus*[12]
	Pusa hispida	23	*Themisto*[12]

[*] benthic-associated but captured in zooplankton nets; References: [1]Soreide et al. 2008; [2]Dunton and Schell 1987; [3]Pages et al. 1996;[4] LaRoche 1982;[5] Pepin and Penney 1997; [6]Pearre Jr. 1973;[7] Bell and Sargent 1985;[8] Petersen et al. 2003;[9] Hudon 1983;[10] Steneck and Watling 1982;[11]Himmelman and Hamel 1993;[12] B.C. McMeans, unpublished data from Cumberland Sound ;[13] Scott and Scott 1988;[14] Moore and Moore 1974;[15] Cardinale 2000

Table 3.2. Sampling year, mean ± SD of $\delta^{13}C$ and $\delta^{15}N$ (‰) and mean relative trophic positions (TP), proportional reliance on pelagic carbon (α) and carbon:nitrogen (C:N) for Cumberland Sound species sampled in August.

Species	Date	*n*	Tissue	$\delta^{13}C$	$\delta^{15}N$	TP	α	C:N
Primary producers								
POM	2008	1	W	-22.13	8.24			8.5
Fucus sp.	2008	3	Leaf	-14.87 ± 1.17	6.40 ± 1.08			29.5
	2009	3		-15.13 ± 1.80	7.49 ± 1.29			32.1
Invertebrates								
Aglantha digitale	2008	7	W	-20.46 ± 0.26	10.12 ±	2.07	99	3.3
Chlamys islandica	2008	5	M	-18.63 ± 0.65	9.65 ± 0.16	1.93	59	3.3
	2009	5	M	-18.79 ± 0.20	8.89 ± 0.38	1.71	53	3.3
Hiatella arctica	2008	5	Ma	-19.52 ± 0.23	8.14 ± 0.43	1.49	71	3.9
Littorina sp.	2009	5	W	-16.13 ± 0.62	9.39 ± 0.50	1.85	5	4.4
Buccinum cyaneum	2008	5	F	-17.27 ± 0.63	12.92 ±	2.90	46	3.5
Tectura testudinalis	2008	5	F	-15.96 ± 0.46	9.87 ± 0.19	2.00	4	3.7
Nudibranch	2008	2	W	-16.81 ± 0.23	13.54 ±	3.08	39	3.8
Polychaete	2008	3	W	-16.18 ± 0.80	11.21 ±	2.39	13	3.8
Calanus hyperboreus	2008	5	W	-20.37 ± 0.14	9.88 ± 0.53	2.00	98	3.5
	2009	5	W	-20.84 ± 0.49	9.90 ± 0.34	2.00	96	3.7
Gammarus oceanicus	2008	7	W	-18.55 ± 0.29	9.48 ± 0.71	1.88	57	5.0
Mysis oculata	2009	5	W	-20.79 ± 0.10	9.02 ± 0.13	1.74	95	3.6
Sagitta sp	2008	2	W	-19.25 ± 0.47	14.1 ± 0.01	3.17	94	3.2
Elasmobranchs								
Somniosus microcephalus	2008	15	M	-17.74 ± 0.67	17.07 ±	4.55	77	3.3
Amblyraja hyperborea	2007	1	M	-18.37	16.79	3.89	100	3.3
Teleosts								
Clupea harengus	2007	1	M	-19.85	13.40	2.89	100	3.4
Salvelinus alpinus	2008	10	M	-18.61 ± 0.23	14.51 ±	3.36	85	3.3
Mallotus villosus	2008	7	M	-19.37 ± 0.15	13.51 ±	3.07	96	3.3
Myoxocephalus scorpius, la	2008	16	W	-20.54 ± 0.44	10.54 ±	2.19	95	3.4
Myoxocephalus scorpius, S	2008	3	M	-17.99 ± 0.58	15.07 ±	3.53	74	3.3
Myoxocephalus scorpius, L	2008	4	M	-16.79 ± 1.07	17.17 ±	4.14	58	3.3
Stichaeus punctatus, la	2009	18	W	-21.09 ± 0.22	10.63 ±	2.22	100	3.4
Mammals								
Phoca groenlandica (Pl)	2008	6	M	-17.95 ± 0.13	14.66 ±	3.40	71	3.3
Pusa hispida (Pl)	2008	4	M	-18.40 ± 0.38	14.92 ±	3.48	82	3.4

la=larval fish;S=small *M. scorpius* (<24cm); L=large *M. scorpius* (>24cm); Tissue analyzed-W: whole, M: muscle, Ma: mantle, F: foot

Table 3.3. Fatty acids (% of total, mean ±SD) of organisms sampled from Cumberland Sound. Fatty acids were used as indicators of reliance on either phytoplankton (^{P}) or macroalgae (^{M}) among consumers. Tissue analyzed is the same as for stable isotopes (see Table 3.2), with the exception that blubber was analyzed for mammal fatty acids.

Species	Date	*n*	% Lipid	16:1n-7^{P}	18:2n-6^{M}	20:4n-6^{M}	22:6n-3^{P}	w3to6^{P}
POM (Stevens et al. 2004)[1]	1999		nr	15.5 ± 4.5	1.7 ± 0.7	0.4 ± 0.3	8.5 ± 3.6	12.5 ± 3.6
Fucus sp.	2008	3	4.3 ± 3	1.9 ± 1	13.7 ± 0.4	9.9 ± 3.6	0.5 ± 0.4	0.5 ± 0.1
Invertebrates								
Chlamys islandica	2008	4	5.3 ± 0.4	3.2 ± 0.3	1.6 ± 1.2	1.5 ± 0.2	28.3 ± 1.4	13.2 ± 3.8
	2009	5	5.1 ± 0.2	2.7 ± 0.4	1.4 ± 0.8	1.4 ± 0.2	26.1 ± 2.5	6 ± 1.3
Hiatella arctica	2008	5	9.4 ± 2	16.1 ± 3.2	1.8 ± 0.3	1.6 ± 0.6	14.7 ± 3.6	6.1 ± 0.4
Buccinum cyaneum	2008	7	6.2 ± 0.8	1.1 ± 0.3	2.9 ± 3.8	4.6 ± 0.9	9.6 ± 1.3	3.3 ± 0.7
Tectura testudinalis	2008	5	9 ± 3.1	4.7 ± 3.8	5 ± 3.3	12.9 ± 4.2	0.9 ± 0.2	1.1 ± 0.4
Nudibranch	2008	1	10.9	1.1	8.6	8.7	18.9	2.5
Polychaete	2008	3	8.4 ± 1.2	4.7 ± 1	2.3 ± 0.3	3.4 ± 0.3	2 ± 0.1	3.3 ± 0.3
Calanus hyperboreus	2008	5	36 ± 3	17.3 ± 0.7	3.5 ± 0.1	0.2 ± 0	8.9 ± 1	3.9 ± 0.2
Gammarus oceanicus	2008	2	10.4 ± 0.3	10.8 ± 0.4	4.6 ± 0.8	1.6 ± 0.2	5.1 ± 0.8	2.2 ± 0
Mysis oculata	2009	5	10.3 ± 0.7	3.8 ± 1.2	1.8 ± 0.1	1.2 ± 0.1	24.1 ± 1.8	7.3 ± 1.1
Fishes								
Somniosus microcephalus	2008	15	54.6 ± 3.3	6.8 ± 0.7	1.1 ± 0.1	1.5 ± 0.2	8.4 ± 0.8	4.5 ± 0.3
Amblyraja hyperborea	2007	1	6.5	4.4	1.3	3.7	25.6	7.1
Salvelinus alpinus	2008	7	22.7 ± 10.6	16.4 ± 6.1	1.5 ± 0.5	0.4 ± 0.1	10.9 ± 2.3	6.9 ± 1
Mallotus villosus	2008	7	17 ± 10.2	7.2 ± 2.9	1.2 ± 0.2	0.4 ± 0.1	24.6 ± 10.4	14.9 ± 4.6
Myoxocephalus scorpius	2009	16	15.1 ± 2.8	7.4 ± 4.5	1.4 ± 0.7	1.0 ± 0.5	24.9 ± 5.8	9.7 ± 4.7
Myoxocephalus scorpius (small)	2008	3	6.4 ± 0.5	7.1 ± 1.6	1.7 ± 0.4	2.3 ± 0.5	24.5 ± 3.4	8.3 ± 1.9
Myoxocephalus scorpius (large)	2008	4	5.4 ± 1.1	4.6 ± 0.6	1.3 ± 0.1	4.4 ± 1.5	25.1 ± 4	6.9 ± 2.9
Stichaeus punctatus (larval)	2009	17	13.9 ± 1.2	3.3 ± 0.6	0.7 ± 0.1	0.5 ± 0.1	34.1 ± 3.7	16.6 ± 3.3
Mammals								
Phoca groenlandica	2008	6	88.6 ± 18.8	18.1 ± 3	1.8 ± 0.3	0.4 ± 0.1	9.3 ± 1.4	5.3 ± 0.3
Pusa hispida	2008	6	89.9 ± 8.1	22 ± 5.1	1.6 ± 0.2	0.5 ± 0.3	9.5 ± 1.8	5.7 ± 1

[1] POM/seston from Stevens et al. 2004: sampled Autumn 1999 from southeast stations of North Water Polyna in surface waters. nr: not reported

Table 3.4. Significant differences in several food web metrics among Cumberland Sound functional groups based on three ANOVAs and one Kruskal-Wallis non-parametric ANOVA.

Metric	Functional Group	Test statistic	DF	*P*
Vertical food web structure				
δ^{15}N	zooplankton = benthos < consumers	*F*=255.01	2,150	<0.001
TP	zooplankton = benthos < consumers	*F*=46.174	2,150	<0.001
Horizontal food web structure				
δ^{13}C	zooplankton < consumers < benthos	*F*=134.57	2,150	<0.001
α	benthos < consumers < zooplankton	χ^2=108.36	2	<0.001

TP: δ^{15}N-derived trophic position; α: δ^{13}C-derived % reliance on pelagic carbon; DF: degrees of freedom

Fig. 3.1. Percent (%) reliance on pelagic carbon (α) and trophic positions of benthos (black), zooplankton (white) and fish and marine mammal consumers (grey) from Cumberland Sound (mean ± SE, see Table 3.1 for number codes). Values of α are the results of a two-source $\delta^{13}C$ mixing model with primary consumers of phytoplankton and macroalgae as baselines. Trophic positions were calculated using a one-source, $\delta^{15}N$-based model.

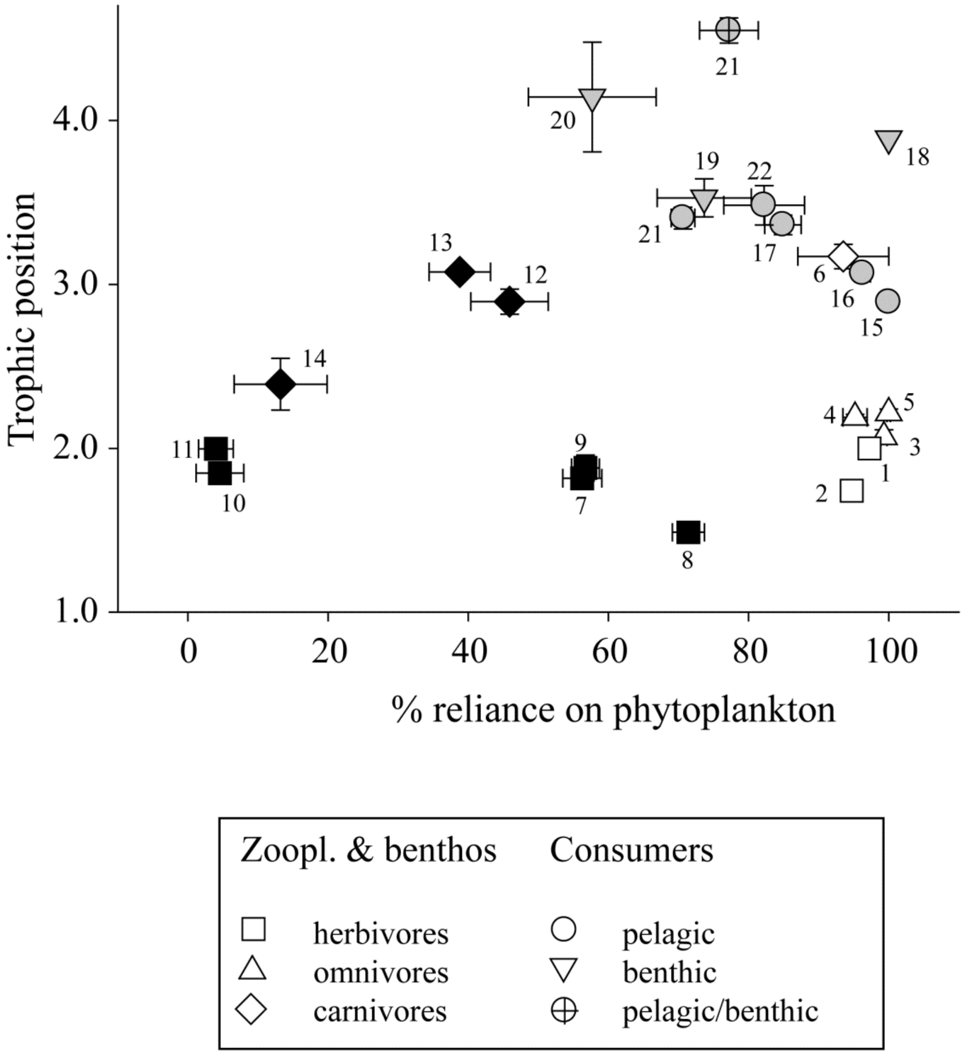
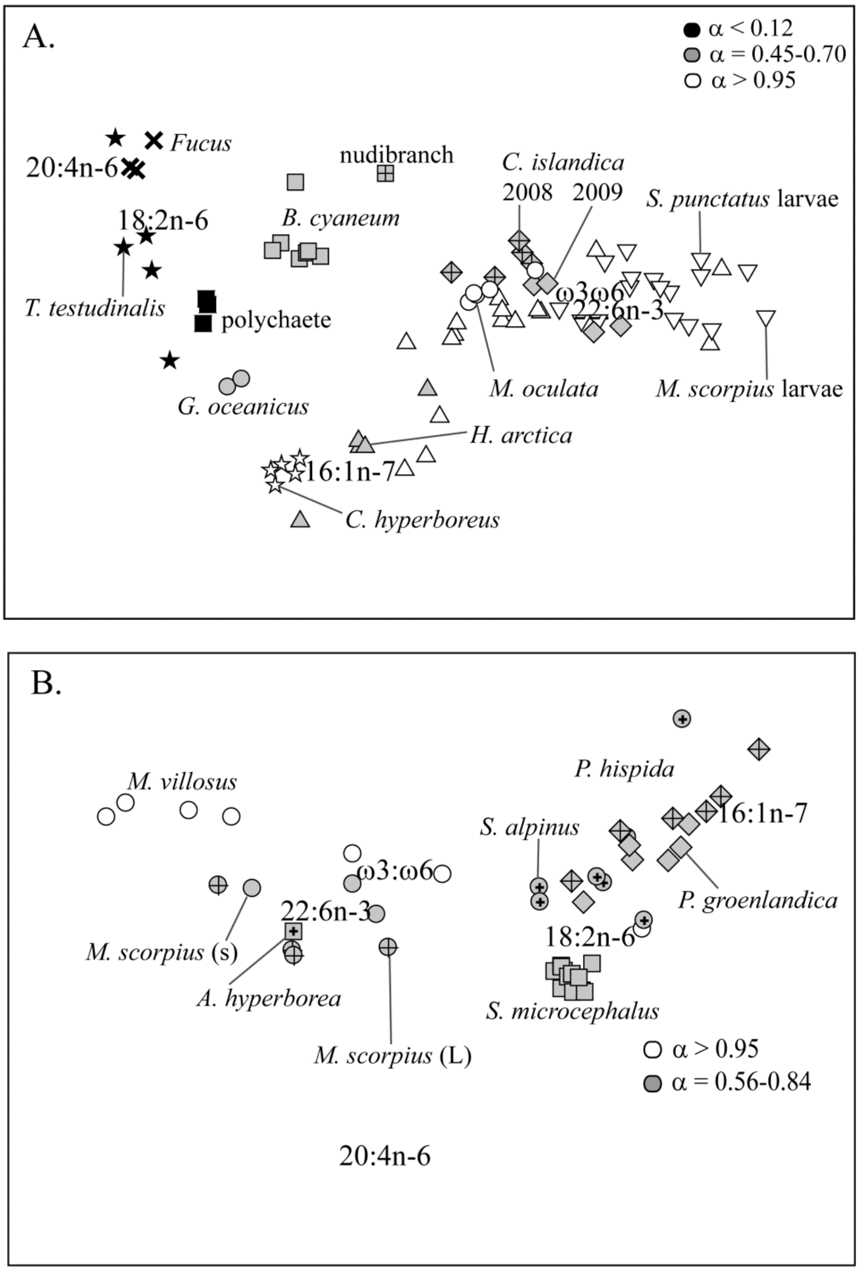
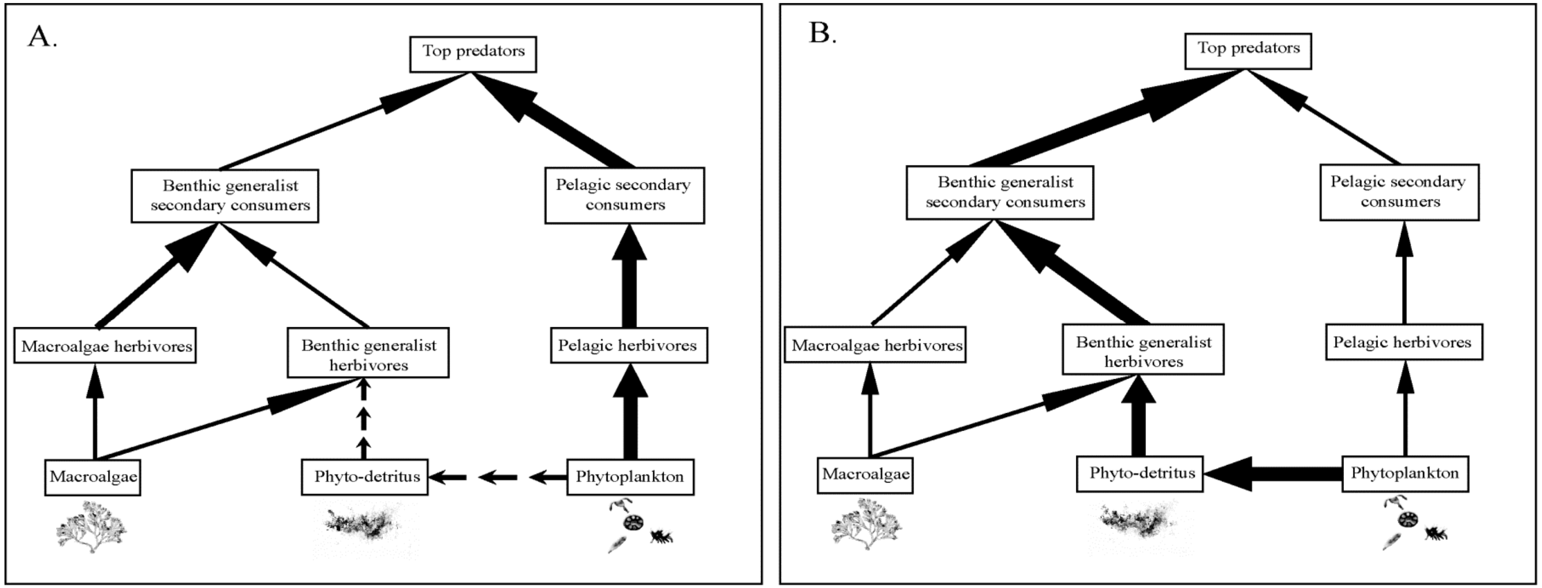


Fig. 3.2. Results of non metric multidimensional scaling performed on: A) *Fucus*, zooplankton and benthos (dimensions = 2, stress = 0.04), and B) fish and marine mammal consumers (dimensions = 2, stress = 0.02) sampled during August in Cumberland Sound. Symbol colours reflect percent reliance on pelagic carbon (α) calculated from δ^{13}C.



'L' and 's': large (>24cm) and small (<24cm), respectively

Fig. 3.3. Hypothetical transfer of energy through fast (phytoplankton) and slow (macroalgae and phytodetritus) channels in an arctic marine food web during the spring/summer bloom (A) and towards the end of the bloom in late summer/fall (B). During the bloom, energy is rapidly and efficiently transferred through the pelagic pathway (some phytoplankton settling to the benthos indicated by dashed arrows, (A). As the bloom progresses, ample phytoplankton is reaching the sea floor, is exploited by the benthos and is eventually transferred through the benthic pathway (B). Macroalgae continues to be transferred from benthos to upper trophic levels during early (A) and late bloom (B) scenarios, although in lower quantities than phytoplankton (A) and phytodetritus (B).



CHAPTER 4

SIMILARITY BETWEEN PREDATOR AND PREY FATTY ACID PROFILES IS TISSUE DEPENDENT IN GREENLAND SHARKS (SOMNIOSUS MICROCEPHALUS): IMPLICATIONS FOR DIET RECONSTRUCTION

McMeans, BC, Arts, MT, Fisk, AT. Similarity between predator and prey fatty acid profiles is tissue dependent in Greenland sharks (*Somniosus microcephalus*): implications for diet reconstruction. Submitted to Journal of Experimental Marine Biology and Ecology

INTRODUCTION

Sharks are important predators in marine and brackish waters, affecting prey populations both directly (i.e. predation) and indirectly (e.g. by generating predator avoidance behaviour) (Ferretti et al. 2010). However, a complete understanding of how sharks affect energy flow through food webs requires a detailed knowledge of their feeding ecology (Myers et al. 2007). Fatty acids (FA), which serve a multitude of biochemical functions in animals (e.g. cell membrane constituents, precursors to eicosanoids, energy source, Tocher 2003), are a promising tool for investigating the diet of marine predators like large sharks (Schaufler et al. 2005) that are difficult to study via traditional stomach content analysis. For example, the 'essential' FAs, arachidonic acid (ARA, 20:4n-6), eicosapentaenoic acid (EPA, 20:5n-3) and docosahexaenoic acid (DHA, 22:6n-3), can often be used as dietary tracers because they cannot be biosynthesized by most marine consumers in amounts sufficient to meet their needs (Parrish 2009). Although some FAs (e.g. 16:0 and 18:0) can be biosynthesized by fishes, while others can be modified via chain shortening (e.g. 20:1n-9 to 18:1n-9) or elongation (e.g. 16:1n7 to 18:1n-7) (Tocher 2003), it is generally accepted that the tissue FA profile of a consumer largely reflects FAs retained from the diet (Iverson 2009).

Fatty acids have only recently been applied to investigate the diet of elasmobranchs (Schaufler et al. 2005; Semeniuk et al. 2007; Pethybridge et al. 2011; Wai et al. 2011). However, the current lack of data regarding how sharks alter dietary FAs prior to tissue incorporation is a major concern with this application. Predators are widely acknowledged to modify dietary FAs to meet their needs, which could lead to divergence between predator and prey profiles (Iverson 2009). Thus, the question becomes, how much, on a tissue-specific basis, will a predator modify dietary FAs and other lipids?

Based on the comprehensive work of Pethybridge et al. (2010), who identified inter-tissue differences in the lipid class and FA profiles of 16 deep water Chondrichthyans from Australian waters, shark liver is high in storage molecules (e.g. triacylglycerol, TAG) and MUFA, whereas muscle is high in phospholipids and polyunsaturated fatty acids (PUFA). Subsequently, Chondrichthyan muscle can be more similar to PUFA-rich prey, and liver to MUFA-rich prey (Pethybridge et al. 2011). Based on results of the above studies, it is clear that elasmobranchs are selectively incorporating dietary FAs into different tissues.

It is still unclear, however, to what extent shark tissue FA profiles differ from FA profiles of dominant prey, or which tissue provides the most accurate information regarding diet. Captive feeding studies will help unravel the origin of FAs in shark tissues, although these studies will most likely be restricted to young and/or small sharks. Because differences in locomotory mode and phylogeny contribute to differences in lipid classes and FA profiles among shark species (Pethybridge et al. 2010), researchers wishing to apply FAs to study the ecology of large sharks in the wild would benefit from a directed assessment of how FAs differ between tissues of a large, mobile shark and those of known prey.

Here, within- and among-tissue variability in FA profiles of muscle, liver and blood plasma of 18 individual Greenland sharks sampled from Cumberland Sound, Nunavut, Canada, was investigated to identify the degree that shark tissue FA profiles differed from those of known prey items (based on stomach contents). The goal was to identify which tissues are the most useful for diet studies, and which tissues are the most altered by these sharks. Because elasmobranch liver functions as the major site of: 1) FA catabolism (i.e. beta oxidation), 2) ketone body biosynthesis, and 3) buoyancy regulation (achieved through retention of lipids) (Ballantyne 1997), liver FAs are predicted to be the most modified by the sharks and to differ the most from prey profiles. Plasma, on the other hand, functions in transporting dietary FAs to other elasmobranch tissues via lipoproteins (e.g. chylomicrons) (Ballantyne 1997), and plasma FA are predicted to be the most similar to prey profiles. Elasmobranch muscle lacks the enzymes necessary to catabolize FA, and typically has low lipid levels (Ballantyne 1997). However, neutral, storage lipids, like TAG, are still present in shark muscle (Sargent et al. 1973), and muscle FAs are therefore predicted to provide some information about shark diet. The data presented here should help future researchers to more accurately apply FA to reconstruct the dietary history of large sharks.

MATERIALS AND METHODS

Sampling of Greenland sharks

Greenland sharks were sampled for the present study from Cumberland Sound, Nunavut, Canada. The Greenland shark is one of only two sharks known to regularly inhabit polar, ice-covered waters that reach temperatures <0ºC (the other being the Pacific sleeper shark, *S. pacificus*, Bigelow and Schroeder 1948). They reach a large size (of at least 6 m, Bigelow and Schroeder 1948), feed on a both teleost and marine mammal prey in Cumberland Sound (Fisk et al. 2002), and move throughout the water column from near the surface to several hundred meters depth in arctic waters (Skomal and Benz 2004). Greenland sharks were sampled via bottom long line (set times=2-24 h) baited with either seal blubber or squid. Greenland sharks were sampled for the present study in April 2008 as part of a larger field campaign, which included subsequent sampling dates in August 2008, April 2009 and August 2009. Trends between Greenland shark and prey fatty acids were similar when considering only the April 2008 data, or the pooled data (i.e. from all sampling dates combined). The data for the latter-sampled three seasons were therefore retained to present elsewhere to explore, in detail, seasonal and inter-annual variability in diet of the Greenland shark (see Chapter 5).Greenland sharks were euthanized upon capture via an incision made through the dorsal surface (immediately behind the head, anterior to the gills) to sever the spinal cord and dorsal aortae, followed directly by a second incision through the brain. Blood was allowed to flow from the dorsal cut for several seconds before being collected into a centrifuge tube, immediately centrifuged in the field, removing the plasma using a sterile pipette, and transferring into a 2 mL cryovial. Five grams of dorsal muscle were collected ~2 cm above the vertebrae. Liver biopsies were taken by removing a cross section of one lobe, at approximately the mid-way point along the lobe's length, dissecting ~5 g from the center. All samples were immediately put on ice, and were frozen at -80°C (via dry ice or liquid nitrogen) within 1 h from the time of collection. Stomach contents were identified to as low a taxonomic level as possible and counted for all 18 Greenland sharks (Table 4.1). Squid and mammal bait identified in shark stomachs was not included in these counts. However, hooked Greenland halibut that were found in the sharks' stomachs were included in counts because Greenland sharks are known to eat hooked halibut off of fishing lines during the winter artisinal fishery in Cumberland Sound (McMeans, Fisk, unpublished data), and because we used shark-specific fishing gear (i.e. metal leads and gangions), these halibut were not associated with our fishing operations. The exploitation of halibut off of Inuit fishermen's lines would affect the FA profile of the sharks and is therefore relevant to the present study.

Prey sampling

Known prey of the Cumberland Sound Greenland sharks sampled here, based on stomach contents (Table 4.1), were sampled for fatty acid analysis and included: arctic skate (*Amblyraja hyperborea*), Greenland halibut (*Reinhardtius hippoglossoides*) and ringed seal (*Pusa hispida*). In addition, several potential prey of Greenland sharks were also sampled for fatty acid analysis, which have been previously identified in the stomachs of Greenland sharks from Cumberland Sound (B.C. McMeans, A.T. Fisk, unpublished data), and included arctic char (*Salvelinus alpinus*), harp seal (*Phoca groenlandica*) and narwhal (*Monodon monoceros*). The data for potential prey were included in the present study to assess how Greenland sharks tissue fatty acids compared to that of known prey (Table 4.1) as well as potential prey that may not have been captured by the sharks' stomachs contents. All prey species were collected from the shark sampling sites (near the mouth of Pangnirtung fjord, see Fig. 2.1 for a map of sampling locations). Char were collected via gill nets, skate and halibut via bottom long line (set times 2-4 h) and marine mammals were harvested by local Inuit hunters. Narwhal were sampled during August 2007, skate and halibut during April 2008 and Arctic char, ringed seal and harp seal during August 2008.

Because fish were found in shark stomachs either whole or as fragments of muscle and bone (Table 4.1), muscle was sampled from the dorsal surface of fish for FA analysis. The FA profile of Greenland halibut muscle reported here (Table 4.2), which was the dominant teleost prey of the Greenland sharks (Table 4.1), is similar to that reported for conspecifics homogenized and analyzed whole (Andersen et al. 2004). For example, Greenland halibut analyzed whole (Andersen et al. 2004) and as muscle only (Table 4.2) had 18:1n9 in high and similar proportions (mean±SD = 15.8±0.2 and 15.5 ± 2.3%, respectively). Thus, muscle likely accounted for most of the elasmobranch and teleost biomass consumed by Greenland sharks, and is a useful proxy for the FA profile of the dominant teleost prey. Because marine mammal tissue was found in Greenland shark stomachs predominantly as pieces of blubber (Table 4.1), and because blubber would contribute the most lipids to Greenland shark consumers (vs. other mammal tissues), the inner half of the dorsal surface blubber layer was sampled from marine mammals for FA analysis. All muscle and blubber samples for FA were placed in cryovials and frozen at -80°C within one hour after sampling.

Fatty acids were analyzed as detailed in Chapter 2 and McMeans et al. (2012).

Data analysis

Data were obtained for 50 individual FAs, but analyses were restricted to 15 FAs that contributed mean values >1% to at least one shark tissue (these 15 FA are listed in Table 4.2). Together, these 15 FAs accounted for 92% of total shark plasma FAs and 95% of total muscle and liver FAs. Coefficients of variation were calculated to compare variability in each FA proportion among Greenland shark tissues. Principal components analysis (PCA) was used to explore relationships between Greenland shark and prey FAs. Separate PCAs were performed on proportional data (Table 4.2) and absolute $\mu g^{\bullet} mg^{-1}$ data (Table 4.3). FAs reported as $\mu g^{\bullet} mg^{-1}$ are highly sensitive to the % lipid of a sample, but are a useful way to ensure that, for example, high proportions of one FA are not driven by low proportions of another FA. PCA was a straightforward way to identify: 1) which FAs explained the largest amount of variance in the data, and 2) which shark tissue was most similar to prey tissues based on underlying similarities in FA profiles. FA data were standardized to a mean of 0 and variance of 1 prior to inclusion in the PCAs and were left untransformed because logit transformation (i.e. $\log[FA_i/(1 - FA_i)]$), which is effective for increasing normality and linearity of proportional data (Warton and Hui 2011), did not alter PCA outputs. FA variable weights were extracted 'unscaled' (i.e. scaling=0) from the first two principal components (PC1 and PC2), and FA 'loadings' (i.e. correlations between each FA variable and each PC axis) were calculated by multiplying the unscaled FA weight by the square root of the eigenvalue for that principal component (McGarigal and Cushman 2000). Variables with loadings >0.63 were considered highly influential to that component (McGarigal and Cushman 2000). All analyses were performed in R (R Development Core Team 2010) and package 'vegan' (Oksanen et al. 2010) was used for the PCA.

RESULTS

Greenland halibut and ringed seal (adults and pups) were the most commonly identified prey in the Greenland sharks' stomachs (% occurrence=72.2 and 33.3%, respectively, Table 4.1). Greenland halibut muscle and ringed seal blubber (Table 4.1), had different FA profiles, with the former being dominated by proportions of 18:1n-9, 20:1n-9, and 22:1n-11, and the latter having 16:1n-7, 18:1n-9 and DHA in the highest proportions (Table 4.2). FAs reported on a $\mu g^{\bullet} mg^{-1}$ basis supported this pattern (Table 4.3). Greenland shark plasma, liver and muscle had 18:1n-9 and 20:1n-9 in the highest proportions (Table 4.2). Plasma also had high proportions of DHA (10.6 ± 2.1%) and EPA (9.1 ± 1.8%) and muscle had high proportions of 16:0 (10.1 ± 0.8%) and DHA (8.8

± 1.3%). Liver, on the other hand, had 22:1n-11 and 18:1n-7 in the next highest amounts, and combined with 18:1n-9 and 20:1n-9, these four MUFA contributed to 67.0% of total liver FAs (Table 4.2). Blood plasma and liver were more variable than shark muscle based on their higher CV for FA proportions (Table S4.1).

The PCA of shark and prey proportions (Fig. 4.1A) revealed that the greatest amount of variance in the data was explained by the difference between Greenland shark liver and marine mammal blubber, based on the observation that PC1 separated shark liver from mammal blubber due to higher proportions (positive loadings) of 20:1n-9, 22:1n-11, 22:1n-9, and 24:1n-9 in the former and higher proportions (negative loadings) of 18:2n-6, EPA and 22:5n-3 in the latter (Fig. 4.1A). PC2 revealed a separation between skate (positive scores) and narwhal (negative scores) (Fig. 4.1A). All three Greenland shark tissues overlapped to some extent with at least one prey species, but shark muscle, liver and plasma all overlapped with Greenland halibut on PC1 (Fig. 4.1A). Shark muscle and plasma separated closer to marine mammal on the PCA than liver, and based on their overlap on PC1, shark muscle was more similar to plasma than liver (Fig. 4.1A).

Absolute μg•mg^{-1} data supported results from the FA proportions because shark muscle was more similar to the dominant prey, halibut and ringed seal, whereas shark liver was the most distant from the prey samples on the μg•mg^{-1} PCA (Fig. 4.1B). Thus, Greenland shark muscle was more similar to prey FA in both relative proportions (Fig. 4.1A) and absolute μg•mg^{-1}values (Fig. 4.1B) than shark liver. Plasma had much lower FAs on a μg•mg^{-1} basis relative to shark muscle and liver, and therefore separated from the other shark tissues on the μg•mg^{-1} PCA.

Qualitative comparisons of FA proportions were made among individual Greenland sharks and individuals of dominant prey (halibut and ringed seal) (Fig. 4.2). Based on this comparison, FAs can be grouped into one of three categories as follows: 1) FAs that were generally similar (i.e. within a few %) in all three shark tissues to Greenland halibut and ringed seal (i.e. 18:0, 18:1n-7, 18:2n-6, 22:5n-3, Fig. 4.2A), 2) FAs that were higher in shark liver than prey values (i.e. 20:1n-9, 22:1n-11, 22:1n-9, 24:1n-9, Fig. 4.2B), and 3) FAs that were higher in plasma and/or muscle than prey tissues (i.e. 18:1n-9, ARA, EPA, DHA, Fig. 4.2C). Specifically, for the latter group, shark muscle (and liver) were higher in proportions of 18:1n-9, shark muscle and plasma were higher in ARA, and shark plasma was higher in EPA and DHA relative to dominant prey species (Fig. 4.2C, Table 4.2). Absolute µg•mg^{-1} data for shark muscle and liver (but not plasma due to low FA µg•mg^{-1}) generally supported the above categorizations. For example, from group 1, mean 18:1n-7 was between 36 and 39 µg·mg^{-1} in shark muscle and liver (Table 4.3). However, ringed seal had higher µg•mg^{-1} values of 22:5n-3 (43.9±17.0 µg·mg^{-1}) than shark tissues, but proportionally, all three shark tissues fell within the extreme values of 22:5n-3 exhibited by Greenland halibut and ringed seal (Table 4.2, Fig. 4.2A). From group 2, all prey had mean 22:1n-11 less than 60 µg·mg^{-1}, but shark liver had a mean value of 115 µg·mg^{-1} (Table 4.3). From group 3, ARA was higher in shark muscle (8 µg·mg^{-1}) than in any of the prey (all means ≤4.1 µg·mg^{-1}) (Table 4.3), which supports the proportional data (Table 4.2).

DISCUSSION

The Greenland sharks sampled here consumed predominantly Greenland halibut and ringed seal based on stomach contents, which agrees with previously reported contaminant and stomach content data from Cumberland Sound Greenland sharks (Fisk et al. 2002). However, based on shark tissues-halibut overlap on PC1 of the proportions PCA, muscle, liver and plasma FA of Greenland sharks indicated a greater reliance on Greenland halibut. Agreement between stomach contents and FA indicates that all three tissues will therefore provide some information about diet for future explorations focused on the feeding ecology of these sharks. Because elasmobranch liver turns over more quickly than muscle (MacNeil et al. 2006), and plasma is known to be a short-term dietary indicator (Käkelä et al. 2009), differences in the relative magnitude of FAs between slow and fast turnover tissues could be used to identify differences in feeding behaviour over time. However, in agreement with previous findings from 16 species of Chondrichthyan (Pethybridge et al. 2010), inter-tissue differences were apparent, and Greenland sharks had higher PUFA in their muscle (∑PUFA=21.8% versus liver=14.6%) and higher MUFA in their liver (∑MUFA=78.8% versus muscle=65.4%). This pattern hints at underlying, baseline differences between the tissues that are likely related to different tissue requirements and roles in FA metabolism (Ballantyne 1997; Tocher 2003), and stresses the need to consider tissue differences when interpreting FAs as indicators of shark diet.

Greenland sharks appeared to retain 18:0, 18:1n-7, 18:2n-6, and 22:5n-3 in their tissues in generally similar proportions that existed in their diet. Proportions of 18:0 and 18:1n-7 were similar between Greenland halibut and ringed seal and all three shark tissues, whereas proportions of 18:2n-6 and 22:5n-3 in shark tissues generally fell in between the values exhibited by dominant prey (Fig. 4.2A). Thus, the tissues of shark consumers should reflect a mixture of prey sources in these FA. Muscle and liver of European sea bass (*Dicentrarchus labrax*) were also similar to dietary proportions of 18:0, 18:1n-7, 18:2n-6 and 22:5n-3 regardless of whether fish were fed a diet of 100% fish oil, or a mixed diet (40% fish and 10% rapeseed oil, Mourente and Bell 2006). It is noteworthy that several individual Greenland sharks had high proportions of plasma 22:5n-3 that matched those observed in ringed seal (Fig. 4.2A), which could reflect recent seal consumption.

Lower 16:1n-7 proportions (Table 4.2) and $\mu g \cdot mg^{-1}$ values (Table 4.3) in shark tissues vs. prey indicates that this FA was selectively catabolized or was continually elongated to 18:1n-7 (Tocher 2003). Higher C_{20}-C_{22} MUFA in shark liver vs. prey, on the other hand, indicates either selective retention of these FA from the diet, or accumulation as the products from chain shortening (partial beta oxidation, e.g. 22:1n-9 to 20:1n-9). Differences between shark liver and prey FA profiles, and high variability in liver FA among individual Greenland sharks, supports the prediction that liver would exhibit a high degree of FA modification, likely to meet requirements associated with metabolism and buoyancy (Ballantyne 1997).

Greenland shark muscle was the most similar of the tissues sampled to both halibut and ringed seal FA profiles, suggesting that dietary FAs are incorporated into the shark's muscle with little modification, and that Greenland shark muscle provides an accurate view of diet. Lower CV of muscle FAs indicates that muscle FA proportions were likely regulated to meet tissue-specific requirements to a greater degree than liver or plasma (Parrish 2009). Atlantic salmon muscle proportions of EPA and DHA did not reflect differences obtained in their experimental diet, suggesting that these FA could be maintained at species-specific levels (Budge et al. 2011). However, calculated CVs were often similar among muscle, liver and plasma (e.g. 20:1n-9 CV: plasma=0.21, liver=0.18, muscle=0.16, Table S4.1), indicating that variability was present in muscle FAs among individual Greenland sharks that could have arisen from dietary differences.

Because polar lipids respond less to changes in diet than neutral lipids (Regost et al. 2003), one might expect shark muscle to be less responsive to diet than tissues like liver that are dominated by neutral storage molecules. The similarity between Greenland shark muscle and prey FA profiles is therefore somewhat surprising considering that shark muscle lacks the enzymes necessary to catabolize FAs (Zammit and Newsholme 1979), and typically has low % lipid and high contribution of phospholipids (Pethybridge et al. 2010). However, shark species differ in muscle total lipid (Davidson et al. 2011) and % contribution of neutral lipids (Sargent et al. 1973), suggesting that the ability to store FAs in muscle, and subsequently the responsiveness of shark muscle FA composition to diet, may also differ among shark species. Interestingly, Greenland shark muscle has higher % lipid (19±4%, ww, converted from dw values provided on Table 4.2 using % water content of individual samples, B.C. McMeans unpubl. data) than other shark species analyzed to date (e.g. range among species reported in Pethybridge et al. 2010: 0.37-1.87% ww). Squalids, including *S. acanthias* and the Pacific sleeper shark, also appear to have a higher contribution of storage molecules in their muscle than other sharks (e.g. *S. acanthias* muscle TAG+DAG=84.2%, Malins et al. 1965; Pacific sleeper shark muscle=73% TAG, Schaufler et al. 2005). Therefore, the muscle of sharks with lower % lipid may not align so closely with prey FA profiles as observed here in

Greenland sharks. Clearly, further work is required to determine the role of muscle lipids in some sharks, which could function as additional energy stores, or in buoyancy regulation (Malins and Barone 1970).

Because sharks likely do not mobilize large quantities of FAs from the liver to other tissues for energy (most extra-hepatic tissues rely on ketone bodies, Speers-Roesch and Treberg 2010), Greenland shark plasma FAs were expected to closely reflect dietary FAs. In support of this prediction, plasma FA proportions were similar to the Greenland halibut and ringed seal for most FAs (Fig 4.2). The similarity between shark plasma and muscle proportions supports the contention that muscle FA were of dietary origin. However, in addition to neutral FAs like TAG, the total lipid fraction of shark plasma also contains polar lipids (Craik 1978) that could feasibly be of both dietary and non dietary origin (e.g. inter-tissue routing of membrane lipids). The presence of non dietary lipids could explain the higher ARA, EPA and DHA proportions observed in Greenland shark plasma vs. dominant prey. Closer agreement between prey and plasma FA would be expected if the isolated chylomicron fraction were analyzed (e.g. Cooper et al. 2006) instead of total plasma lipids. However, even plasma FAs extracted from the total lipid fraction generally reflect dietary differences (Käkelä et al. 2009). The high variability in plasma FAs among Greenland sharks (i.e. high CV) suggests that shark plasma FA likely reflect a combination of differences in diet, inter-tissue routing of membrane FA and the duration since the last meal.

Our results for Greenland shark muscle, liver and plasma support findings from previous research in teleosts (Mourente and Bell 2006) and seabirds (Käkelä et al. 2009) that the relationship between consumer and dietary FAs is not always 1:1, and that fatty acid differences among-species can be greater than variability within-species (Budge et al. 2002). However, qualitative differences in diet could still be explored by comparing FA profiles between- or within-shark species, because sharks that consume a greater quantity of a certain FA should still have higher proportions of that FA versus sharks that consume less. For example, C_{20} and C_{22} MUFA are biosynthesized by *Calanus* copepods and should differ among sharks that obtain different amounts of these FA in their diet. In fact, Greenland sharks from Cumberland Sound had 18% and 25% 20:1n-9 in their muscle and liver, respectively (Table 4.2), but Pacific sleeper shark muscle and liver from the Gulf of Alaska, as well as blubber from the Pacific sleeper sharks' stomachs, had <6% (Schaufler et al. 2005). Cumberland Sound halibut had high 20:1n-9 proportions (17.7±1.1%) and are a likely source of observed 20:1n-9 proportions in Greenland shark tissues. It therefore appears that C_{20} and C_{22} MUFA are useful dietary indicators in sharks, as long as similar proportions are not expected between shark liver and prey.

Results from the present field study provide new information about the degree that tissue FA profiles of a large shark differ from those of dominant prey. Further work is required to establish if the observed similarities and differences in shark-prey FA proportions (i.e. Fig. 4.2) are applicable to other elasmobranchs. Due to the multitude of habitats and temperatures that elasmobranchs occupy, and their wide range of locomotory modes and diets, differences among species are likely. Greenland sharks (and Pacific sleeper sharks) are clearly unique in their habitat (i.e. ice-covered seas), and their higher % lipid (Table 4.2) and contribution of MUFA to their muscle (Table S4.2). At ~40%, the deep-water *Centroscymnus coelolepis* and the coastal *Carcharhinus obscurus*, which are both highly mobile species (Compagno 1984a, b), come the closest to the muscle

∑MUFA of the Greenland shark (Table S4.2), but further work is required to determine the ubiquity of shark muscle as a dietary indicator. The liver of Greenland sharks, on the other hand, has a more comparable FA composition to other shark species, but is most similar to that of mobile, deep water species like *Dalatias licha* (Table S4.3). Thus, results for specific shark-prey FA differences identified here may be most directly applicable to large, mobile squaliforms. Based on inspection of Tables S4.2 and S4.3, it is clear that future work should address what factors govern differences in FA profiles among shark species.

Several general conclusions can be drawn from the present analysis that should be applicable to other sharks. First, researchers should not expect that shark FA profiles will *exactly* match that of dominant prey items, which is somewhat obvious and expected, but has implications for inferring diet based on shark-prey overlap on multivariate ordinations. Second, liver FA should be interpreted with care, due to potentially high modification of dietary FA profiles by shark consumers. Third, muscle fatty acid profiles of Greenland sharks were the most similar to that of known prey, but future studies are tasked with determining the ubiquity of this trend in other shark species. Finally, plasma FA are likely sensitive to the presence of some non-dietary lipid (if the total lipid fraction is analyzed), digestion and the timing since the last meal, but still appear useful for inferring shark diet. The sampling of muscle and plasma could be useful for future studies focused on large sharks that may be endangered or protected. Additional insights into the retention/ metabolism of dietary FAs could be gained from other FAs like polymethylene-interrupted FA and through controlled feeding studies performed on a variety of elasmobranch species.

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Table 4.1. Stomach contents from 18 Greenland sharks (*Somniosus microcephalus*) sampled in Cumberland Sound, Nunavut, Canada.

Sampling Date	% occurrence[a]	Tissue found
Invertebrates		
Buccinum cyaneum	22.2	Whole or operculum
Strongylocentrotus droebachiensis	11.1	Whole
Squid spp.	11.1	Beaks
Gorgonocephalus arcticus	5.6	Whole
Scavanging amphipods[b]	33.3	Whole
Elasmobranchii		
Amblyraja hyperborea	11.1	Sections of wing
Teleostei		
Reinhardtius hippoglossoides[b]	72.2	Whole or pieces of skin and muscle[3]
Myoxocephalus scorpius	27.8	Whole
Lycodes reticulatus	11.1	Whole
Lumpfish	5.6	Pieces of skin and muscle
Mammalia		
Pusa hispida	16.7	Pieces (blubber/ muscle) or intact body sections
Pusa hispida pup	16.7	Whole
Other		
skate egg	5.6	Whole
unidentified teleost	38.9	Pieces of muscle
Total fish[c]	77.8	
Total mammal	33.3	

a. % occurrence = # of stomachs containing that prey · total # of stomachs $^{-1}$ *100; b.including *Orchomenella* spp., *Onisimus* spp., *Menigrates* spp.; c. Total fish and mammal=# of stomachs containing any fish or mammal species, respectively, divided by total # stomachs

Table 4.2. Fatty acid proportions (% of total, mean±SD) from the total lipid extract of *Somniosus microcephalus* and representative prey from Cumberland Sound.

Species	Tissue[a]	*n*	16:0	16:1n-7	18:0	18:1n-9	18:1n-7	18:2n-6	20:1n-9	18:3n-3	22:1n-11
S. microcephalus	BP	12	8.8 ± 1.4	4.3 ± 1	2.4 ± 2.2	15.3 ± 2.1	4.5 ± 1.4	1.1 ± 0.3	16.4 ± 3.4	0.5 ± 0.7	9.9 ± 3.1
	L	18	4.2 ± 0.8	4.0 ± 1.6	1.3 ± 0.3	18.3 ± 2.2	6.1 ± 1.2	0.7 ± 0.2	24.7 ± 4.3	1.6 ± 1.2	17.9 ± 4.6
	M	18	10.1 ± 0.8	6.7 ± 1.3	1.3 ± 0.3	19.8 ± 2.1	7.1 ± 1	1.1 ± 0.1	17.9 ± 2.9	1.5 ± 0.6	9.5 ± 2.1
A. hyperborea	M	5	18.1 ± 0.7	3.0 ± 0.3	4.4 ± 0.5	8.1 ± 0.4	6.3 ± 0.4	1.5 ± 0.1	4.4 ± 0.9	0.3 ± 0	0.8 ± 0.5
S. alpinus	M	7	12.3 ± 1.9	16.4 ± 6.1	2.1 ± 0.3	11 ± 1.7	3.4 ± 1	1.5 ± 0.5	10.6 ± 6.7	0.5 ± 0.6	10.5 ± 5.1
R. hippoglossoides	M	9	10.0 ± 0.4	10.5 ± 0.6	2.0 ± 0.2	15.5 ± 2.3	6.6 ± 1.1	0.9 ± 0.1	17.7 ± 1.1	0.9 ± 0.8	16.2 ± 2.3
P. hispida	B	8	5.5 ± 0.9	21.3 ± 4.5	0.7 ± 0.3	18.5 ± 4	7.2 ± 1.2	1.7 ± 0.2	7.8 ± 3	0.4 ± 0.1	2.3 ± 2.8
P. groenlandica	B	15	5.4 ± 2.1	16.8 ± 2.8	0.9 ± 0.3	16.5 ± 4.1	6 ± 1.1	1.9 ± 0.3	12 ± 2.6	0.6 ± 0.2	5.5 ± 4.6
M. monoceros	B	7	6.4 ± 0.8	24.9 ± 2.4	1.1 ± 0.3	22 ± 1.8	6 ± 0.4	1.1 ± 0.1	9.9 ± 1.1	0.4 ± 0	4.2 ± 1.1

Species	22:1n-9	20:4n-6	20:5n-3	24:1n-9	22:5n-3	22:6n-3	∑SAFA	∑MUFA	∑PUFA	%lipid[b]
S. microcephalus	2.9 ± 0.6	2.4 ± 0.7	9.1 ± 1.8	1.5 ± 0.3	2.7 ± 1.7	10.6 ± 2.1	12.9 ± 4.3	58.9 ± 5.8	28.2 ± 3.7	14.4 ± 4.8
	3.9 ± 0.6	0.8 ± 0.3	3.1 ± 1	1.9 ± 0.5	1.5 ± 0.7	5.1 ± 1.9	6.5 ± 1.3	78.8 ± 4.2	14.6 ± 3.5	78.8 ± 11.2
	2.0 ± 0.2	1.6 ± 0.3	5.6 ± 0.9	0.8 ± 0.1	1.7 ± 0.4	8.8 ± 1.3	12.7 ± 0.8	65.4 ± 2.2	21.8 ± 2.2	56.8 ± 5.9
A. hyperborea	0.5 ± 0.1	3.3 ± 0.3	10.3 ± 1.3	0.3 ± 0.0	2.2 ± 0.2	30.5 ± 1.2	24.6 ± 0.9	25.3 ± 2.1	50.1 ± 1.9	6.6 ± 1.1
S. alpinus	1.8 ± 0.7	0.4 ± 0.1	7.3 ± 2.5	0.6 ± 0.2	1.3 ± 0.3	10.9 ± 2.3	19 ± 1.5	56.7 ± 6.2	24.3 ± 5.2	22.7 ± 10.6
R. hippoglossoides	2.3 ± 0.2	0.4 ± 0.1	3.7 ± 0.7	0.7 ± 0.1	0.6 ± 0.1	4.8 ± 1.5	15.9 ± 0.6	70.9 ± 3	13.3 ± 2.5	39.9 ± 10.2
P. hispida	0.5 ± 0.4	0.5 ± 0.2	8.5 ± 2	0.1 ± 0.1	5.4 ± 1.3	9.5 ± 1.5	10.6 ± 1.9	61 ± 3.6	28.3 ± 3.2	85.5 ± 11.7
P. groenlandica	0.9 ± 0.5	0.3 ± 0.1	7.8 ± 1.9	0.2 ± 0.1	4.4 ± 1.2	9.6 ± 2.3	10.6 ± 3.3	62 ± 4.8	27.4 ± 4.6	73.9 ± 19.6
M. monoceros	1 ± 0.2	0.3 ± 0	2.7 ± 0.7	0.1 ± 0.1	1.2 ± 0.3	2.5 ± 0.6	16.4 ± 1.4	73.9 ± 2.3	9.7 ± 1.7	70.1 ± 21

a. BP=blood plasma, M=muscle, L=liver, B=blubber; b. Percent (%) lipid= mass of lipid • dry weight of sample^{-1}; Full species names: *Somniosus microcephalus, Ambylraja hyperborea, Salvelinus alpinus, Reinhardtius hippoglossoides, Pusa hispida, Phoca groenlandica, Monodon monoceros*

Table 4.3. Absolute fatty acid values (µg·mg^{-1} dry tissue, mean±SD) of *Somniosus microcephalus* and representative prey.

Species	Tissue[a]	16:0	16:1n-7	18:0	18:1n-9	18:1n-7	18:2n-6	20:1n-9	18:3n-3	22:1n-11
S. microcephalus	BP	4.3±2.2	2.1±1.4	1.1±0.8	7.6±4.4	2.4±1.9	0.5±0.3	8±4.8	0.4±0.7	4.9±3.4
	L	26.8±6.9	25.4±12.6	8.3±1.7	116.1±23.5	38.4±9.2	4.7±1.5	148±65.8	10.7±8.2	114.8±36.5
	M	50.9±6.9	34.5±10.8	6.7±1.8	100.2±17.8	35.9±7.3	5.7±1.1	89.6±16.7	7.2±3.1	47.9±12
A. hyperborea	M	5.4±1.1	0.9±0.3	1.3±0.4	2.4±0.6	1.9±0.5	0.5±0.1	1.4±0.6	0.1±0	0.3±0.2
S. alpinus	M	22±9	29.1±12.9	3.7±1.5	21.3±11.5	7.1±5.6	2.9±1.5	22±22.4	1.1±1.3	23.4±22.3
R. hippoglossoides	M	36.7±9.3	39.6±12.6	7.2±1.7	58.7±22.3	24.9±9.5	3.4±1.1	65.9±19.2	3±2.8	59.9±18.5
P. hispida	B	43.3±9.8	173.4±61.1	5±1.8	150.1±53.7	58.3±20	13.1±2.9	59.9±22.4	3.1±1.1	15.9±18
P. groenlandica	B	32.7±15.1	103±35.5	4.9±1.7	102.5±45.6	37.2±14.4	11.6±3.1	73.6±27.3	3.3±1.8	33.5±26.2
M. monoceros	B	34.2±12.9	133.4±44.6	5.8±1.9	116.7±36.4	32.5±11.9	5.8±2	52.3±18.9	2.1±0.8	22.4±11.2

Species	22:1n-9	20:4n-6	20:5n-3	24:1n-9	22:5n-3	22:6n-3	∑SAFA	∑MUFA	∑PUFA
S. microcephalus	1.4±0.7	1.2±0.9	4.4±2.6	0.7±0.3	1.1±0.5	5±2.6	6.1±3.2	28.7±15.9	13.5±7.5
	24.8±6	4.9±1.6	20.1±8.7	12.2±3.4	9.7±5.1	33.1±14.2	41.1±9.9	504.1±94.4	94.5±31.9
	10.0±1.8	8.0±1.8	28.6±7.2	3.9±0.8	8.6±3.2	44.3±10.2	64.2±9.5	331±51.7	110.6±22.1
A. hyperborea	0.2±0.1	1.0±0.1	3.1±0.6	0.1±0	0.7±0.1	9.2±1.9	7.4±1.6	7.7±2.2	15±2.8
S. alpinus	3.6±2.4	0.6±0.1	12.4±3.8	1.3±0.8	2.3±0.9	18.8±5.6	35.4±17.3	112.6±73.3	42.3±14.1
R. hippoglossoides	8.3±2	1.3±0.3	13.3±2.6	2.6±0.7	2±0.6	16.5±2.4	58.7±15.5	265±81.6	47.1±7.6
P. hispida	3.7±2.8	4.1±2.7	69.2±26	0.5±0.5	43.9±17	75±17.9	83.2±15.7	487.8±119.2	227.8±62.6
P. groenlandica	5.5±3.6	1.9±0.7	48.1±18.1	1±0.8	27±11.6	59.6±23.3	64.4±25.5	381.5±119.9	168.3±57.5
M. monoceros	5.4±2	1.5±0.6	15±8	0.4±0.5	6.7±3.4	14±7.5	88.3±30.3	393.6±127.2	53.4±25.2

a. BP=blood plasma, M=muscle, L=liver, B=blubber; Full species names: *Somniosus microcephalus, Ambylraja hyperborea, Salvelinus alpinus, Reinhardtius hippoglossoides, Pusa hispida, Phoca groenlandica, Monodon monoceros*

Fig. 4.1. Principal component analysis of fatty acid proportions (A: % of total) and µg fatty acid • mg dry tissue^{-1} values (B) of Greenland sharks (*Somniosus microcephalus*) (muscle, liver and plasma) and several known teleost and marine mammal prey. Fatty acids that were highly correlated (>0.63) with each principal component axis are provided.

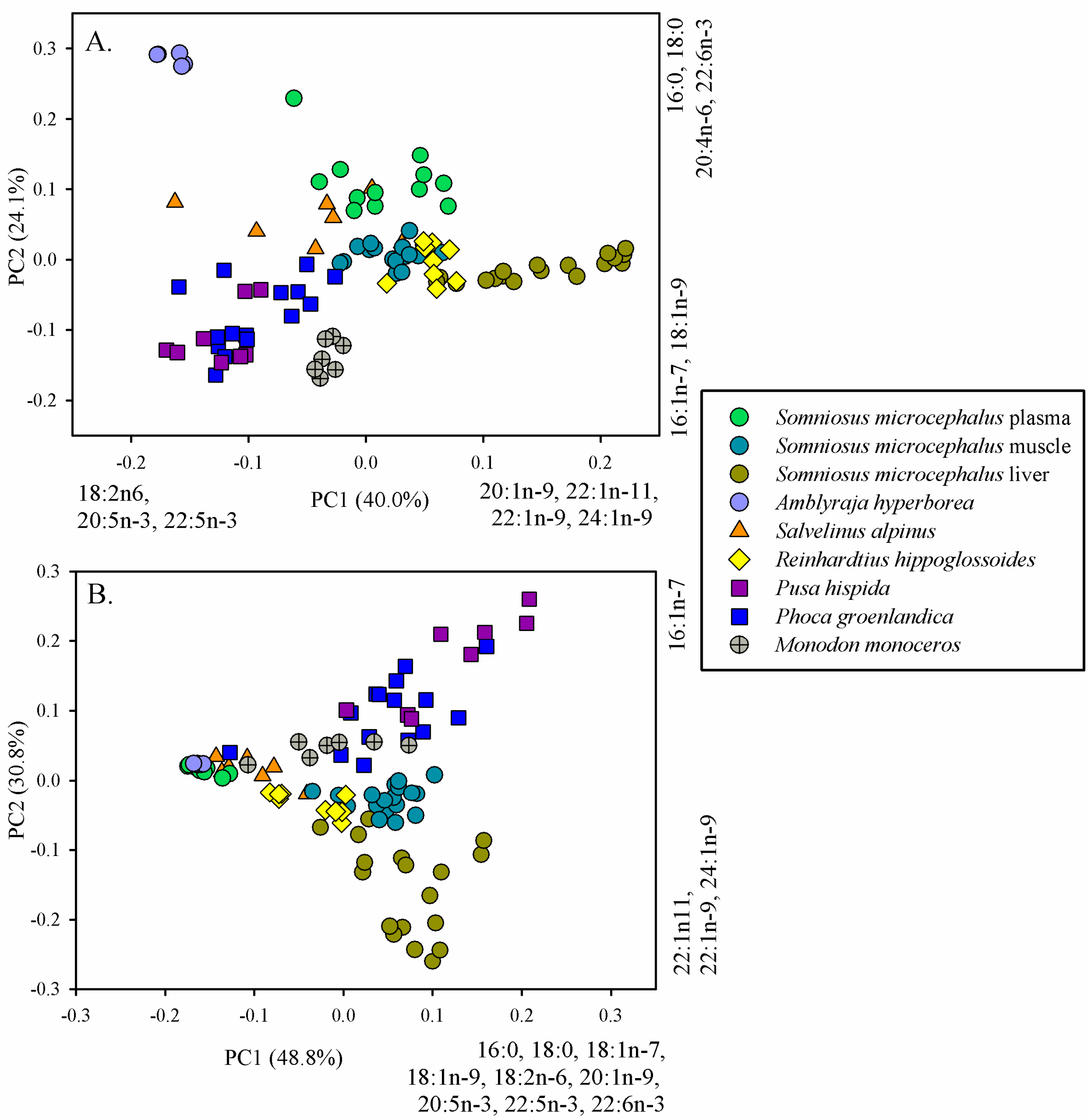
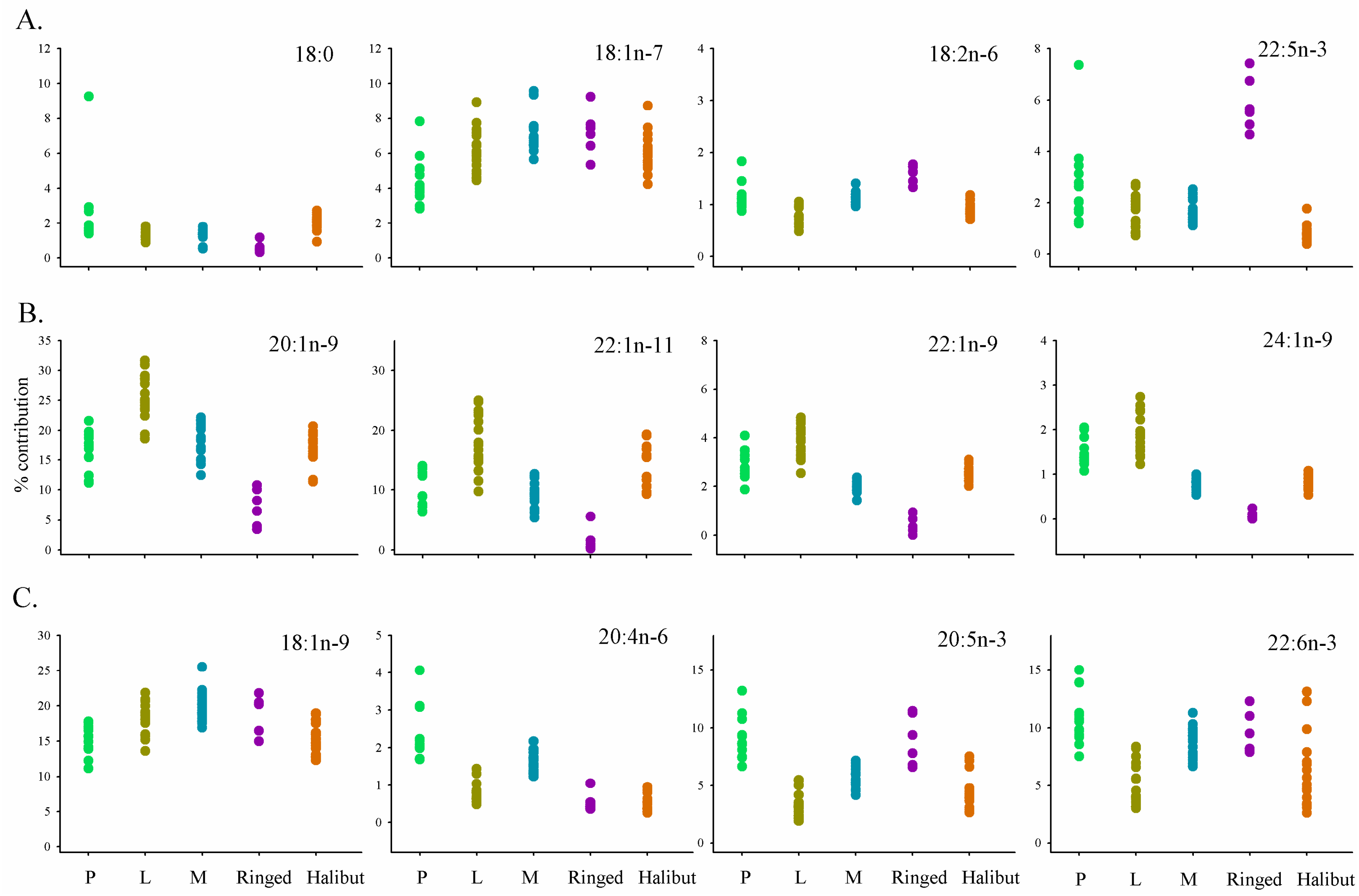


Fig. 4.2. Fatty acid proportions (% of total) of individual Greenland shark plasma (P), liver (L), and muscle (M) and values for the sharks' dominant prey, Greenland halibut (muscle) and ringed seal (blubber). Fatty acids are separated by shark-prey: A) similarity, B) higher values in shark liver, and C) higher values in shark plasma and/or muscle. Note the different scales of the y axes.



SUPPLEMENTARY MATERIAL

Table S4.1. Coefficients of variation for *Somniosus microcephalus* tissue fatty acid proportions.

Fatty acid	Plasma	Liver	Muscle
n	12	18	18
16:0	0.16	0.20	0.08
16:1n-7	0.24	0.39	0.20
18:0	0.90	0.21	0.23
18:1n-9	0.14	0.12	0.11
18:1n-7	0.30	0.20	0.14
18:2n-6	0.23	0.25	0.10
20:1n-9	0.21	0.18	0.16
18:3n-3	1.43	0.75	0.42
22:1n-11	0.31	0.26	0.22
22:1n-9	0.21	0.17	0.11
20:4n-6	0.30	0.32	0.17
20:5n-3	0.20	0.32	0.15
24:1n-9	0.21	0.24	0.16
22:5n-3	0.61	0.45	0.25
22:6n-3	0.20	0.36	0.15
∑SAFA	0.33	0.20	0.06
∑MUFA	0.10	0.05	0.03
∑PUFA	0.13	0.24	0.10
%lipid	0.33	0.14	0.10

Table S4.2. Muscle ∑saturated fatty acids (SAFA), ∑monounsaturated fatty acids (MUFA), and ∑polyunsaturated fatty acids (PUFA) (proportions, mean values) for various shark species sampled from northern, tropical and subtropical waters.

Order Family	Species	SAFA	MUFA	PUFA	Sampling location	Reference	Dominant habitat
Squaliformes							
Centrophoridae	*Centrophorus squamosus*	20.3	25.5	54.3	North Atlantic	Økland et al. 2005	rare above 1000m[a]
	Centrophorus zeehaani	31.3	21.9	42.3	Australia	Pethybridge et al. 2010	upper slope, 200-650m[c]
	Deania calcea	23.9	21.7	48.1	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[c]
Dalattidae	*Dalatias licha*	26.2	30.5	38.0	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[c]
Etmopteridae	*Centroscyllium fabricii*	17.9	26.0	56.1	North Atlantic	Økland et al. 2005	200-500m[a]
	Etmopterus baxteri	20.2	30.6	39.7	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[c]
Somniosidae	*C entroselachus crepidater*	24.8	25.0	45.5	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[c]
	Centroscymnus coelolepis	15.3	36.7	48.0	North Atlantic	Økland et al. 2005	bathypelagic usually> 400m[a]
	Centroscymnus owstoni	24.7	21.9	44.7	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[c]
	Proscymnodon plunketi	26.5	21.7	46.0	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[c]
	Somniosus microcephalus	13.0	64.3	22.7	Nunavut	this study	benthopelagic, 0-1200m[a]
	Somniosus pacificus	17.4	59.5	23.1	Gulf of Alaska	Schaufler et al. 2005	benthopelagic, 0-2000m[a]
Sqalidae	*Squalus acanthias*	18.4	34.5	34.0	Australia	Pethybridge et al. 2010	shelf, 0-200m[c]
	Squalus megalops	27.7	23.4	44.0	Australia	Pethybridge et al. 2010	shelf, 0-200m[c]
Carcharhiniformes							
Carcharhinidae	*Carcharhinus brevipinna*	29.0	35.0	23.0	South Africa	Davidson et al. 2011	coastal, shelf[b]
	Carcharhinus leucas	31.0	29.0	35.0	South Africa	Davidson et al. 2011	coastal, estuarine[b]
	Carcharhinus limbatus	32.0	26.0	40.0	South Africa	Davidson et al. 2011	coastal[b]
	Carcharhinus obscurus	30.0	40.0	21.0	South Africa	Davidson et al. 2011	coastal, shelf[b]
	Galeocerdo cuvier	30.0	30.0	33.0	South Africa	Davidson et al. 2011	coastal, shelf[b]
Scyliorhinidae	*Apristurus sinensis*	26.7	24.5	45.0	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[c]
	Figaro boardmani	27.3	20.9	45.8	Australia	Pethybridge et al. 2010	upper slope, 200-650m[c]
Sphyrnidae	*Sphyrna lewini*	31.0	22.0	44.0	South Africa	Davidson et al. 2011	coastal, shelf, semioceanic[b]
	Sphyrna zygaena	31.0	22.0	35.0	South Africa	Davidson et al. 2011	coastal, shelf, semioceanic[b]
Lamniformes							
Lamnidae	*Carcharodon carcharias*	35.0	25.0	30.0	South Africa	Davidson et al. 2011	coastal, shelf[a]
Odontaspididae	*Carcharias taurus*	31.0	25.0	36.0	South Africa	Davidson et al. 2011	coastal, shelf[a]

a. Compagno, L.J.V. 1984. FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1-Hexanchiformes to Lamniformes. FAO Fish. Synop. 125(4/1): 1-249. b. Compagno, L.J.V. 1984. FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2-Carcharhiniformes. FAO Fish. Synop. 125(4/2): 251-655. C. Daley, R.K., Stevens, J.D., Last, P.R., Yearsley, G.K. 2002. Field guide to Australian sharks and rays. CSIRO, Victoria., b)

Table S4.3. Mean proportions of liver ∑saturated fatty acids (SAFA), ∑monounsaturated fatty acids (MUFA), and ∑polyunsaturated fatty acids (PUFA) for various shark species sampled from northern, tropical and subtropical waters.

Order Family	Species	SAFA	MUFA	PUFA	Sampling location	Reference	Dominant habitat
Hexanchiformes							
Hexanchidae	*Notorynchus cepedianus*	29.1	41.9	26.5	Australia	Pethybridge et al. 2010	shelf, 0-200m[b]
Squaliformes							
Centrophoridae	*Centrophorus moluccensis*	25.6	62.2	0.6	Australia	Bakes and Nichols 1995	outer shelves, 130-800m[a]
	Centrophorus zeehaani	26.7	57.9	12.1	Australia	Pethybridge et al. 2010	upper slope, 200-650m[b]
	Deania calcea	26.4	63.0	8.1	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[b]
Dalattidae	*Dalatias licha*	15.2	70.9	11.6	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[b]
Etmopteridae	*Etmopterus baxteri*	16.2	76.9	4.6	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[b]
	Etmopterus granulosus	15.0	80.0	2.5	Australia	Bakes and Nichols 1995	outer shelves, 200-600m[a]
Somniosidae	*C entroselachus crepidater*	17.9	71.6	8.4	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[b]
	Centroscymnus coelolepis	18.6	60.0	20.2	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[b]
	Proscymnodon plunketi	11.9	81.8	3.9	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[b]
	Somniosus microcephalus	6.9	77.6	15.5	Nunavut	this study	benthopelagic, 0-1200m[a]
	Somniosus pacificus	16.2	70.2	13.6	Gulf of Alaska	Schalufler et al. 2005	benthopelagic, 0-2000m[a]
	Somniosus pacificus	12.5	72.0	13.3	Australia	Bakes and Nichols 1995	benthopelagic, 0-2000m[a]
Sqalidae	*Squalus acanthias*	23.1	57.3	14.7	Australia	Pethybridge et al. 2010	shelf, 0-200m[b]
	Squalus chloroculus	20.4	61.6	13.4	Australia	Pethybridge et al. 2010	shelf, 0-200m[b]
	Squalus megalops	15.8	58.8	15.8	Australia	Pethybridge et al. 2010	upper slope, 200-650m[b]
Carcharhiniformes							
Carcharhinidae	*Carcharhinus brevipinna*	43.3	29.8	26.9	South Africa	Davidson and Cliff 2002	coastal, shelf [b]
	Carcharhinus leucas	41.5	40.6	18.0	South Africa	Davidson and Cliff 2002	coastal, estuarine [b]
	Carcharhinus limbatus	43.8	32.1	24.4	South Africa	Davidson and Cliff 2002	coastal [b]
	Carcharhinus obscurus	39.3	38.4	22.6	South Africa	Davidson and Cliff 2002	coastal, shelf [b]
	Galeocerdo cuvieri	39.0	42.8	18.2	South Africa	Davidson and Cliff 2002	coastal, shelf [b]
Scyliorhinidae	*Apristurus sinensis*	15.8	72.6	9.8	Australia	Pethybridge et al. 2010	mid slope, 650-1200m[c]
	Figaro boardmani	23.2	45.3	29.4	Australia	Pethybridge et al. 2010	upper slope, 200-650m[c]
Sphyrnidae	*Sphyrna lewini*	36.2	43.1	20.8	South Africa	Davidson and Cliff 2002	coastal, shelf, semioceanic
Lamniformes							
Odontaspididae	*Carcharias taurus*	37.1	36.4	26.6	South Africa	Davidson and Cliff 2002	nearshore, coastal[a]

a. Compagno, L.J.V. 1984. FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1-Hexanchiformes to Lamniformes. FAO Fish. Synop. 125(4/1): 1-249. b. Compagno, L.J.V. 1984. FAO Species Catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2-Carcharhiniformes. FAO Fish. Synop. 125(4/2): 251-655. C. Daley, R.K., Stevens, J.D., Last, P.R., Yearsley, G.K. 2002. Field guide to Australian sharks and rays. CSIRO, Victoria.

CHAPTER 5

INDIVIDUAL SPECIALIZATION IN GREENLAND SHARKS (SOMNIOSUS MICROCEAPHLUS)

INTRODUCTION

It has been widely hypothesized that generalist vs specialist feeding behaviour (i.e. whether a given species consistently consumes many and variable vs few and invariable types of prey) directly affects food web persistence in ecological communities (MacArthur 1955). MacArthur (1955) suggested that in regions of low diversity, such as at high latitudes, species consume a wider range of prey items, thereby increasing food web persistence. Empirical studies have shown that generalist feeding at multiple trophic levels across spatial and temporal boundaries is common in real food webs (Polis 1991; Polis and Strong 1996; Vander Zanden and Vadeboncoeur 2002). Theoretical models further suggest that the ability of generalists to move across spatial boundaries and consume multiple resources as they become available (i.e. spatial resource coupling) imparts a flexible nature to food webs (Rooney et al. 2006). These results strongly suggest that consumers, especially those inhabiting low diversity and/or temporally variable environments, should feed as generalists (MacArthur 1955). However the way in which generalist populations moderate food web persistence is complicated by recent evidence that many generalist populations are in fact composed of specialist individuals that feed on a specific subset of the populations' total resources (reviewed by Bolnick et al. 2003; Araújo et al. 2011).

Distinguishing between populations with high amounts of individual generalism (IG) and those dominated by individual specialization (IS) is not trivial and has major consequences for food web-level processes (Bolnick et al. 2011). While high IS in a predator population may be destabilizing by limiting the extent of spatial resource coupling (Bolnick et al. 2011), it may also promote food web persistence by increasing the frequency and decreasing the strength of any one inter-specific interaction (McCann et al. 1998; Bolnick et al. 2011). The offsetting of these IS effects in generalist populations suggest generalist feeding may be both less common and potentially less important for food web persistence than previously thought. Further complicating this issue is the potential for IG and IS to vary in time within a population (e.g. with season, Herrera et al. 2008).

To understand the extent and dynamics of IS and IG within populations requires a metric for specialization that can be readily compared within and among populations. Because an individual specialist will have a smaller niche (i.e. lower diet variance) relative to the populations' total niche than an individual generalist, the degree of IS in a given population can be estimated as the ratio of within-individual diet variation (WIC, within-individual component) to the diet variation of the total population (TNW, total niche width, equal to WIC + the level of between-individual diet variation (BIC, between-individual component); (Bolnick et al. 2002). Values of WIC/TNW close to zero indicate high IS and values approaching 1 indicating high IG (Bolnick et al. 2002).

Chemical tracers, such stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) are useful for estimating WIC and TNW because they are integrated within consumers tissues over time (Bolnick et al. 2002). High variance in stable isotopes among tissues with different turnover times is indicative of a consistently variable diet over time (i.e. IG), whereas low variance indicates IS (Bolnick et al. 2002; Bolnick et al. 2003; Araújo et al. 2011). However, stable isotopes normally provide information only about the proteinacious diet component, as tissues are conventionally lipid extracted prior to analysis to remove the bias associated with ^{13}C-depleted lipids (Post et al. 2007; Hussey et al. 2010). Fatty acids on the other hand, being dietary tracers that are integrated into a predator's tissues over time (Iverson 2009), could provide information about IS in predators with high fat diets (e.g. mammal blubber, fatty fish). Fatty acids have been successfully used to track resource use in arctic animals, from zooplankton (Falk-Petersen et al. 2009) and benthic fish (Graeve et al. 1997) to sharks (Schaufler et al. 2005), seals (Falk-Petersen et al. 2009) and polar bears (Grahl-Nielsen et al. 2003).

Here, fatty acids were analyzed in three tissues (muscle, liver, plasma) of Greenland sharks (*Somniosus microcephalus*) sampled from Cumberland Sound, Canada during summer (August) and winter (April) of 2008 and 2009, to answer two questions: (1) What is the extent of individual diet specialization in a theoretically generalist, high-latitude population, and (2) does the level of individual specialization present vary with season and/or year? The Greenland shark is the only shark to inhabit ice-covered seas in the North Atlantic, and is widely presumed to feed as an opportunist/generalist (recently reviewed by MacNeil et al. 2012). Because the Greenland shark's diet includes lipid-rich prey (e.g. fatty teleosts like Greenland halibut, *Reinhardtius hippoglossoides* and marine mammals like ringed seal, *Pusa hispida*, see Chapter 4), fatty acids are an appropriate tool for exploring resource use among individual sharks. Although no population size estimates exist for Greenland sharks, the species is commonly caught in Cumberland Sound (>15 individuals 100 hooks^{-1} using shark-specfic gear, MacNeil et al. 2012) and is therefore likely abundant. As such, intra-specific competition could be high and the prediction is that IS will be high (Svanbäck and Bolnick 2005; Araújo et al. 2011). Although no biomass data exist for Cumberland Sound, winter marine food webs tend to be less complex than summer food webs due to migration (Johnson et al. 2009). Thus, a more diverse array of prey are expected to be available in summer, with the prediction being that the extent of IS in Greenland sharks will change with season and be higher in summer than in winter (see Fig. 1.2 for visual representation of these hypotheses).

MATERIALS AND METHODS

Sample collection

Four sampling events were performed in Cumberland Sound: two during summer, open water (August 2008 and 2009) and two during winter, ice cover (April 2008 and 2009). All samples were collected within or up to 30 km of the mouth of Pangnirtung fjord (see Chapter 2, Fig. 2.1 for map of sampling locations). Greenland sharks were caught via bottom long-lines, set from boats during summer and through holes cut in the sea ice in winter, and immediately euthanized via an incision through the dorsal surface (immediately anterior to the first gill slit) to sever the spinal cord followed by a second incision through the brain. Blood was allowed to flow from the dorsal cut for several seconds before being collected into a centrifuge tube with no lining or additives. One exception is the blood sampled in August 2009, which was collected from the caudal vein using a syringe. Blood was centrifuged immediately in the field and the plasma portion was separated from the whole blood fraction using a sterile pipette. There was no effect of blood collection method on fatty acids because the range of August 2009 plasma 22:5n-3 was within the range of the other sampling dates (Table S5.1), and there was no significant difference in plasma 22:5n-3 among sampling dates (see Results section). Approximately 5 g of dorsal muscle were collected ~2 cm above the vertebrae and liver biopsies (~5 g) were taken from the mid-way point along one liver lobe's length. In total, 59 Greenland sharks were sampled, but data are only presented for sharks that had all three tissues sampled. Based on the Greenland sharks' stomach contents, the dominant prey items, Greenland halibut and ringed seal (Chapter 4), were sampled for fatty acids. Greenland halibut were sampled during April 2008 and 2009 using bottom long-lines set through the sea ice, and ringed seals were shot during Inuit subsistence hunting during August 2008 and April 2008. Muscle and blubber were sampled from halibut and ringed seal, respectively, because these tissues should represent the largest biomass of lipid consumed by Greenland sharks. All samples were placed immediately on ice and were frozen on dry ice or in liquid nitrogen within 1 h.

Lipids were extracted from all tissue samples using a 2:1 chloroform: methanol solution (Folch et al. 1957) and fatty acid methyl esters (FAME) were generated from the total lipid extract as detailed in Chapter 2 and McMeans et al. (2012).

Choice of fatty acid

It is widely acknowledged that the fatty acid proportions observed in a predators tissues do not match the proportions observed in the diet (e.g. Andersen et al. 2004, Budge et al. 2011, Grahl-Nielsen et al. 2003, 2011). However, to effectively interpret variable or similar values of a given fatty acid among shark tissues as evidence for IG or IS, respectively, required that: 1) sharks have similar magnitudes of this fatty acid among the three tissues when at equilibrium and 2) that the fatty acid value of the sharks' tissues reflect the amount of that fatty acid obtained in the diet. A preliminary assessment of the tissue fatty acid data revealed that 22:5n-3 appeared to meet both of these requirements (Chapter 4, B.C. McMeans, M.T. Arts, A.T. Fisk, submitted manuscript). Specifically, although there was no way of assessing what the fatty acid profile of a Greenland shark would be at equilibrium, the magnitude of 22:5n-3 is generally similar among Greenland shark muscle, liver and plasma, unlike other fatty acids like 22:6n-3 that tend to accumulate in muscle and 20:1n-9 that accumulate in the sharks' liver (Chapter 4, B.C. McMeans, M.T. Arts, A.T. Fisk, submitted manuscript). Second, values of 22:5n-3 in Greenland shark muscle, liver and plasma fall in between the extreme values exhibited by Greenland halibut muscle and ringed seal blubber, such that the sharks appear to incorporate similar amounts of this fatty acid into their tissues as obtained in the diet (Fig. 5.1). Previous controlled feeding trials have found that dietary differences in 22:5n-3 are reflected in the tissues of both fish (Bell et al. 2003; Arts et al. 2010; Budge et al. 2011) and avian predators (Iverson 2009), supporting the use of 22:5n-3 as a dietary indicator in the present study.

Choice of tissues and tissue turnover

A major assumption of the present work is that fatty acids of different tissues reflect different time frames of the sharks' diet. To this end, shark tissues were sampled, based on knowledge derived from captive feeding studies performed predominantly in mammals, which function in fatty acid storage and are dominated by molecules like triacylglycerol (TAG). Such tissues should have faster turnover times than tissues which have structural functions or have low % lipid and tend to be dominated by phospholipids (Budge et al. 2006). The large, lipid-rich liver is the major fatty acid storage site in sharks (Ballantyne 1997), such that liver should have a faster turnover rate than more structural tissues like muscle. This does appear to be the case in the protein portion of shark liver vs muscle based on stable isotopes (MacNeil et al. 2005). Further, the Greenland shark has high % lipid in both liver and muscle, such that both tissues likely function in fatty acid storage (Chapter 4, B.C. McMeans, M.T. Arts, A.T. Fisk, submitted manuscript) and should both be good indicators of diet. The fact that the Pacific sleeper shark (*Somniosus* *pacificus*) has liver and muscle dominated by storage molecules (78 and 73% TAG, respectively, Schaufler et al. 2005) and that both tissues reflected the sharks' consumption of planktivorous whales supports this suggestion. Plasma was chosen for analysis in addition to liver and muscle because it is the vehicle for transferring dietary fatty acids to the tissues, and will logically have a faster turnover time than lipids incorporated into muscle or liver (Budge et al. 2006).

Unfortunately no studies exist to estimate the specific turnover time of fatty acids in shark muscle, liver or plasma. Previous controlled feeding studies performed on Atlantic salmon, a teleosts with high fat in both muscle and liver (i.e. similar to Greenland sharks), indicated that postsmolts, which grew to 30 cm over the course of the experiment, reflected the fatty acid profile of their diet in both muscle and liver after 12 weeks (Budge et al. 2011). Adipose tissue of seabirds also reflects past diet on the scale of weeks (Budge et al. 2006). Finally, Hazel and Neas (1982) found that microsomal membrane lipids of rainbow trout (*Salmo gairdneri*) turned over faster in liver ($t_{1/2}$=3.4-6.8 d) than muscle ($t_{1/2}$=8.1-14.8 d), supporting the sampling of muscle and liver as indicators of different dietary time frames for the present study. Due to the large size and cold habitat of the Greenland shark, their muscle and liver fatty acids likely reflect diet incorporation on the scale of months, not weeks. Regarding plasma, a previous controlled feeding study in herring gulls, *Larus argentatus*, revealed that consumption of different fish species (with different fatty acid signatures) was reflected in the birds' plasma within 5 d (Käkelä et al. 2009). Digestion is slow in Greenland sharks (Leclerc et al. 2012), such that plasma could reflect a longer incorporation time in sharks than seabirds, although turnover is almost certainly faster than the sharks' muscle or liver, and on the scale of days or weeks instead of months.

Data analysis

Three separate ANOVAs followed by Tukey's post hoc comparisons were used to compare proportions of 22:5n-3 in muscle, liver and plasma among sampling dates (i.e. April 2008, August 2008, April 2009, August 2009). Liver 22:5n3 was logit transformed prior to analysis to increase normality (Warton and Hui 2011). ANOVA and Welch's *t* test were used to compare 22:5n-3c in ringed seals and Greenland halibut among sampling dates, respectively.

The four metrics defined by Bolnick et al. (2002) for continuous data were calculated to quantify IS in Greenland sharks: 1) BIC, 2) WIC, 3) TNW = BIC+WIC and 4) WIC/TNW (Table 5.1). Metrics were estimated in two ways. First, a linear mixed-effects model was run on proportions of 22:5n-3, with tissue (muscle, liver, plasma) as a fixed effect and individual shark as a random effect. BIC was estimated from the among-individual variation (in the random intercepts) while WIC was given by the residual variation at the individual level. TNW was obtained by summing WIC and BIC estimates obtained from the model. The program IndSpec (Bolnick et al. 2002) was also used to obtain estimates of population-level BIC, WIC, and TNW.

The BIC, WIC and TNW metrics provide only population-level indications of diet variation among individuals. Therefore, to obtain an estimate of IS for each Greenland shark, the variance of 22:5n-3 was calculated among the three tissues for each individual Greenland shark was calculated and labelled 'WIC_{ind}.' Using the population-level TNW derived from the linear mixed-effects model, the ratio of WIC_{ind}/TNW was calculated as a metric of IS for each individual shark. Kruskal Wallis followed by pair-wise comparisons were used to compare WIC_{ind}/TNW among sampling dates, Pearson's product moment correlation to explore the relationship between WIC_{ind}/TNW and Greenland shark length and Welch's t test to identify any effect of sex. One individual shark from April 2008 had a very high WIC_{ind} /TNW (i.e. 6.86) attributed to a very high three-tissue variance (i.e. 11.53, Table S5.1) and was excluded from the aforementioned comparisons. All analyses, except for those performed using the IndSpec program (Bolnick et al. 2002), were performed in R (R_Development_Core_Team 2010).

RESULTS

Proportions of 22:5n-3 were generally similar among the three shark tissues when considered across all sampling dates (mean±SD: muscle=2.4±0.8, liver=2.4±1.3, plasma=3.4±1.3). However among sampling dates, mean proportions of 22:5n-3 in muscle, liver and plasma were higher in April and August 2009 vs April and August 2008, although these differences were not always significant (Table 5.2). Greenland halibut muscle had less variable proportions of 22:5n-3 than ringed seal blubber, but proportions of 22:5n-3 did not differ between sampling dates in either species (Table 5.2). Relative to prey, 2008 sharks had tissue proportions of 22:5n-3 that were closer to Greenland halibut muscle, whereas tissues of 2009 sharks were more similar to ringed seal blubber (Table 5.2, Fig. 5.1). Regardless of season, however, all shark tissue values fell within the extreme values exhibited by halibut and ringed seal (Fig. 5.1).

Individual specialization metrics calculated using the linear mixed-effects model agreed with results from IndSpec, revealing that the WIC of the Greenland sharks was 43% and 36% of the TNW based on IndSpec and the glm, respectively (Table 5.3).

Relative to bull (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*), the extent of IS was lower for Greenland sharks (i.e. WIC/TNW was higher, Table 5.3).

The mean of WIC_{ind}/TNW among all 44 Greenland sharks was 0.39 (when the one shark with very high WIC_{ind}/TNW was removed, see Data Analysis section and Table 5.3), which agrees with the population-level WIC/TNW obtained from the glm and IndSpec methods (i.e. 0.36 and 0.43, respectively, Table 5.3), indicating that this is an appropriate metric to explore IS in each Greenland shark. The standard deviation of WIC_{ind}/TNW was high (i.e. 0.33) and indicates variability in the extent of IS among individuals. Visual inspection of the data reveals that 22:5n-3 proportions were less variable among shark tissues sampled during April and August 2008 (with the exception of one individual with a very large 22:5n-3 range from April 2008) than in April and August 2009 (Fig. 5.1). In fact, IS was lower in April and August 2009 based on higher mean WIC_{ind}/TNW (2008: April=0.17±0.17, August=0.31±0.22; 2009: April=0.38±0.26, August=0.83±0.41), although only the differences between August 2009 and both Aprils were significant (Fig. 5.2). Values of WIC_{ind}/TNW were not correlated with shark length and did not differ between sexes (both $P>0.05$).

DISCUSSION

Greenland sharks from Cumberland Sound exhibited an intermediate level of IS based on WIC/TNW= ~0.4 (Bolnick et al. 2003). Compared to a recent review of 78 studies published since 2003 (performed on plants, gastropods, crustaceans, insects, fishes, amphibians, reptiles, birds and mammals; (mean WIC/TNW=0.66, Araújo et al. 2011), these Greenland sharks exhibited greater than average IS (i.e. lower WIC/TNW) when considered across taxa. However comparisons among WIC/TNW from different populations must be made with care due, for example, to differences in prey fatty acid variability (Araújo et al. 2011). It is likely more appropriate to compare values of WIC/TNW among shark species, because sharks have a much larger potential TNW than other taxa (e.g. due to their high mobility, variable diet and exploitation of sporadic scavenging events). The level of IS in the present study was lower than the only other study to investigate IS in sharks, which found that bull and tiger sharks feed as individual specialists (WIC/TNW=0.05, Table 5.3) and individual generalists (WIC/TNW=0.33, Table 5.3), respectively (Matich et al. 2011). Based on the agreement between WIC/TNW in Greenland sharks and tiger sharks (Matich et al. 2011), it appears that the population of Greenland sharks sampled in the present study predominantly fed as individual generalists, which is consistent with Greenland sharks commonly containing multiple prey in a given stomach (Leclerc et al. 2012), and having a propensity for scavenging (Leclerc et al. 2011; MacNeil et al. 2012).

Although WIC/TNW metric is useful for gauging the extent of IS in a given population, it also masked considerable variation in the level of IS among individual Greenland sharks. Based on the individual-level metric WIC_{ind}/TNW, this generalist population included multiple individuals feeding as specialists (i.e. sharks with values of WIC_{ind}/TNW approaching zero, Table S5.1). These sharks appeared to feed on a subset of the populations' total resources at least long enough to be reflected in their muscle, liver and plasma (i.e. likely for many months or longer), lending support to the prediction that IS could be high in Greenland sharks. Thus, IS can arise even within generalist populations inhabiting temporally variable and seasonal environments, and a population can be composed of both individual specialists and individual generalists.

Because populations exhibiting temporally stable IS will be more susceptible to density-dependent population fluctuations (Bolnick et al. 2003), the temporal constancy of IS was explored in the present study. The comparison of WIC_{ind}/TNW among sampling dates revealed that IS in Greenland sharks did not remain constant through time, similar to previous observations in mammal consumers (Herrera et al. 2008). Based on this result, even if IS arises in Greenland sharks, it is not a permanent feature of the Greenland sharks' feeding ecology. Using the terminology of Bolnick et al. (2003), Greenland sharks are individual generalists that occasionally act as 'short-term specialists'. Such a flexible feeding behaviour should allow Greenland sharks to rapidly respond to changes in prey availability or environmental disturbance (Bolnick et al. 2003).

Higher 22:5n-3 (i.e. more similar to seal proportions) but lower IS (i.e. higher WIC_{ind}/TNW) in the 2009 sharks suggests that these sharks were including a larger portion of seal in their diets but were not specializing on seal. This was reflected in their stomach contents, where seal was found only in conjunction with fish remains (B.C. McMeans, unpubl. data). However, 22:5n-3 was lower (more similar to Greenland halibut) in 2008 and IS was higher (i.e. lower WIC_{ind}/TNW, Fig. 5.2), suggesting the 2008 sharks were exploiting different subsets of the populations' resources, perhaps by exploiting different relative amounts of Greenland halibut (i.e. sharks with consistently low 22:5n-3) and Greenland halibut and seal (i.e. sharks with more intermediate 22:5n-3, Fig. 5.2). The fact that IS varied between sampling years supports the prediction that the extent of IS in Greenland sharks would vary with time. Considered within a given year, but not across both years, the mean WIC_{ind}/TNW was higher in the summer vs winter (i.e.

IS was lower in the summer vs winter of a given year), which deviates from the expectation of higher IS in summer than winter.

Although the separation of April and August sampling dates of a given year by only 4 months was likely insufficient time for muscle or liver to capture a seasonal diet change, blood plasma should have captured a consistent diet change if one existed. Differences in mean 22:5n-3 proportions in all three shark tissues between August 2008 and April 2009 (Table 5.3), however, indicate that 8 months was sufficient time to allow for fatty acid turnover to reflect a new diet. Additional feeding studies focused on sharks will help better pinpoint the specific turnover time of fatty acids, and allow more specific identification of the timing of past feeding behaviour. The range of 22:5n-3 reported here for ringed seals (i.e. 5.0-7.8%) captures the variability that would be encountered by Greenland sharks feeding throughout the Canadian Arctic (previously reported to be ~5.5 to 7.0%, Thiemann et al. 2007). As such, the annual differences between 2008 and 2009 sharks most likely arose from dietary differences and not from, for example, sharks feeding in a different location outside of Cumberland Sound prior to capture.

The individual-level feeding behaviour identified in the present study has several implications from the perspective of food webs. First, the flexible feeding behaviour of the Greenland shark supports the hypothesis that species should feed as generalists in low diversity systems like the Arctic (MacArthur 1955), and that omnivory is a common and important mechanism acting in food webs (Polis and Strong 1996). Second, Greenland sharks are known to scavenge (Leclerc et al. 2011; MacNeil et al. 2012), and among the sharks sampled in Cumberland Sound, 37% (22 of 59) exhibited evidence of scavenging (i.e. the presence of scavenging invertebrates like *Onisimus* in shark stomachs).

Scavenging has often been overlooked regarding its role in food webs until recently (Wilson and Wolkovich 2011). Instead of being a 'dead end', consumption of high quality carrion by consumers is likely very important for the flow of energy through food webs by, for example, increasing the number of trophic links and making food webs more reticulate (Wilson and Wolkovich 2011). Further, by feeding on both live and dead prey, Greenland sharks are effectively acting as resource couplers of fast and slow resource compartments, which can increase the flexibility of food webs in response to perturbations and promote persistence (Rooney et al. 2006).

Although it is unknown what mechanism was driving changes in the extent of IS with time, drastic differences in prey availability are an unlikely explanation because Greenland halibut and ringed seals were present in Cumberland Sound throughout the study period (B.C. McMeans, personal observation). However, local variability in prey abundance may have played a role as catch per unit effort of Greenland halibut in Cumberland Sound are known to exhibit inter-annual variability (Dennard et al. 2010). Future work is tasked with identifying whether IS arises in other arctic marine species, and with linking both the extent and temporal constancy of IS exhibited among species in a given ecosystem (Matich et al. 2011) and within populations (this study, Rosenblatt and Heithaus 2011) with their importance for food web structure and persistence. The flexible feeding behaviour of Greenland sharks identified in the present study could be an important mechanism for the structure, and even the persistence, of arctic food webs. As the physical environment and biological community structure of arctic ecosystems continues to change (MacNeil et al. 2010), such flexibility may become increasingly important for arctic animals.

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Table 5.1. Metrics used to estimate individual specialization in Cumberland Sound Greenland sharks.

Metric		Level	Method of estimation
BIC	between-individual variation	population	glm and IndSpec*
WIC	within-individual variation	population	glm and IndSpec
TNW	total niche variation	population	glm and IndSpec
WIC/TNW	individual specialization, specialist 0↔1 generalist	population	glm and IndSpec
WIC_{ind}	individual-level variance	individual	3 tissue variance for each individual
WIC_{ind}/TNW	individual specialization, specialist 0↔1 generalist	individual	glm / 3 tissue variance

glm: linear mixed-effects model performed on proportions of 22:5n-3 (dependent variable), including tissue (muscle, liver, plasma) as a fixed effect and individual as a random effect; *Bolnick et al. 2002

Table 5.2. Proportions of 22:5n-3 (mean ± SD) in tissues of Greenland sharks (*S. microcephalus*) and two dominant prey. Significant differences in Greenland shark muscle, liver and plasma between sampling dates, based on ANOVA, are indicated by different letters (similar values share the same letter). The overall mean (i.e. among sampling dates) for halibut and ringed seal is presented in Fig. 5.1.

Species	Date	*n*	Tissue		
Somniosus microcephalus			Muscle	Liver	Plasma
(Greenland shark)	April 2008	12	1.7 ± 0.5^{a}	1.6 ± 0.7^{a}	2.7 ± 1.7^{a}
	August 2008	8	1.8 ± 0.3^{a}	1.9 ± 0.7^{ab}	2.7 ± 0.7^{a}
	April 2009	17	3.1 ± 0.7^{b}	2.7 ± 1.2 ^{ab}	3.9 ± 1.2^{a}
	August 2009	7	2.6 ± 0.7^{ab}	4.3 ± 1.4^{b}	4.4 ± 0.8^{a}
R. hippoglossoides			Muscle		
(Greenland halibut)	April 2008	11	0.7 ± 0.4^{a}		
	April 2009	33	1.0 ± 0.3^{a}		
Pusa hispida			Blubber		
(ringed seal)	April 2008	3	6.9 ± 0.9^{a}		
	August 2008	6	5.8 ± 1.1^{a}		

Muscle ANOVA: $F_{3,40}$=15.83, P<0.001, Liver ANOVA: $F_{3,38}$=7.70, P<0.001, Plasma ANOVA: P>0.05, Greenland halibut Welch's t test: P>0.05; Ringed seal Welch's t test: P>0.05

Table 5.3. Individual specialization metrics for Greenland sharks (*Somniosus microcephalus*) sampled in Cumberland Sound, calculated from 22:5n-3 proportions of shark muscle, liver and plasma. Previously published values for bull (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*) are shown. The values of WIC_{ind}/TNW is the mean ± SD calculated for all 44 individual Greenland sharks (excluding one outlier from April 2008).

Level	Metric	Greenland shark		Tiger shark*	Bull shark*
Population		IndSpec	glm	IndSpec	IndSpec
	BIC	1.05	0.95	0.04	0.04
	WIC	0.59	0.73	0.02	0.002
	TNW	1.68	1.64	0.06	0.04
	WIC/TNW (↓ = ↑ ind. spec.)	0.43	0.36	0.33	0.05
Individual	WIC_{ind}/TNW	NA	0.39 ± 0.33	NA	NA

*Data from Matich et al. 2010, metrics derived from δ^{13}C values of three tissues (muscle, blood, plasma for bull sharks and fin, blood, plasma for tiger sharks)

Fig. 5.1. Proportions of 22:5n3 (% of total) in 44 individual Greenland sharks sampled in Cumberland Sound during two summers (August) and two winters (April). Each horizontal line corresponds to one individual shark and is the range of 22:5n-3 among muscle, liver and plasma. Mean (dashed vertical line) ± 1 SD of ringed seal and Greenland halibut 22:5n-3 (from across all sampling dates, see Table 5.2) are also shown.

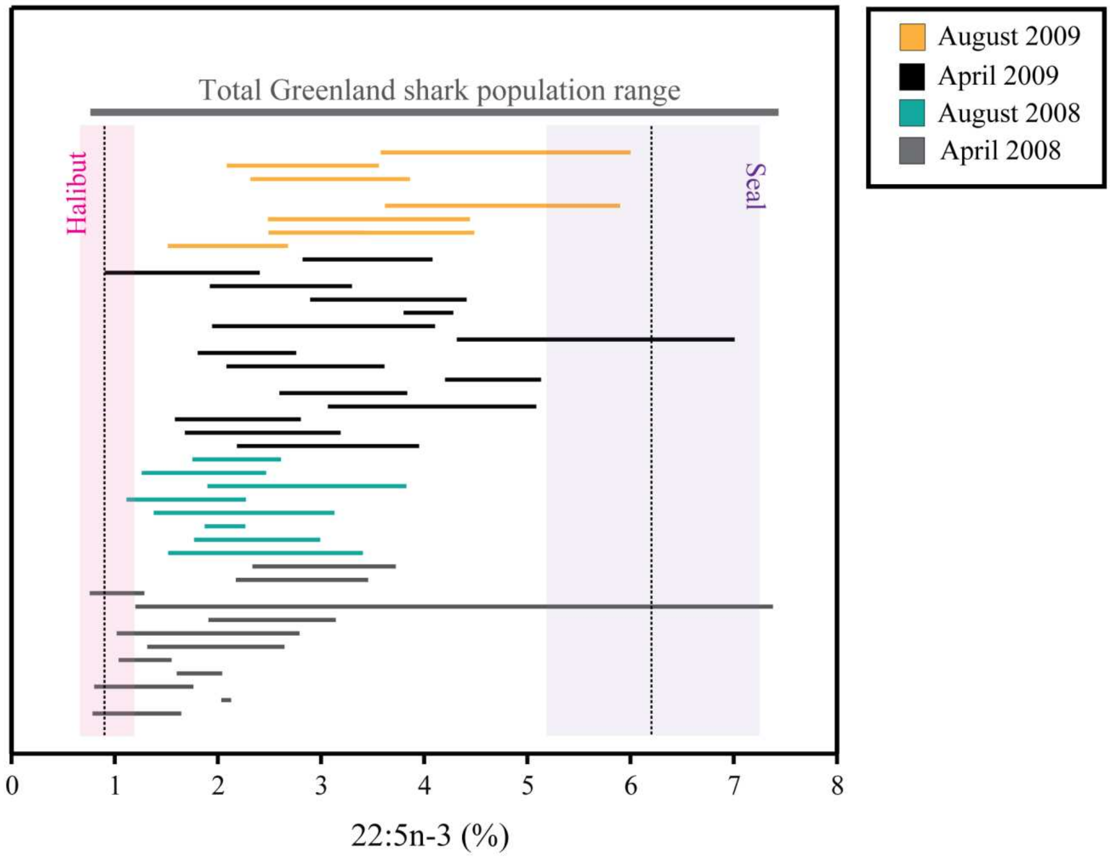
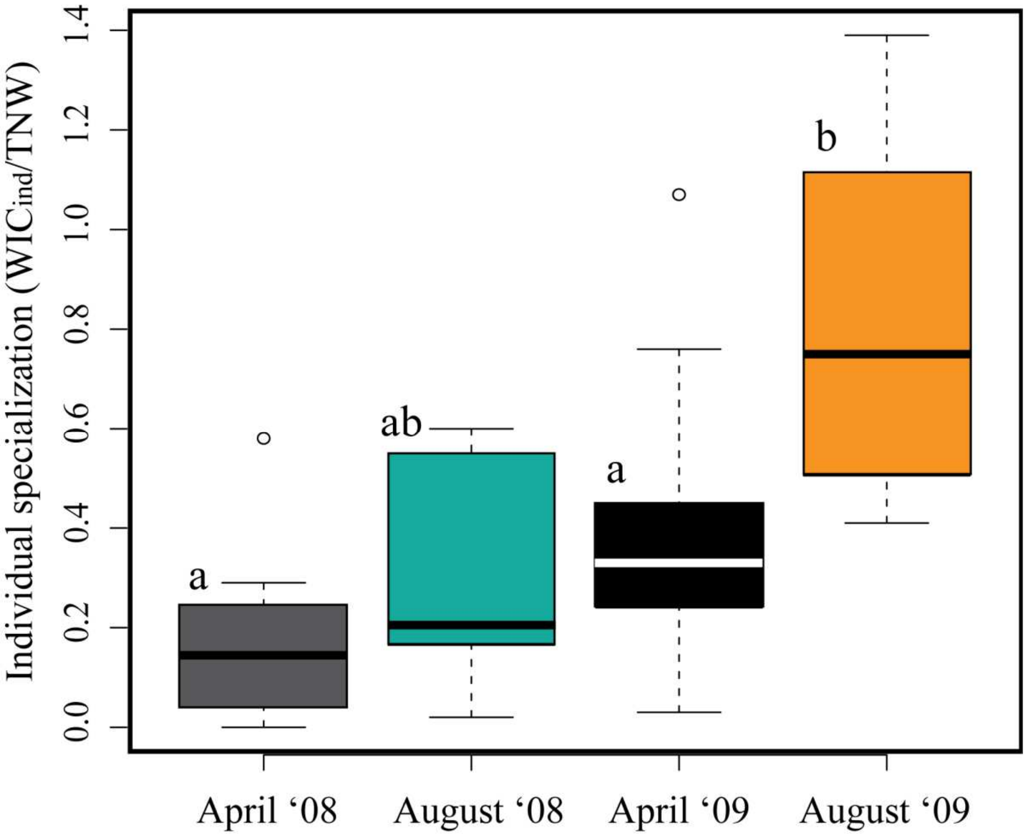


Fig. 5.2. Boxplots of WIC_{ind}/TNW calculated for individual Greenland sharks sampled in Cumberland Sound during two summers (August) and two winters (April). Lower values indicate greater individual specialization. Letters indicate significant differences (Kruskal-Wallis, $\chi^2=15.61$, df=3, $P<0.05$) and similar values share the same letter.



SUPPLEMENTARY MATERIAL

Table S5.1. Proportions of plasma (BP), liver (L) and muscle (M) 22:5n-3, sampling season and year, length (cm) and sex for 44 individual Greenland sharks. The within-individual variance (WIC_{ind}) is the variance of the three tissues, TNW is the populations' total variance estimated from a linear mixed effects model (Table 5.2) and the individual specialization metric for each shark is WIC_{ind}/TNW.

Individual	Season	Sex	Length	BP	L	M	WIC_{ind}	WIC_{ind}/TNW
1	April 08	M	269	1.6	0.8	1.3	0.17	0.10
2	April 08	F	345	2.1	2.1	2.1	0.00	0.00
3	April 08	M	250	1.7	0.8	1.6	0.24	0.14
4	April 08	M	277	2.0	1.7	1.6	0.04	0.03
5	April 08	F	259	1.2	1.1	1.5	0.06	0.04
6	April 08	M	262	2.6	2.2	1.3	0.43	0.25
7	April 08	M	258	2.8	1.0	1.1	0.97	0.58
8	April 08	M	224	3.1	1.9	2.5	0.36	0.21
9	April 08	M	248	7.4	1.2	1.8	11.53	6.86*
10	April 08	M	280	1.3	0.8	1.2	0.07	0.04
11	April 08	F	291	3.4	2.6	2.2	0.40	0.24
12	April 08	M	293	3.7	2.7	2.4	0.49	0.29
13	August 08	M	277	3.4	1.8	1.5	1.00	0.60
14	August 08	F	320	1.8	3.0	2.2	0.36	0.21
15	August 08	M	270	1.9	2.2	2.0	0.04	0.02
16	August 08	F	295	3.1	1.5	1.4	0.93	0.56
17	August 08	F	255	2.3	1.1	1.4	0.34	0.20
18	August 08	M	320	3.8	2.7	1.9	0.90	0.54
19	August 08	F	252	2.4	1.3	1.9	0.34	0.20
20	August 08	M	305	2.6	1.8	1.8	0.22	0.13
21	April 09	F	249	3.9	2.9	2.2	0.75	0.45
22	April 09	F	210	3.2	1.7	2.8	0.58	0.35
23	April 09	M	291	2.8	1.6	2.5	0.38	0.23
24	April 09	M	213	5.1	4.5	3.1	1.03	0.61
25	April 09	F	294	3.8	2.6	2.8	0.43	0.25
26	April 09	F	270	5.1	4.5	4.2	0.21	0.13
27	April 09	M	275	3.6	2.1	3.4	0.64	0.38
28	April 09	M	255	2.4	1.8	2.7	0.21	0.13
29	April 09	M	283	7.0	5.4	4.3	1.79	1.07

30	April 09	M	273	4.1	2.0	3.7	1.28	0.76
31	April 09	M	278	4.3	3.8	3.9	0.06	0.03
32	April 09	M	254	4.4	2.9	3.8	0.55	0.33
33	April 09	M	274	3.3	1.9	2.1	0.52	0.31
34	April 09	M	264	2.4	0.9	2.3	0.67	0.40
35	April 09	F	343	4.1	2.8	3.2	0.40	0.24
36	April 09	M	255	2.6	1.5	2.7	0.40	0.24
37	April 09	M	244	4.5	3.4	2.5	0.96	0.57
38	August 09	M	288	3.9	4.4	2.5	0.98	0.58
39	August 09	M	285	5.0	5.9	3.6	1.26	0.75
40	August 09	F	285	4.4	NA	2.3	2.30	1.37
41	August 09	F	322	3.8	3.8	2.3	0.73	0.43
42	August 09	M	290	3.5	2.1	2.1	0.68	0.41
43	August 09	M	307	6.0	5.1	3.6	1.45	0.86
44	August 09	F	270	4.0	NA	1.8	2.33	1.39

*treated as an outlier and excluded from statistical analyses

CHAPTER 6

TEMPORAL RESOURCE ASYNCHRONY AND SEASONAL DIET SWITCHING IN ARCTIC FOOD WEBS: COMPARISONS BETWEEN EMPIRICAL PATTERS AND THEORETICAL PREDICTIONS

INTRODUCTION

Linking food web structures with mechanisms that promote food web persistence (i.e. the continued existence of a food web through time) has been an elusive but important goal of ecologists for decades (MacArthur 1955; May 1973; Yodzis 1981). There has long been a suspicion among ecologists that spatial resource subsidies and flexible consumer feeding behaviour are important for food web complexity (Elton 1927; Polis 1991), and the ability of food webs to adapt in the face of perturbations (Levin 1998). Recent theoretical models have largely confirmed that persistence is greatly increased when food webs are structured such that resources vary asynchronously in space (i.e. exhibit different relative abundances), which are 'coupled' by generalist predators (i.e. when consumers move throughout the landscape consuming abundant resources) (Rooney et al. 2006). The coupling of spatially asynchronous resources imparts persistence to food webs because: 1) the resource asynchrony provides a steady source of food to consumers, 2) resources and consumers within the fast energy channel rapidly recover from perturbations, and 3) because consumers 'decouple' from (i.e. stop consuming) declining resources, thereby allowing scarce resources to recover (Rooney et al. 2006; McCann and Rooney 2009). Consumers are also known to couple resources as they vary in time. For example, frugivorous birds switch their diets to exploit seasonally varying abundances of insects and fruit, which is thought to promote species coexistence and diversity (Carnicer et al. 2008). However, very few data have been collected to categorize temporal changes in trophic interactions at the scale of an entire food web (e.g. Johnson et al. 2009). It therefore remains unknown if the coupling of temporally asynchronous resources is a common structure in food webs.

Temporal variability in resources is more the 'norm' than the exception in terrestrial and aquatic environments, and could affect food webs in a number of ways. For example, drawing on Noy-Meir's (1973, 1974) pulse-reserve hypothesis, Polis et al. (1996) contended that the copious amounts of detritus produced during productive periods, and converted into detritivore biomass, can act as an alternative resource for consumers during non-productive periods. The ability of consumers to switch between feeding on abundant phytoplankton-based resources during productive periods to feeding on detritus-consuming prey during non productive periods (i.e. coupling temporally asynchronous resources, Fig. 1.3) is synonymous with the movement of consumers in space to exploit abundant and abandon declining resources (Eveleigh et al. 2007). The coupling of temporal resource asynchrony could therefore promote persistence in a similar manner to that previously described for spatial coupling (Rooney et al. 2006). If temporal mechanisms are important for food web structure and persistence, two patterns are expected (McCann et al. 2005): 1) multiple resources that vary asynchronously through time should exist (i.e. as the abundance of one resource declines, another resource increases) and 2) consumers should act as temporal couplers of this resource variability by exploiting abundant (i.e. temporal coupling) and abandoning scarce resources (i.e. temporal decoupling). The arctic is one of the most temporally variable marine environments on earth (Weslawski et al. 1991) and should therefore be a fruitful location to investigate the effects of temporal resource variability on food web structure, and to determine whether empirical food web structures are consistent with theoretical predictions.

What is known about the seasonal changes of arctic marine ecosystems and the effect of seasonality on arctic food webs? Generally, open-water diatom blooms in the summer months fuel pelagic food chains (Falk-Petersen et al. 2000; Falk-Petersen et al. 2007) and settle to the sea floor to support a diverse benthos (Forest et al. 2008; Renaud et al. 2011). The phytoplankton bloom eventually becomes nutrient and light limited as ice forms, winter progresses, and very little pelagic algae are present during the dark, ice-covered period (Carey 1992). When light returns in early spring, under-ice algae provide early nutrition to pelagic and benthic consumers (Carey 1992), which is followed by the phytoplankton bloom, completing the annual cycle. Periods of > 9 months can separate times of phytoplankton production in arctic seas (Weslawski et al. 1991) and as a result, arctic consumers are broadly considered to feed as opportunists all year (Lovvorn et al. 2005; Renaud et al. 2011), or to cease feeding entirely during winter and enter diapause (i.e. some calanoid copeods, Falk-Petersen et al. 2009). Opportunistic feeding behaviour has been invoked to explain the lack of seasonal changes in the diets of arctic biota (Werner and Auel 2005; Renaud et al. 2011; Legezynska et al. 2012), which is consistent with an 'unstructured' food web (Isaacs 1973). However, arctic ecosystems are known to experience seasonal changes in primary production (Carmack and Wassmann 2006), lower biomass and diversity in winter (Weslawski et al. 1991), and a switch from phytoplankton to detritus fueling the summer and winter food webs, respectively (Forest et al. 2008). Further, some consumers, like ringed seals (*Pusa hispida*), are known to switch their diet with season, exploiting higher trophic position prey in the winter (Lowry et al. 1980; Weslawski et al. 1994). Unfortunately, much empirical work in the arctic to date has been highly regional (Carmack and Wassmann 2006) and no attempt has been made to broadly unite empirical observations from the arctic with patterns predicted by recent food web theory. Further, most studies that report winter feeding behaviour focus on one species (e.g. *Pusa hispida*, Weslawski et al. 1994), functional group (e.g. sympagic amphipods, Werner and Auel 2005) or only a portion of the food web (e.g. benthic food web, Renaud et al. 2011). It therefore remains unclear which view of arctic food webs, as structured or unstructured, is correct.

The goal of the present study was to determine whether temporal coupling of asynchronous resources is an apparent structure within arctic food webs when sampled between summer and winter. Specifically, the following questions were asked: 1) do resources in arctic food webs vary asynchronously through time?, and, 2) do arctic consumers switch their diet away from declining and towards abundant resources as they vary through time (i.e. 'couple' resources in time)? To answer these questions, previously published data were compiled from arctic seas to assess: 1) seasonal variability in basal resources (i.e. phytoplankton, detritus and macroalgae) and in the biomass of zooplankton, benthos and fishes (to establish whether resources and prey availability varied asynchronously) and 2) seasonal diet switching by consumers (to establish whether consumers altered their diet in response to temporal resource asynchrony if observed). To further explore seasonal changes in food web structure, data collected in Cumberland Sound, Baffin Island, Canada during summer and winter periods are presented. Primary production was expected to only occur during summer and the biomass of zooplankton was predicted to decline in winter (Weslawski et al. 1991). If resources are observed to vary asynchronously, for example, if the biomass of some resources decline in winter and availability of other resources increase in winter, and consumers alter their feeding behaviour in time to exploit abundant resources and decouple from declining resources, then the observed pattern would agree with that predicted by theory (McCann et al. 2005) (i.e. Fig. 1.3, Ho). One alternative possibility is no apparent temporal pattern in the overall structure of the food web (Fig. 1.3, Ha).

MATERIALS AND METHODS

Literature review

The literature review was restricted to studies that reported data from an arctic food web (categorized as defined by Carmack and Wassmann 2006) during both summer and winter (i.e. data were not compiled from studies that only reported winter or summer data only) and to studies focused on marginal ice sea areas that experience periods of both open water and ice cover (e.g. not on pack ice food webs). Data were compiled for summer and winter only (although other seasons obviously occur in the arctic), because summer and winter are the times of maximum and minimum phytoplankton production and arguably represent the most disparate conditions experienced by most arctic organisms. The timing of summer and winter differ among arctic locations, but most arctic studies define these seasons in a similar manner (e.g. Weslawski et al. 1991; Carmack and Wassmann 2006). Arctic summer is the time of predominantly open water, no or little ice cover and high solar radiation, salinity stratification and high phytoplankton productivity. Winter is defined as the time of 100% ice cover, and low water column stratification, solar radiation and primary productivity. The review of biomass and consumer diet changes was attempted to be exhaustive. The review of changes in basal resources was not exhaustive because it quickly became clear that phytoplankton peaked in the spring or summer and was at a minimum in the winter, which is a known characteristic of arctic seas (Carmack and Wassmann 2006).

Cumberland Sound sampling

Several lower and upper trophic level species, as well as primary producers, were sampled for stable isotope and fatty acid analysis (see Chapter 2 for a description of Cumberland Sound and Fig. 2.1. for a map of sampling locations) during summer (August) and winter (April) of 2007-2010 (see Table 6.1 for species sampled and putative diet information, and Tables S6.1 and S6.2 for sampling dates). Zooplankton were captured using a 243-μm plankton net (Wildlife Supply Company®, Buffalo, New York) by performing horizontal and vertical tows (from near bottom to surface) in open water (summer) and vertical hauls through holes cut in the ice during winter. Benthos were sampled using a dredge, Ponar or dip nets in summer. One exception was scavenging amphipods (*Onisimus* spp.), which were caught using bottom traps baited with seal blubber (wrapped in mesh to prevent consumption). Sculpin (*Myoxocephalus scorpius*) were captured using baited fishing line and elasmobranchs (arctic skate: *Amblyraja hyperborea,* Greenland shark: *Somniosus microcephalus*) using bottom long lines (set from a boat during summer and through ice holes in winter). Ringed seals were collected during Inuit subsistence hunts. Samples collected for stable isotopes and fatty acids (see Table S6.1 and S6.2 for tissues sampled, respectively) were immediately frozen at -20°C and -80°C.

In an attempt to capture a seasonal diet switch if one existed in upper trophic levels, tissues thought to have fast turnover times were sampled (MacNeil et al. 2005; MacNeil et al. 2006; Käkelä et al. 2009). Specifically, plasma was sampled from

Greenland sharks and liver from arctic skate (for both stable isotopes and fatty acids). Liver and blubber of ringed seals were analyzed for stable isotopes and fatty acids, respectively. It is important to note, however, that the sampling of different tissues limits the ability to compare stable isotope values among these species due to differences in tissue-specific diet-tissue discrimination values (Caut et al. 2009; Hussey et al. 2012). However this will not affect the purpose of this study, as the goal was not to compare between species but between seasons, within species. Samples were analyzed for stable isotopes as described in McMeans et al. (2009) and for fatty acids as described in Chapter 2 and McMeans et al. (2012).

Analysis of Cumberland Sound data

Two-way ANOVAs (factors=functional group*season) were used to determine the effect of season on $\delta^{13}C$ and $\delta^{15}N$ after accounting for differences among functional groups and ensuring normality (q-q plots) and homoscedacity (Levene's test). When $n \geq 3$, Welch's *t* tests (two groups) or ANOVA (≥3 groups) were used to compare $\delta^{13}C$ and $\delta^{15}N$ values of individual species between sampling dates. Non-metric multidimensional scaling (dimensions = 2, distance measure = Euclidean) was used to explore differences in fatty acids among: 1) primary producers, zooplankton and benthos and 2) fish and marine mammal consumers. Data were generated for 50 fatty acids, but analyses were performed on 5 fatty acids known to be informative regarding resource use and diet (Table 6.2). All analyses were performed in R (R Development Core Team 2010) and the significance level was set at 0.05.

Trophic positions and carbon sources of Cumberland Sound species

Stable isotopes are useful for calculating relative trophic positions and for tracing the use of isotopically distinct carbon sources through arctic food webs (Dunton and Schell 1987; Søreide et al. 2006; Tamelander et al. 2006). To do so, however, requires first correcting upper trophic level isotope values by both diet-tissue discrimination (i.e. Δ^{13}C and Δ^{15}N) and for temporal variability in stable isotopes at the base of the food web (Vander Zanden and Rasmussen 1999; Vander Zanden and Rasmussen 2001; Post 2002). Specifically in arctic seas, POM and macroalgae are known to change their isotopic signature by becoming more enriched and depleted, respectively, in winter compared to summer due to increased bacterial degradation in winter (Fig. S6.1). To overcome these issues, a one-source and a two-source model, respectively, were used to calculate relative trophic positions (TP) and relative reliance on pelagic carbon (α). Relative TPs were calculated for summer- and winter-sampled individuals using the mean δ^{15}N of the filter-feeding clam (*Mya eideri,* $\text{TP}_{\text{baseline}}$=2) from summer and winter, respectively (Table S6.1), as the baseline and 3.4‰ as the Δ^{15}N in the following equation:

$$TP_{consumer} = TP_{baseline} + \frac{\delta^{15}N_{consumer} - \delta^{15}N_{clam}}{\Delta^{15}N} \qquad \text{Eqn. 1}$$

To identify changes in horizontal food web structure, values of α were calculated using a modified two-source mixing equation (Post 2002; Vander Zanden and Vadeboncoeur 2002) that incorporates enrichment of consumer ^{13}C at each trophic step (i.e. Δ^{13}C) above the primary consumer baselines as follows:

$$\alpha = \frac{\delta^{13}C_{consumer} - [\Delta^{13}C \times (TP_{consumer} - 2)] - \delta^{13}C_{polychaete}}{\delta^{13}C_{clam} - \delta^{13}C_{polychaete}} \qquad \text{Eqn. 2}$$

$\Delta^{13}C$ was set at 0.8‰ (Dunton and Schell 1987; Fredriksen 2003), $TP_{consumer}$ is the result of the one source TP model for each individual (Eqn. 1) and 2 is the TP of the baselines. The filter-feeding clam and deposit-feeding polychaete (*Cistenides granulata*) were used as the two baselines for phytoplankton and benthic carbon, respectively. Thus, relative values of α represent % reliance on pelagic vs. benthic carbon. These species are appropriate baselines because they likely feed all year on available carbon and should therefore reflect changes in the isotopic signature of carbon between summer and winter, unlike other previously used baselines like *Calanus* (Hobson et al. 2002) that do not feed in the winter (Søreide et al. 2008).

RESULTS

Temporal resource variability

As expected, total particulate organic carbon (POC) flux was consistently higher in summer versus winter in all 6 arctic regions (Table S6.3). The seasonal variability observed for total POC was mirrored by trends in specific types of POC: phytoplankton, detritus and fecal pellets (Fig. 6.1). Total POC in summer was predominantly represented by fresh phytoplankton and zooplankton fecal pellets, whereas detritus dominated total POC in winter (Fig. 6.1). Fecal pellet flux tended to be higher in summer than winter (Table S6.3), but based on results presented by Forest et al. (2008), the proportion of degraded fecal pellets increased in winter (Fig. 6.1), indicating increased reliance on coprophagy. Macroalgae detritus is also thought to contribute substantially to the detrital pool and to act as an important resource to consumers during winter (Table S6.3, Dunton and Schell 1987).

Temporal changes in biomass

Herbivorous zooplankton declined in biomass from summer to winter, whereas a larger proportion of omnivorous and carnivorous zooplankton had higher abundance or biomass in the winter (vs herbivores, Fig. 6.2). For example, smaller copepods like omnivorous *Microcalanus pygmaeus* and *Pseudocalanus* sp., as well as copepod naupulii, were reported in higher numbers in winter than summer (Table S6.4). However, changes in zooplankton abundance and biomass are intricately linked to water currents (Søreide et al. 2003; Hop et al. 2006) and life history (e.g. the 'ontogenetic escalator' described by Conover 1988), such that declining biomass does not necessarily only represent mortality.

Abundance or biomass of deposit/filter feeding (DF/ FF) benthos also varied with seasonal changes in primary production because these species often, but not always, declined in abundance or biomass during the winter (Fig. 6.2). Upper trophic level benthos, which included omnivorous, carnivorous, scavenging (O/C/S) amphipods, on the other hand, commonly maintained biomass between seasons, but were also reported to increase or decrease during winter (Fig. 6.2, Table S6.4). The biomass of transient species like arctic char (*Salvelinus alpinus*) and capelin (*Mallosus villosus*) obviously declined in winter (Table S6.4). No data could be located regarding if and how resident species, like ringed seals, change in biomass or abundance between summer and winter. Resident arctic consumers like ringed seals produce and rear young in late winter (Lydersen and Gjertz 1986; Ferguson et al. 2005), so a decline in biomass would not be expected.

Seasonal diet switching by consumers

Compiled data from the literature indicated that diet switching between summer and winter in arctic consumers is variable within and between functional groups (Fig. 6.3, Table S6.5). Herbivorous zooplankton exhibited the most consistent response by switching from a phytoplankton diet in summer to relying on internal reserves in winter (Fig. 6.3). This is a well known mechanism of the genus *Calanus* (e.g. Falk-Petersen et al. 2009) which survive the winter by decreasing their respiration rate (Fig. 6.4) and relying on stored lipids. DF/FF benthos generally exhibited no change in diet with season, although reports of reliance on internal reserves or increased contribution of benthic or macroalgae carbon were found (Fig. 6.3, Table S6.5).

A greater range of diet changes between summer and winter was exhibited by omnivores and carnivores (Fig. 6.3). Not changing diet with season was commonly reported (i.e. ≥50%) in carnivorous zooplankton, O/C/S benthos and in fish, marine mammal and seabird consumers (Fig. 6.3). The observation that not all arctic species switch their diet with season is supported by the known response of some consumers, including certain amphipods (e.g. *Onisimus*), to maintain the same respiration rate through winter, unlike herbivorous copepods (Fig. 6.4). However, switching to a higher trophic position in winter was also reported for consumers and some O/C/S benthos (Fig. 6.3).

Data from Cumberland Sound allowed further exploration of seasonal diet switches and changes in overall food web structure (i.e. α vs TP). At the level of functional groups, two way ANOVAs revealed that season and the functional group*season interaction term was significant for $\delta^{15}N$ (Table 6.3). Based on Tukey's post hoc comparisons, carnivorous zooplankton, carnivorous benthos and pelagic consumers were the only functional groups to exhibit significantly higher $\delta^{15}N$ in winter than summer. At the species level, Welch's *t* tests and ANOVAs revealed that $\delta^{15}N$ was significantly different between summer and winter for clam (DF/FF benthos), whelk (*Buccinum cyaneum,* O/C/S benthos), sculpin (fish consumer) and ringed seal (marine mammal consumer), and that $\delta^{13}C$ significantly differed in the wandering anemone (unknown species, O/C/S benthos) and sculpin (Table S6.1, Fig. 6.5). Based on calculated values of relative TP and α, anemone, jellyfish (*Aglantha digitale,* O/C zooplankton), whelk and ringed seal fed at a higher trophic position, and anemone, whelk and sculpin fed on higher amounts of benthic carbon in winter vs summer (Table S6.1). Higher POM $\delta^{15}N$ in winter vs summer and more similar seasonal values of macroalgae $\delta^{15}N$ (Fig. S6.1) corresponded to significantly higher $\delta^{15}N$ in clam and similar values in polychaete between winter and summer (Table S6.1, Fig. 6.5). This result supports the contention that clams consume pelagic carbon and polychaetes consume macroalgae and/or benthic carbon year round and incorporate the signature of available carbon during summer (fresher material) and winter (more degraded material).

Fatty acids supported stable isotope results from Cumberland Sound (Table S6.2). For example, *C. hyperboreus* exhibited higher 20:1n-9 and other MUFA (e.g. 18:1n-9) and lower PUFA like 20:5n-3 in winter (Table S6.2, Fig. 6.6), which reflects the selective retention and catabolism of certain FA during overwintering (Chapter 2, Lee 1974; McMeans et al. 2012). Based on the NMDS of primary producers and zooplankton, FA profiles of whelk in winter separated from summer due to higher carnivory markers in the former (Fig. S6.2), supporting their higher calculated TP (Table S6.1). Higher ARA (Table S6.2) in winter sculpin supported higher α (Table S6.1) in indicating that winter sculpin relied more heavily on benthic carbon (Table 6.4). Combined, stable isotope and fatty acid results revealed that 50% of Cumberland Sound species sampled exhibited a seasonal diet switch, and that the specific responses of consumer diets between seasons were variable within all functional groups except for carnivorous zooplankton (Table 6.4).

Food web structure

The overall structure of the Cumberland Sound food web (i.e. α vs TP) differed between summer and winter with a shift in structure that was driven by increases in TP and decreases in α (i.e. greater reliance on benthic sources in winter) by several species (Fig. 6.7). Based on results of the literature review and data from Cumberland Sound, a conceptual model of changes in arctic food webs between summer and winter was generated, which aims to capture temporal resource asynchrony, biomass changes and associated changes in consumer diet (Fig. 6.7) in the context of their importance for food web persistence (based on food web theory, McCann 2005). General roles of functional groups in arctic food webs were assigned to illustrate the *potential* function of species belonging to a given function group. Assigning one function or behaviour to an entire functional group is clearly an oversimplification given that seasonal changes in species' biomass (Fig. 6.2) and diet (Fig. 6.3) were variable within functional groups. Illustrated linkages among species are also oversimplified because most species would consume prey from multiple functional groups and because links to the detrital sediment 'food bank' would almost certainly be higher (Mincks et al. 2005). However, this model (Fig. 6.7) is useful for considering observed patterns in arctic food webs in the context of food web theory.

DISCUSSION

Relating empirical patterns with predictions from food web theory

Evidence for both temporal resource asynchrony and consumer coupling of resources in time were found in the present study. Results presented here therefore provide empirical support for the hypothesis that, in a similar manner to spatial coupling (Rooney et al. 2006), the coupling of temporally asynchronous resources is important for the maintenance of food web complexity (Carnicer et al. 2008) and food web persistence (McCann et al. 2005). The existence of multiple, temporally asynchronous resources could promote the persistence of food webs by providing consumers with a stable resource base during both productive and non productive times (Polis et al. 1996). Consumer switching behaviour would allow declining resources to recover, further promoting food web persistence (McCann et al. 2005). Combined, the above mechanisms would impart a flexible nature to food webs and increase their ability to respond in the face of perturbations (Levin 1998).

Temporal resource asynchrony existed in arctic seas because phytoplankton production and herbivore biomass peaked in the summer, and several species of O/C/S zooplankton and amphipods, young stages of herbivorous zooplankton, and benthos peaked during winter months. Higher $\delta^{15}N$ in filter-feeding clams from Cumberland Sound and lower $\delta^{13}C$ in the deposit-feeding polychaete in winter indicate that phytoplankton and macroalgae were consumed as detritus or more refractory forms in winter than summer, supporting previous contentions that arctic food webs are driven by detritus in the winter (Forest et al. 2008). Consumers exploited the abundant phytoplankton growth or the large numbers of herbivorous zooplankton during the summer, and switched to more refractory carbon, higher TPs, or greater amounts of benthic carbon when summer resources became scarce in the winter (Fig. 6.7). This coupling-decoupling of different resource compartments is precisely the structure that is predicted by food web theory to impart persistence (McCann et al. 2005). To the best of my knowledge, this is the first time that the temporal characteristics of arctic marine food webs have been discussed in the context of recent food web theory.

The persistence-promoting mechanisms that arise from both spatial and temporal coupling of asynchronous resources are similar (McCann et al. 2005; Rooney et al. 2006), but the mechanisms *generating* resource asynchrony could differ. Consumer selection of specific resources is an important, top-down mechanism that drives resource asynchrony in spatial landscapes (Rooney et al. 2006; McCann and Rooney 2009). On the other hand, changing levels of sunlight and nutrients (i.e. bottom-up factors) would be the primary drivers of temporal resource asynchrony (e.g. timing of tree fruiting, Carnicer et al. 2008). Interestingly, bottom-up processes are likely important for the generation of both spatial and temporal resource asynchrony in arctic or other highly seasonal environments, because, even within the productive period, the pulsed nature of primary production is the primary driver of differences in availability of resources in both space (Chapter 3) and time (this study). In this way, the mechanisms generating spatial and temporal resource asynchrony could differ between arctic and temperate or tropical locations.

The observation that about 50% of Cumberland Sound species sampled exhibited a seasonal diet switch and that this response varied within and between functional groups is consistent with the results of data compiled from the literature. For example, both amphipods and whelk had higher 20:1n-9 and lower 20:5n-3 in the winter (Fig. 6.6), which, based on their known opportunistic and scavenging behaviour (Table 6.1), could indicate increased consumption of detritus (low in PUFAs like 20:5n-3, Søreide et al. 2008), or increased scavenging of *Calanus* copepods or consumers of *Calanus* (i.e. high 20:1n-9). The slightly higher TP and 20:1n-9 proportions (Fig. 6.6) of winter Cumberland Sound ringed seals supports previous reports that this species switches its diet from zooplankton and amphipods in the summer to fish like polar cod (*Boreogadus saida*) in the winter (Table 6.4), which are high in 20:1n-9 (Dahl et al. 2000). The varied responses of arctic species to environmental variability could be an important mechanism promoting species coexistence (Abrams 2006; Carnicer et al. 2008), which is an interesting avenue for future research.

The Cumberland Sound data additionally revealed how the shape of an arctic food web (i.e. TP vs α) can shift between summer and winter. Because the top predator, the Greenland shark, did not exhibit a seasonal diet switch, the vertical height of the food web (food chain length) did not differ between seasons. However, increased TPs and decreased values of α for several consumers did result in a shift in the overall shape of the food web (Fig. 6.7). The ubiquity of such shifts in food web structure with time remain to be explored, but likely exists in more temperate oceans as well. For example, using network analysis, Johnson et al. (2009) found that the Chesapeake Bay food web switched from pelagic-dominated in the summer to more detritus and benthic dominated in the winter, which agrees with results from the present study (i.e. from Cumberland Sound) and in previous arctic studies (Dunton and Schell 1987; Forest et al. 2008).

Implications for climate change

Based on food web theory, the removal of spatial or temporal resource asynchrony would leave consumers nothing to respond to, via coupling and decoupling, removing the mechanism thought to promote persistence and resulting in an essentially unstructured food web (McCann et al. 2005; Rooney et al. 2008). Global climate change is a threat to resource asynchrony in arctic seas because predicted consequences include a switch from highly pulsed, intense phytoplankton production driven by diatoms (high quality) to more prolonged, less pulsed phytoplankton production driven by smaller (lower quality) flagellates (Weslawski et al. 2011). The increased constancy and decreased quality of phytoplankton growth (Weslawski et al. 2011) is thought to result in community level changes, whereby communities dominated by the larger, more lipid-rich *C. glacialis* and *C. hyperboreus* are replaced by smaller *C. finmarchicus*, which would be a lower quality food for consumers (Falk-Petersen et al. 2007). Decreases in benthic biomass are also a predicted scenario, due to the potential for diminished benthic-pelagic coupling (Weslawski et al. 2011). Such changes could decrease temporal asynchrony by removing the benthos as an alternative resource for consumers, and replacing the summer 'bloom' of *Calanus* production with a more temporally stable, lower quality resource base (i.e. *C. finmarchicus*) for consumers.

In conclusion, arctic food webs are structured such that temporally asynchronous resources are coupled by consumers, which is consistent with predictions from food web theory (McCann et al. 2005; Rooney et al. 2006). Viewing the seasonal changes in arctic food webs through the lens of recent food web theory, any action that promotes resource synchrony would be detrimental to arctic food webs. Future work is tasked with incorporating more subtle differences in species-specific resource use between seasons into the more general framework developed here. However, based on the present study's results, the coupling of resource compartments, as previously described in space (Rooney et al. 2006), also occurs in time. Therefore, the potential for food webs to be structured on a temporal axis is likely an additional structure that promotes their persistence (McCann et al. 2005), at least in seasonal environments like the arctic.

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Table 6.1. Species sampled from Cumberland Sound, Nunavut during summer (August) and winter (April) and putative diet information.

Functional Group	Species	Diet	Reference
Zooplankton			
Herbivorous	*Calanus hyperboreus*	phytoplankton	Søreide et al. 2008
	Mysis sp.	phytoplankton and macroalgae	Dunton and Schell 1987
O/C	*Aglantha digitale*	copepods, fecal pellets, detritus, dinoflagellates, ciliates	Pages et al. 1996
	Sagitta sp.	copepods	Pearre 1973
Benthos			
DF/FF	*Cistenides granulata*	deposit feeder	Fauchald and Jumars 1979
	Mya eideri	filter feeder	Shumway et al. 1985[2]
O/C/S	Wandering anemone	unknown but likely carnivorous	
	Buccinum cyaneum	polychaetes, bivalves, carrion	Himmelman and Hamel 1993
	Amphipods (likely *Onisimus* sp.)	algae, zooplankton carrion	Werner and Auel 2005
Consumers			
	Somniosus microcephalus	*P. hispida, R. hippoglossoides, M. scorpius*	McMeans, unpub. data[1]
	Amblyraja hyperborea	*Lebbeus polaris*	McMeans, unpub. data
	Myoxocephalus scorpius	isopods, *Mysis*, polychaetes	McMeans, unpub. data, Cardinale 2000
	Pusa hispida	themisto, fish	McMeans, unpub. data

Table 6.2. Indicator fatty acids used to investigate seasonal diet changes in Cumberland Sound biota.

Fatty acid	Diet indication	References
16:1n-7	high in phytoplankton or phytoplankton-consuming prey	1, 2
18:1n-9	high in carnivores	3, 4, 5
20:1n-9	high in *Calanus* copepods and consumers of *Calanus*	2, 3, 6
20:4n-6	high in macroalgae or macroalgae-reliant prey	7
20:5n-3	high in phytoplankton or phytoplankton-consuming prey, low in detritus	1, 2, 5
22:6n-3	high in phytoplankton or phytoplankton-consuming prey	1, 2, 5

1. Graeve et al. 1994, 2. Kattner et al. 1989, 3. Sargent and Falk-Petersen 1981, 4. Sargent and Falk-Petersen 1988, 5. Søreide et al. 2008, 6. Graeve et al. 2005, 7. Kharlamenko et al. 1995

Table 6.3. Results of two-way ANOVAs investigating the effects of functional group (Table 1) and season (summer vs winter) on $\delta^{13}C$ and $\delta^{15}N$ of Cumberland Sound species.

$\delta^{13}C$	df	Sum Sq	Mean Sq	*F* value	*P*
Fun.group	6	215.70	35.95	39.27	< 0.001
Season	1	1.01	1.01	1.10	0.30
Fun.group*Season	6	11.49	1.92	2.09	0.06
Residuals	170	155.61	0.92		

$\delta^{15}N$	df	Sum Sq	Mean Sq	*F* value	*P*
Fun.group	6	1709.01	284.84	379.80	<0.001
Season	1	55.13	55.13	73.51	0.00
Fun.group*Season	6	30.78	5.13	6.84	0.00
Residuals	170	127.49	0.75		

Table 6.4. Seasonal changes in diet between summer and winter in Cumberland Sound biota based on stable isotope (SI: δ^{15}N, δ^{13}C) and fatty acid (FA) evidence.

Fun. Group	Species	Change	How	Evidence
Zooplankton				
Herbivorous	*Calanus hyperboreus*	Yes	phytoplankton in summer, internal reserves in winter	no consistent seasonal differences in SI, higher phytoplankton FA in summer
	Mysis sp.	Yes	consumption of non-phytoplankton food in winter	separation on NMDS due to higher 20:1n9 and lower 20:4n-6 and 22:6n-3 in winter
O/C	*Aglantha digitale*	No	omnivorous/ carnivorous all year	similar TP and α between summer and winter
	Sagitta sp.	No	carnivorous all year	similar δ^{13}C and δ^{15}N, TP and between seasons
Benthos				
DF/FF	*Mya eideri*	Yes	increased reliance on re-worked carbon	significantly higher δ^{15}N
	Cistenides granulata	No	selectively feeds on similar particles year-round	no significant difference in δ^{15}N or δ^{13}C
O/C/S	Wandering anemone	Yes	increased benthic carbon usage	significantly higher δ^{13}C and higher α in winter
	Amphipods (*Onisimus* spp.)	No	generally similar, perhaps more scavenging in winter	no separation on NMDS, although 20:1n-9 was higher in winter
	Buccinum cyaneum	Yes	increased TP	significantly higher δ^{15}N, higher TP and higher 20:1n-9, 18:1n-9 and lower ARA, EPA, DHA in winter
Consumer	*Somniosus microcephalus*	No	likely opportunistic all year	no consistent differences in SI of FA between summer and winter
	Amblyraja hyperborea	No	too few summer data to speculate, but differences warrant further attention	*n*=1 in summer but had higher 18:1n9, 20:1n9 and lower 20:5n-3 in winter vs summer
	Myoxocephalus scorpius	Yes	increased benthic feeding	Significantly higher δ^{13}C,α, 18:1n-9, 20:1n-9 and higher contribution of polychaetes to stomachs in winter[1]
	Pusa hispida	Yes	increased TP	Not always significant, but higher δ^{15}N in winter, slightly higher TP and higher 20:1n9, EPA, DHA in winter

1. B. McMeans, unpublished data; NMDS: non metric multidimensional scaling, used to assess differences in fatty acids among species (Fig. S6.2); TP: δ^{15}N-derived relative trophic positions; α: δ^{13}C-derived reliance on pelagic carbon

Fig. 6.1. Particulate organic carbon flux (POC, mg C m^{-2} d^{-1}) from Forest et al. 2008 sampled in Franklin Bay, Beaufort Sea during summer (light bars) and late winter (March, dark bars). Inset shows % of degraded fecal pellet flux. Redrawn from Forest et al. 2008.

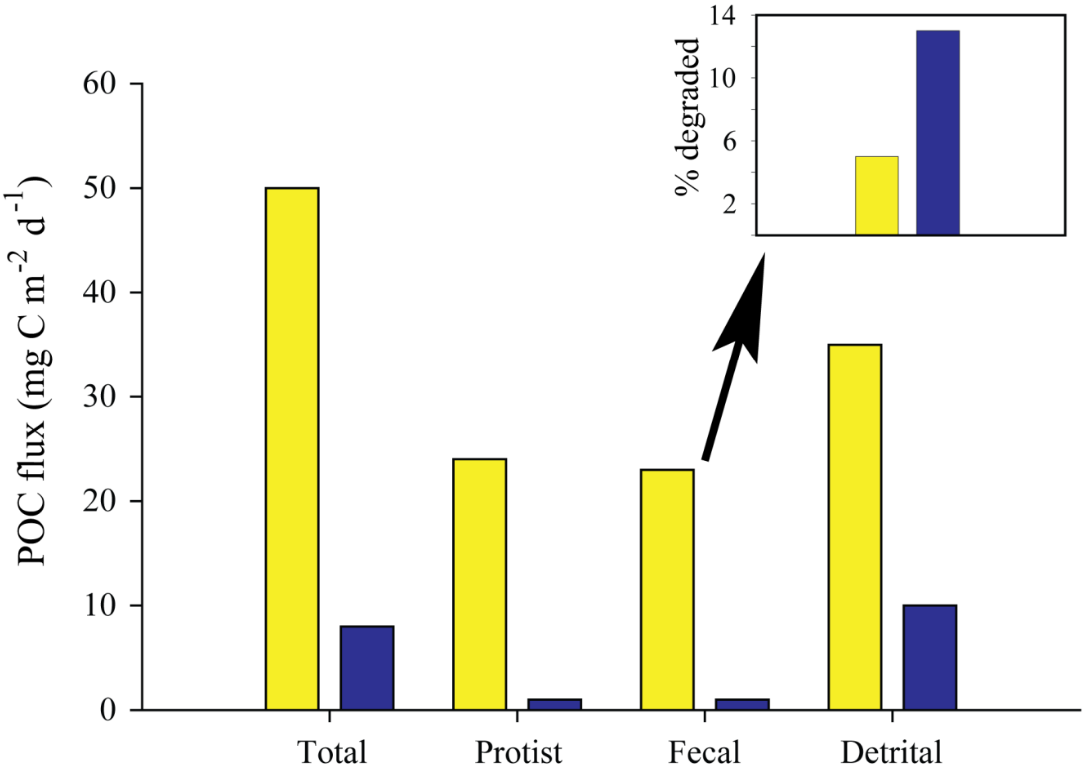


Fig. 6.2. Differences in abundance/ biomass between summer and winter among functional groups sampled from various regions throughout the arctic (number of studies summarized in parentheses, Table S6.4). Piece representing 'no change' is offset.

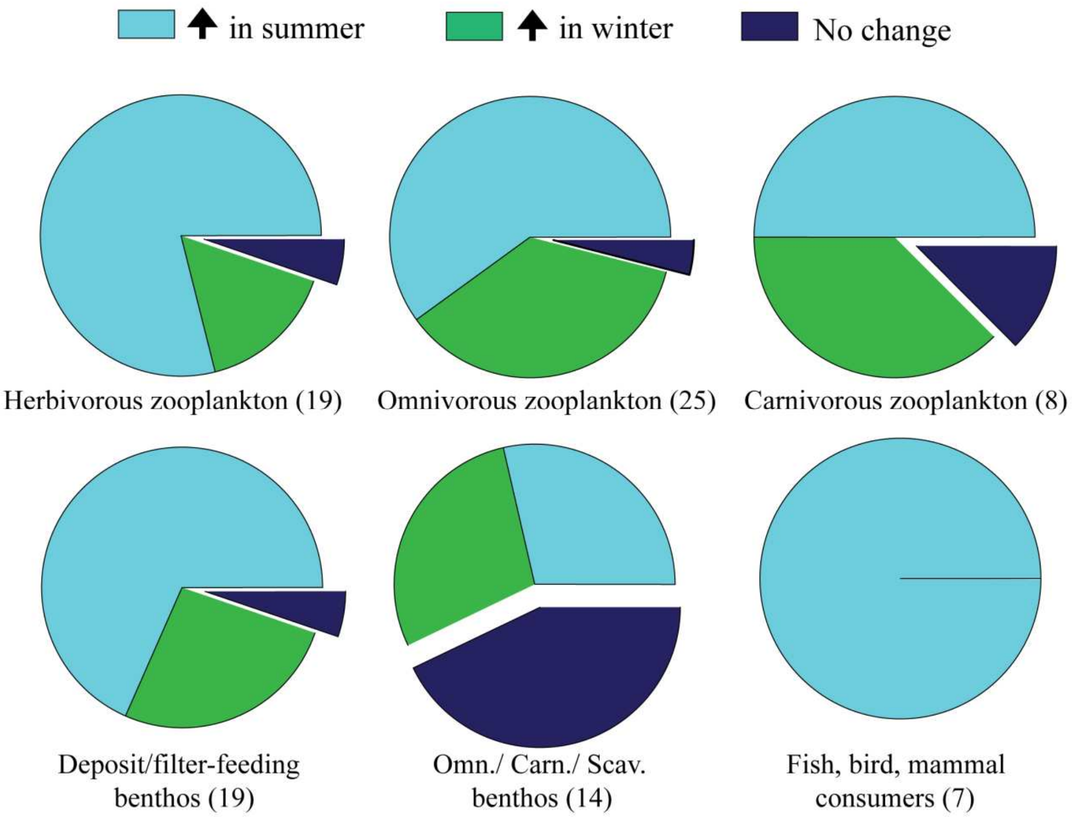
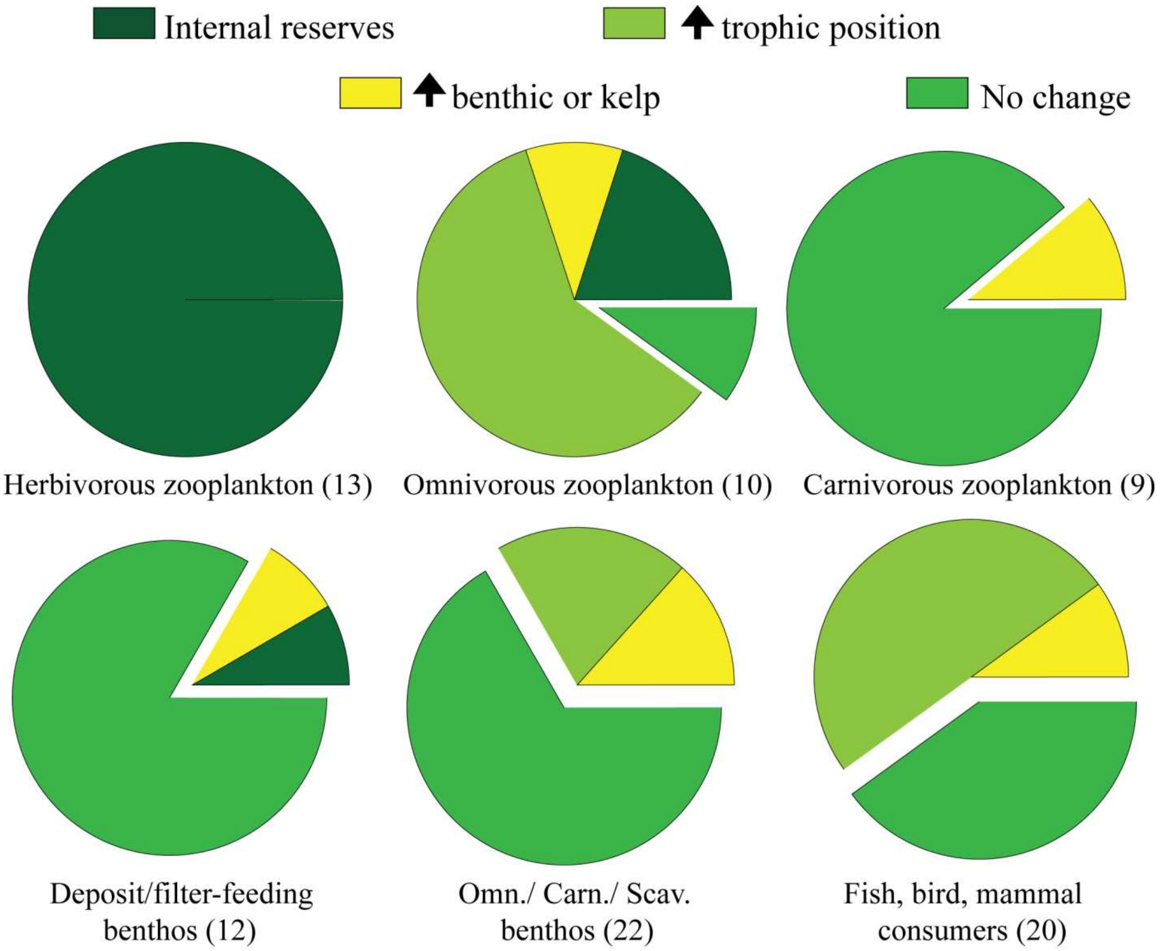


Fig. 6.3. Changes in diet from summer to winter in arctic animals (number of studies summarized in parenthesis, Table S6.5). Piece representing 'no change' is offset.



Herbivorous zooplankton (13)

Omnivorous zooplankton (10)

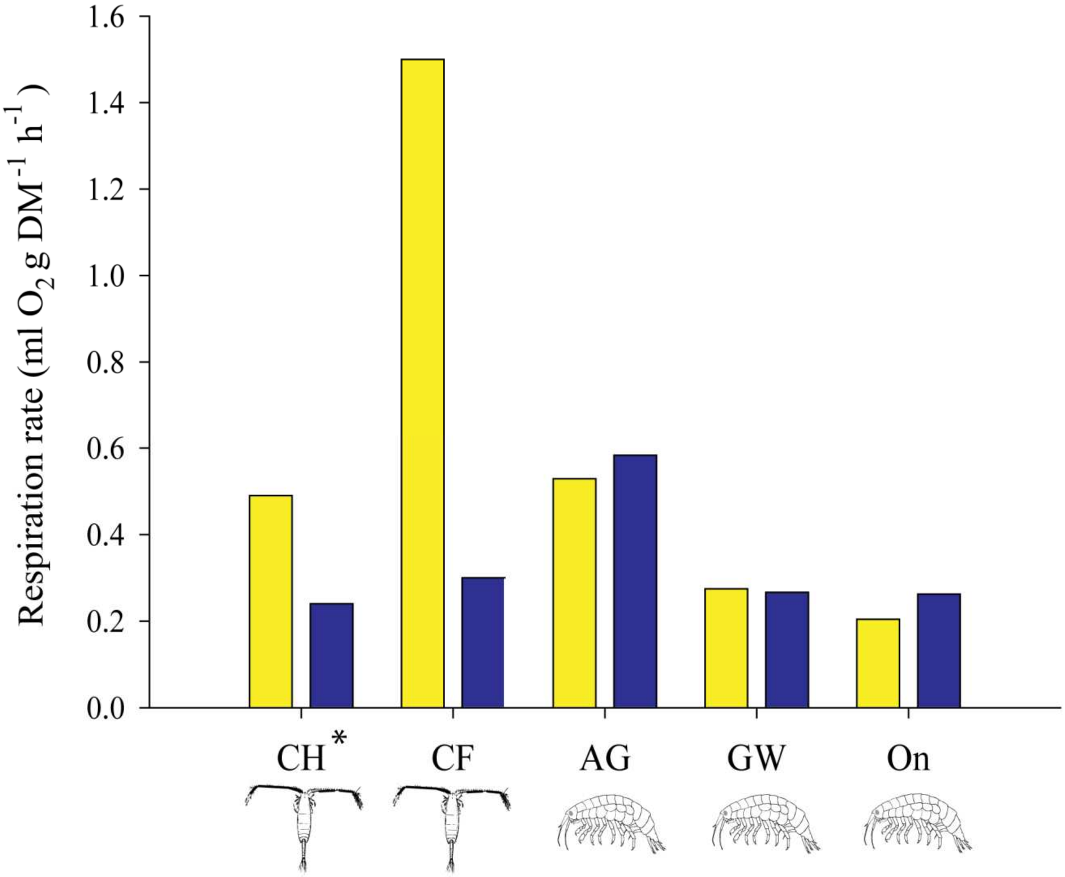
Carnivorous zooplankton (9)

Deposit/filter-feeding benthos (12)

Omn./ Carn./ Scav. benthos (22)

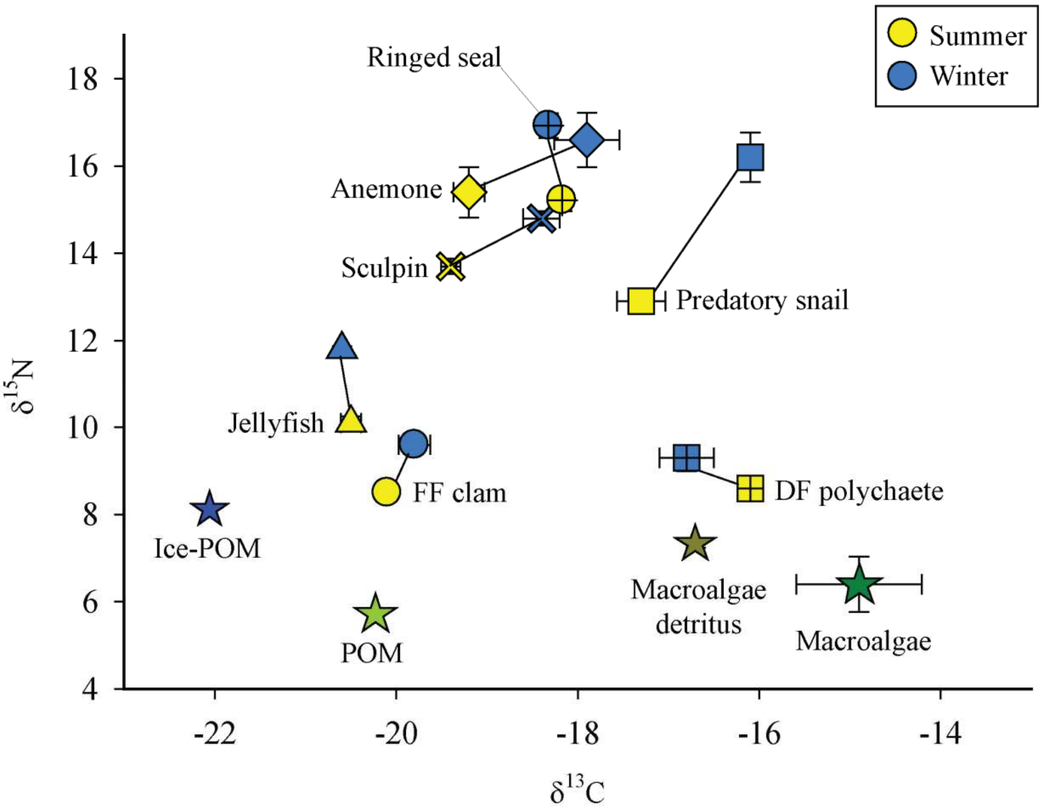
Fish, bird, mammal consumers (20)

Fig. 6.4. Respiration rates for two copepods and three amphipods sampled during summer (light bars) and winter (dark bars) in various arctic regions.



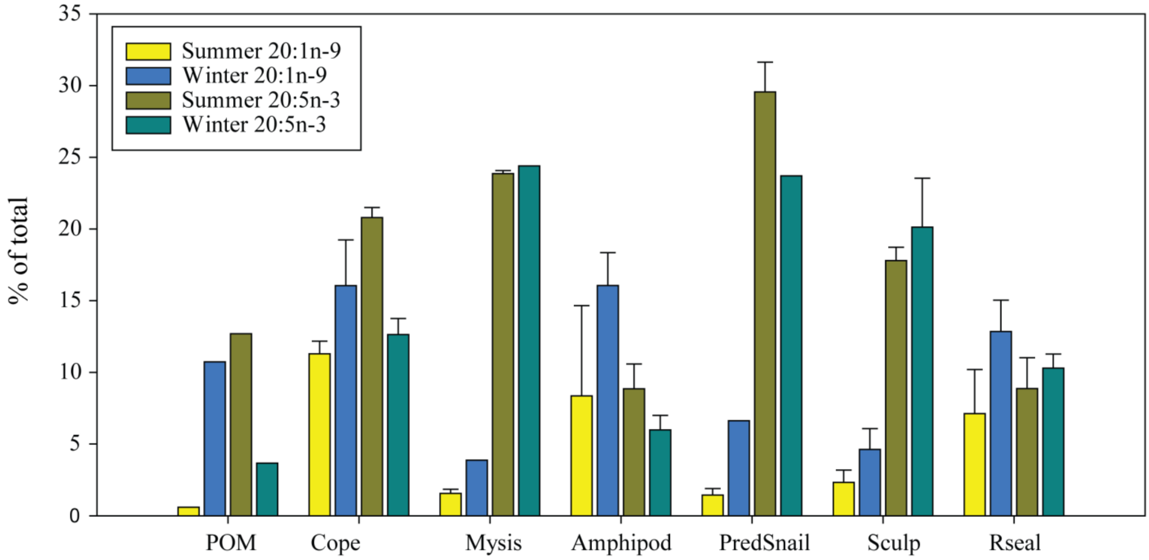
CH*: *Calanus hyperboreus*, both samples were collected during summer, data provided for 'winter' were inactive samples collected in deep water, Auel et al. 2003; CF: *Calanus finmarchicus*, Hirche et al. 1983; AG: *Apherusa glacialis*, GW: *Gammarus wilkitzkii*, On: *Onisimus* spp., Wener and Auel 2005

Fig. 6.5. Mean±SE of stable nitrogen ($\delta^{15}N$) and carbon isotopes ($\delta^{13}C$, both ‰) for selected species sampled in Cumberland Sound, Canada during summer (August) and winter (April, see Table S6.1 for significant differences and full list of species sampled). Summer and winter samples were collected in August 2008 and April 2009, respectively, with the exception of anemone (August 2007 and April 2008), ringed seal (April 2008 and August 2008), DF polychaete and sculpin (both April 2009 and August 2009).



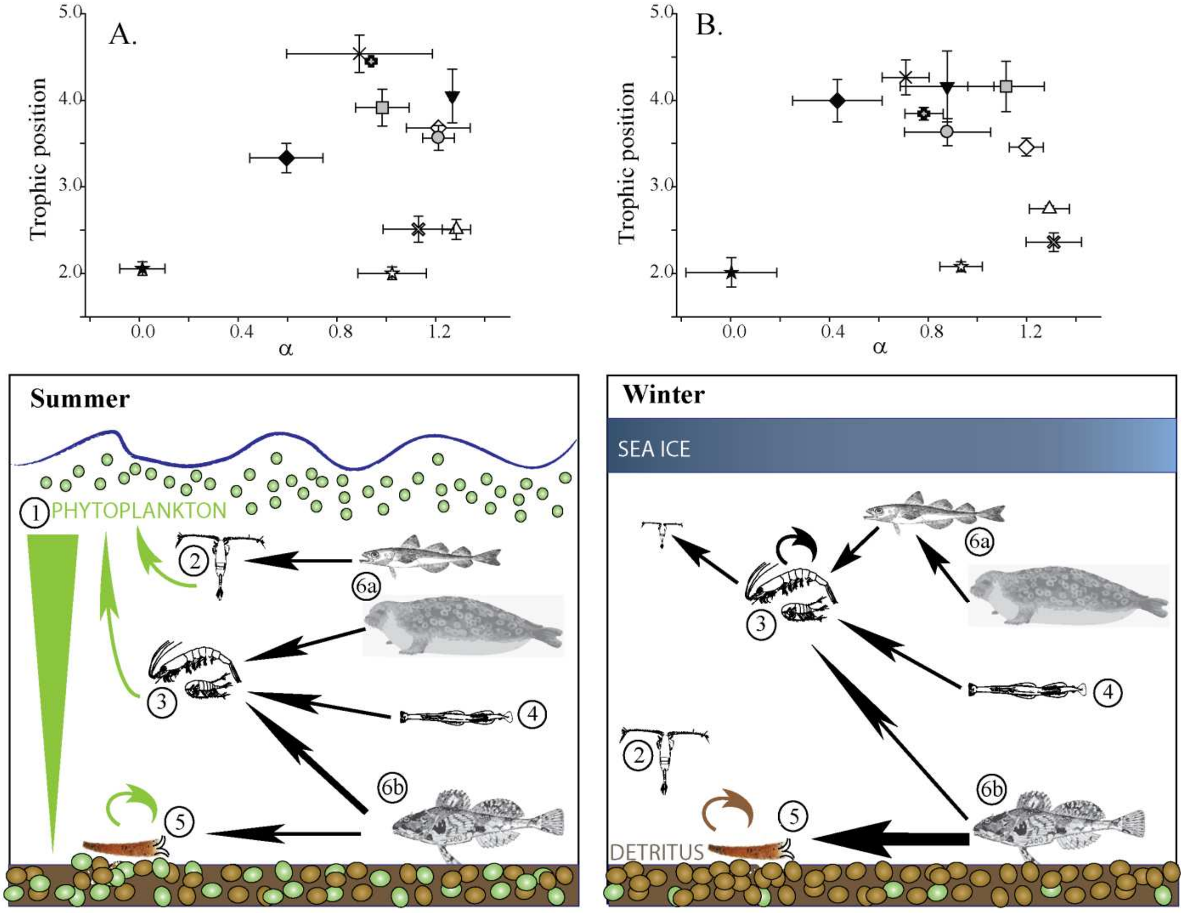
Macroalgae: *Fucus distichus*., DF polychaete: *Cistenides granulata*, FF clam: *Mya eideri*, Jellyfish: *Aglantha digitale*, Predatory snail: *Buccinum cyaneum*, Anemone: unknown species, Sculpin: *Myoxocephalus scorpius*, Ringed seal: *Pusa hispida*

Fig. 6.6. Mean±SD of 20:1n-9 and 20:5n-3 in select Cumberland Sound species between summer (August) and winter (April). Summer and winter samples were collected in August 2008 and April 2009, respectively, with the exception of ringed seal (April 2008 and August 2008), Mysis and sculpin (both April 2009 and August 2009).



Cope: Calanus hyperboreus, Mysis: Mysis sp., Amphipod: likely Onisimus sp., Predatory snail: Buccinum cyaneum, Sculpin: Myoxocephalus scorpius, Ringed seal: Pusa hispida

Fig. 6.7. Cumberland Sound food web structure (% reliance on pelagic carbon (α) vs δ^{15}N-derived trophic position) between summer (A) and winter (B) and conceptual model of temporal changes in arctic food webs (lower panels). Arrows represent use of phytoplankton (green), detritus (brown) or carnivory (black).



①**Temporal resource variability**- high phytoplankton production in summer, minimal in winter ②**Herbivorous zooplankton** - peak biomass in summer; *decouple from phytoplankton in winter* (cease feeding, descend to depth) & *decreased biomass* ③**Omnivorous zooplankton & amphipods** - can act as *temporal couplers* by switching from phytoplankton in summer to zooplankton (including naupulii) in winter, *can maintain or increase biomass in winter* ④**Carnivorous zooplankton** - feed on zooplankton all year, no temporal coupling ⑤**Deposit/filter feeding benthos** - can act as *temporal couplers* of fresh and refractory carbon & *can maintain biomass through winter* ⑥**Consumers** - can act as *temporal couplers* by exploiting abundant zooplankton in summer and switching to higher trophic position (a) or increasing consumption of benthos (b) in winter

SUPPLEMENTARY MATERIAL

Table S6.1. Mean ± SD of δ^{13}C, δ^{15}N, δ^{13}C-derived relative % reliance on pelagic carbon (α), δ^{15}N-derived relative trophic positions (TP) and total length of species sampled from Cumberland Sound, Nunavut during summer (August, S) and winter (winter, W) of 2007-2010. When samples size was ≥3, species' δ^{13}C and δ^{15}N values were compared between summer and winter via Welch's t test (2 groups) or ANOVA (≥3 groups). Results are provided under 'test' columns and similar values share the same letter. Dash (-) indicates not calculated or not reported.

Functional Group	Species name	Tissue	Date	*n*	δ^{13}C (‰)	δ^{13}C test	δ^{15}N (‰)	δ^{15}N test	α	TP	Total length (cm)
Basal											
	POM	Whole	S '08	1	-22.1	-	8.2	-	-	-	-
	IcePOM	Whole	W '08	1	-20.3	-	5.6	-	-	-	-
	Macroalgae (*Fucus distichus*)	Leaf	S '08	3	-14.9 ± 1.2	-	6.4 ± 1.1	-	-	-	-
			S '09	3	-15.1 ± 1.8	-	7.5 ± 1.3	-	-	-	-
	Macroalgae detritus	Leaf	W '09	3	-16.7 ± 0	-	7.3 ± 0.1	-	-	-	-
Zooplankton											
Herbivorous	*Calanus hyperboreus*	Whole	S '07	7	-19.4 ± 0.4	a ☺	10.4 ± 0.4	a	1.0 ± 0.1	2.6 ± 0.1	-
			W '08	2	-20.8 ± 0	-	10.4 ± 0.1	-	1.3 ± 0	2.3 ± 0	-
			S '08	5	-20.4 ± 0.1	b☺	9.9 ± 0.5	a	1.2 ± 0	2.4 ± 0.2	-
			W '09	8	-20.7 ± 0.5	b☺	10.5 ± 0.4	a	1.3 ± 0.1	2.4 ± 0.1	-
	Mysis sp.	Whole	S '09	5	-20.8 ± 0.1	-	9 ± 0.1	-	1.3 ± 0	2.2 ± 0	-
Carnivorous	*Aglantha digitale*	Whole	W '08	2	-20.2 ± 0.2	-	11.8 ± 0.2	-	1.2 ± 0.1	2.7 ± 0.1	-
			S '08	7	-20.5 ± 0.3	-	10.1 ± 0.4	-	1.3 ± 0.1	2.5 ± 0.1	-
			W '09	2	-20.6 ± 0	-	11.8 ± 0.1	-	1.4 ± 0	2.7 ± 0	-
	Sagitta sp.	Whole	W '08	3	-19.4 ± 0.2	-	14.5 ± 0.2	-	1.2 ± 0.1	3.5 ± 0.1	-
			S '08	2	-19.3 ± 0.5	-	14.1 ± 0	-	1.2 ± 0.1	3.7 ± 0	-
			W '09	3	-19.7 ± 0.2	-	14 ± 0.1	-	1.2 ± 0.1	3.4 ± 0	-
Benthos											
DF/FF	*Mya eideri*	Mantle	S '07	5	-19.5 ± 0.4	a	8.3 ± 0.1	a ♪	0.9 ± 0.1	2.0 ± 0.1	-
			S '08	6	-20.1 ± 0.2	a	8.5 ± 0.3	a ♪	1.1 ± 0.1	2.0 ± 0.1	-

			W '09	3	-19.8 ± 0.3	a	9.6 ± 0.2	b ♪	0.9 ± 0.1	2.1 ± 0.1	-
			S '09	1	-20.9	-	8.5	-	1.3 ± 0	2.0 ± 0.0	-
	Cistenides granulata	Whole	W '09	4	-16.8 ± 0.6	a	9.3 ± 0.6	a	0.0 ± 0.2	2.0 ± 0.2	-
			S '09	10	-16.1 ± 0.4	a	8.6 ± 0.3	a	0.0 ± 0.1	2.1 ± 0.1	-
O/C/S	Wandering anemone	Soft	S '07	3	-19.2 ± 0.3	a ♣	15.4 ± 1	a	1.3 ± 0	4.0 ± 0.3	-
			W '08	5	-17.9 ± 0.8	b ♣	16.6 ± 1.4	a	0.9 ± 0.2	4.2 ± 0.4	-
	Buccinum cyaneum	Foot	W '08	5	-16.8 ± 0.7	a	16 ± 0.9	a ☼	0.5 ± 0.2	4 ± 0.3	5.1 ± 1.8
			S '08	5	-17.3 ± 0.6	a	12.9 ± 0.6	b ☼	0.6 ± 0.1	3.3 ± 0.2	4.4 ± 0.9
			W '09	2	-16.1 ± 0.2	a	16.2 ± 0.8	-	0.3 ± 0.1	4 ± 0.2	4.4 ± 0.1
Consumers											
	Somniosus microcephalus	Plasma	W '08	10	-17.4 ± 0.3	a ♥	17.2 ± 0.7	a	0.7 ± 0.1	4.3 ± 0.2	266.1 ± 20.8
			S '08	8	-17 ± 0.3	b ♥	17.1 ± 0.7	a	0.8 ± 0.1	4.6 ± 0.2	286.8 ± 27.3
			W '09	17	-17.3 ± 0.2	a,b ♥	16.9 ± 0.7	a	0.7 ± 0.1	4.2 ± 0.2	266.2 ± 30.7
			S '09	7	-17.9 ± 1.3	a,b ♥	16.9 ± 0.9	a	1.0 ± 0.4	4.5 ± 0.3	292.4 ± 17
	Amblyraja hyperborea	Liver	S '07	1	-17.6	-	16.7	-	0.9	4.4	53
			W '09	6	-17.9 ± 0.3	-	15.6 ± 0.2	-	0.8 ± 0.1	3.8 ± 0.1	57.5 ± 5.7
	Myoxocephalus scorpius	Muscle	W '09	9	-18.4 ± 0.6	a ♦	14.8 ± 0.5	a ◘	0.9 ± 0.2	3.6 ± 0.2	20.8 ± 1.4
			S '09	8	-19.4 ± 0.3	b ♦	13.7 ± 0.5	b ◘	1.2 ± 0.1	3.6 ± 0.1	21.2 ± 1.7
	Pusa hispida	Liver	S '07	3	-18 ± 0	a ♯	14.6 ± 0.4	a ☻	0.9 ± 0.1	3.8 ± 0.1	109.7 ± 3.5
			W '08	4	-18.3 ± 0.2	a ♯	16.9 ± 0.6	b ☻	1.0 ± 0.1	4.2 ± 0.2	-
			S '08	7	-18.2 ± 0.2	a ♯	15.2 ± 0.7	a ☻	1.0 ± 0.1	4 ± 0.2	104.3 ± 16.8
			S '09	6	-18.4 ± 0.4	a ♯	14.7 ± 0.8	a ☻	1.0 ± 0.1	3.8 ± 0.2	111.8 ± 15.1
			W '10	5	-19 ± 0.3	b ♯	16.4 ± 1.2	a ☻	1.2 ± 0.2	4.1 ± 0.4	116.8 ± 14.9

Results from Welch's t tests and ANOVA: ☺$F_{2,15}$=18.62, P<0.001, ♣ t= -3.126, df=5.3, P<0.03, ♥ $F_{3,37}$=3.449, P<0.03, ♦ t=4.104, df=12.41, P<0.002, ♯ $F_{4,20}$=7.055, P<0.001, ♪ $F_{2,11}$=26.64, P<0.0001), ☼ t=6.375, df=6.76, P<0.001, ◘ t=4.578, df=14.95, P<0.001, ☻ $F_{4,20}$=7.038, P<0.001; Relative values of TP were calculated using *M. eideri* as a baseline, and *M. eideri* and *C. granulata* were used as the two endpoints in a two-source mixing model to calculate values of α (see text for details)

Table S6.2. Mean ± SD of indicator fatty acids (reported as relative proportions, %) from Cumberland Sound species sampled during summer (S, August) and winter (W, April) of 2007-2010.

Functional group	Species	Tissue	Date	*n*	16:1n-7	18:1n-9	20:1n-9	20:4n-6	20:5n-3	22:6n-3
Basal	POM[1]	Whole		1	15.5	5.1	0.6	0.4	12.7	8.5
	Fucus sp.	Leaf	S '08	3	1.9±1	10.3±8.9	0.7±0.5	9.9±3.6	8.4±3	0.5±0.4
	Ice POM	Whole	W '09	1	6.8	12.8	10.7	1.2	3.7	3.1
Zooplankton										
Herbivorou	*Calanus hyperboreus*	Whole	S '07	5	16.6±1.3	2.4±0.4	10.5±2.4	0.2±0.1	16.9±2.3	9.3±0.6
			W '08	2	22.9±0.7	5.9±3	17.3±1.9	0.1±0	10.7±1	8.4±0.4
			S '08	5	17.3±0.7	3.9±0.3	11.3±0.9	0.2±0	20.8±0.7	8.9±1
			W '09	5	17.8±0.7	7.6±4	16.1±3.2	0.2±0	12.6±1.1	10.5±0.8
	Mysis sp.	Whole	W '09	1	18.6	9.8	3.9	0.4	24.4	8.9
			S '09	5	3.8±1.2	9.6±0.3	1.6±0.3	1.2±0.1	23.9±0.2	24.1±1.8
Benthos										
O/C/S	amphipods (*Onisimus* sp.)	Whole	S '08	5	12.6±1.7	24.2±6.5	8.4±6.3	1.0±0.3	8.9±1.7	9.9±2.3
			W '09	5	9.4±0.7	20.1±2.0	16.1±2.3	0.7±0.2	6.0±1	4.6±0.6
	Buccinum cyaneum	Foot	S '08	7	1.1±0.3	4.1±0.3	1.4±0.5	4.6±0.9	29.6±2.1	9.6±1.3
			W '09	1	1.9	7.8	6.6	2.5	23.7	8.2
Consumer										
	Somniosus microcephalus	Plasma	W '08	12	4.3±1	15.3±2.1	16.4±3.4	2.4±0.7	9.1±1.8	10.6±2.1
			S '08	8	4.5±1.9	16.1±1.6	16.9±2.1	2±0.5	8.1±1.7	11.3±2
			W '09	17	3.6±1.1	15.1±1.5	16.2±2	3±0.9	10.7±1.9	12.7±2.3
			S '09	7	4.9±2.5	15±1.9	14.6±2.1	2.5±0.8	10.2±1.1	13.3±1.1
	Amblyraja hyperborea	Liver	S '07	1	10.3	12.3	13.1	0.9	9	10.5
			W '09	12	10.1±0.9	13.8±1.7	15.9±1.1	0±0	7±1.3	13.8±1.3
	Myoxocephalus scorpius	Muscle	W '09	10	3.8±2.2	8.4±2.1	4.6±1.5	2.9±0.7	20.1±3.4	25.8±5
			S '09	8	4.6±0.5	7.1±0.6	2.3±0.9	2.0±0.2	17.8±0.9	26.4±2.7
	Pusa hispida	Blubber	S '07	2	19.3±0.1	17.1±8.5	9.7±2.7	0.3±0.1	7.3±1	9.5±0.2
			W '08	3	19.2±0.4	13.4±1.3	12.9±2.2	0.3±0	10.3±1	9.1±0.7
			S '08	6	22±5.1	19±2.7	7.1±3.1	0.5±0.3	8.9±2.2	9.5±1.8

1. Data from Stevens et al. 2004 (southeast North Water Polyna, sampled during Autumn 1999

Table S6.3. Previously reported changes in carbon sources between summer and winter.

POC type	Trend in summer	Trend in winter	ID	Reference
Total POC				
	10.5 ±9.3 mmol C $m^{-2}d^{-1}$ in summer, open water	2.9 ±5.3 mmolC$m^{-2}d^{-1}$ in spring under ice	1	Moran et al. 2005
	high in summer (150-300 mg C $m^{-2}d^{-1}$)	lower in winter (30 -70 mg C $m^{-2}d^{-1}$)	2	Olii et al 2002
	highest POC flux ~100 mg C $m^{-2}d^{-1}$ June and July	lowest POC flux <20 mg C $m^{-2}d^{-1}$April	3	Juul-Pedersen et al. 2010
	more similar between summer and winter than other locations	slightly higher in Feb. - April than summer and dominated by re-suspended material	3	Lalande et al. 2009
	higher in summer (dominated by autochthonous production and river input)	lower in winter, dominated by re-suspended material	3	Lalande et al. 2009
	higher in summer (dominated by autochthonous production and river input)	lower in winter, dominated by re-suspended material	4	Lalande et al. 2009
	maximum of ~7 g C m^{-2} in August	low, ~1 g C m^{-2} during fall and winter	5	Atkinson and Wacasey 1987
	highest value in June	lower but remained stable in winter through spring	5	Juul-Pedersen et al. 2008
	highest in July (dominated by autochthonous production)	low in winter	5	Lalande et al. 2009
	increased between spring and summer	decreased during winter	5	Sampei et al. 2004
	highest in summer	lowest in winter	6	Bauerfind et al. 1997
	234-405 µg C l^{-1}	150-572 µg C l^{-1}	6	Werner 2006
Phytoplankton				
	highest in May/June and August/September	low in winter	2	Bauerfind et al. 2009
	Chl a 50% of total POC	*Chl a* negligible	2	Oliie et al 2002
	Chl a flux increasing to 0.25-0.4 mg C $m^{-2}d^{-1}$May to June	*Chl a* flux <0.1 mg C $m^{-2}d^{-1}$ in Feb.-March and 0.15 in April	2	Renaud et al. 2007
	phaeopigments and *Chl a* in top 9cm of sediments similar from January - July		2	Renaud et al. 2007
	phytoplankton biomass higher in June/July	lower in March	2	Wassmann et al. 2006
	density of cells 99% higher in summer than in winter	very low density (<10 cells L^{-1})	2	Weslawski 191
	protist cells dominated flux in July - August	protist cells minimal in winter	3	Forest et al. 2008
	Chl a flux ~0.7 mg C $m^{-2}d^{-1}$ June	~0.0 mg C $m^{-2}d^{-1}$ March	3	Juul-Pedersen et al. 2010
	sedimenting cells peaked in July - August	negligible in winter	5	Hsaio 1987

	Chl a flux increased to 0.23 mg C $m^{-2}d^{-1}$ in May and 2.0 in June	*Chl a* flux low, 0.01 mg C $m^{-2}d^{-1}$	5	Juul-Pedersen et al. 2008
	increased flux in May to June and from August to September	negligible from October to April	5	Sampei et al. 2002
	maximum phytoplankton carbon flux in May/June (contributed 21% to total POC flux over two years)	lowest in winter	5	Sampei et al. 2004
	Chl a >200 mg C m^{-2} in July and August	negligible in March	5	Welch et al. 1992
	phytoplankton biomass highest in July/August	not present in winter	6	Rysgaard et al. 1999
Fecal pellets	up to 260 mg C m^{-2} d^{-1} but variable among locations	<1 mg C m^{-2} d^{-1}	2	Oliie et al 2002
	vertical flux ~150 mg C m^{-2} d^{-1} but retention was variable among locations (up to 96%)	<3 mg C m^{-2} d^{-1}	2	Riser et al. 2002
	flux highest in July-August and pellets were not degraded	fecal pellets were predominantly degraded	3	Forest et al. 2008
	two large fluxes: one in spring and one in fall	minimum in winter	5	Sampei et al. 2002
	maximum flux July to September (contributed 1% to total POC over two years)	minimum in winter	5	Sampei et al. 2004
	Calanus glacialis produced 0.6 fecal pellets $ind^{-1}h^{-1}$ in late May	0 fecal pellets in early March	3	Seuthe et al. 2007
	C. hyperboreus produced 0.35 fecal pellets $ind^{-1}h^{-1}$ in late May	0 fecal pellets in early March	3	Seuthe et al. 2007
	Metridia longa produced 1.1 fecal pellets $ind^{-1}h^{-1}$ in late May	0 fecal pellets in early March	3	Seuthe et al. 2007
Macroalgae	Macroalgae detritus thought to provide a stable food source to consumers all year		3	Dunton and schell 1987
Detritus	Detrital flux lowest in summer (July-August)	Detrital flux high in winter (high all year except July-August)	3	Forest et al. 2008

Shelf ID (from Carmack and Wassmann 2006): 1. Bering/Chukchi Sea (shallow inflow shelf) 2. Barents Sea (deep inflow shelf) 3. Beaufort Sea (narrow interior shelf) 4. Kara/Laptev/Siberian Seas (wide interior shelf) 5. Canadian archipelago (network outflow shelf) 6. East Greenland (longitudinal outflow)

Table S6.4. Changes in abundance or biomass between summer and winter in arctic zooplankton (Zoo), benthos (Ben) and upper trophic level fish, marine mammal and seabird consumers (Con). Species diet or feeding mode is reported (H: herbivore, O: omniovore, C: carnivore, DF/FF: deposit/filter feeder, O/C/S: omnivorous, carnivorous and/or scavenging). Change was categorized as higher in summer (1), higher in winter (2) or no change (3).

Organism	Diet	Fun. Group	Summer	Winter	Change	Taxon	Shelf ID	Reference
Calanus finmarchicus	H	Zoo	<5 g dw m-2	8.7 g dw m-2	2	Copepoda	2	Soreide et al. 2008
C. glacialis	H	Zoo	peaked in June (1750 ind m^{-2})	lowest in Nov.-Jan. (<250 ind m^{-2})	1	Copepoda	1	Ashjian et al. 2003
C. glacialis	H	Zoo	higher biomass in summer	lower in winter	1	Copepoda	2	Soreide et al. 2003
C. glacialis	H	Zoo	30.6 g dw m^{-2}	<5 g dw m^{-2}	1	Copepoda	2	Soreide et al. 2008
C. glacialis	H	Zoo	>30,000 ind m^{-2}	<1000 ind m^{-2}	1	Copepoda	2	Soreide et al. 2010
C. glacialis	H	Zoo	5 g C m^{-2} August	4 g C m^{-2} January	1	Copepoda	3	Forest et al. 2011
C. glacialis	H	Zoo	August 1964 mg m^{-2}	April 201 mg m^{-2}	1	Copepoda	5	Grainger 1971
C. glacialis	H	Zoo	biomass typically higher in summer than winter but interannual variability high		1	Copepoda	5	Michel et al. 2006
C. glacialis	H	Zoo	August 0.130 g m^{-2}	April 0.100 g m^{-2}	3	Copepoda	5	Conover and Siferd 1993
C. hyperboreus	H	Zoo	abundance peaked in April with high numbers of CI	lowest in Nov-Feb (<3000 ind m^{-2})	1	Copepoda	1	Ashjian et al. 2003
C. hyperboreus	H	Zoo	9.5 g C m^{-2} August	7.5 g C m^{-2} January	1	Copepoda	3	Forest et al. 2011
C. hyperboreus	H	Zoo	biomass typically higher in summer than winter but interannual variability high		1	Copepoda	5	Michel et al. 2006
C. hyperboreus	H	Zoo	August 0.706 g m^{-2}	April 0.304 g m^{-2}	1	Copepoda	5	Conover and Siferd 1993
C. hyperboreus, C. glacialis, C. pacificus, Metridia longa	H	Zoo	August 9 g dw m^{-2}	April 2 g dw m^{-2}	1	Copepoda	3	Forest et al. 2008
cirripede nauplii	H	Zoo	August 3885 mg m^{-2}	April 0 mg m^{-2}	1	Copepoda	5	Grainger 1971
copepod nauplii	H	Zoo	August 1161 mg m^{-2}	April 2 mg m^{-2}	1	Copepoda	5	Grainger 1971
copepoda nauplii	H	Zoo	38.2% of total abundance	70.4%of total abundance	2	Copepoda	4	Abramova and Tuschling 2005

Metridia longa nauplii	H	Zoo	peaked in Aug-Sept (1700-2200 ind m^{-2})	lowest in Dec-Apr (<100 ind m^{-2})	1	Copepoda	1	Ashjian et al. 2003
Microcalanus pygmaeus naupulii	H	Zoo	abundance 0 ind m^{-2} in August	peaked in March (64,000 ind m^{-2})	2	Copepoda	1	Ashjian et al. 2003
Acartia	O	Zoo	August 49 mg m^{-2}	April 12 mg m^{-2}	1	Copepoda	5	Grainger 1971
A. longiremis	O	Zoo	(stage VI) June 95 (*1000 mg m^{-3})	April (stage VI) 1235 (*1000 mg m^{-3})	2	Copepoda	3	Horner and Murphy 1985
A. longiremis	O	Zoo	8.9% of total abundance	3.1%of total abundance	1	Copepoda	4	Abramova and Tuschling 2005
Drepanopus bungei	O	Zoo	14.8% of total abundance	17.3% of total abundance	2	Copepoda	4	Abramova and Tuschling 2005
Harpacticoida	O	Zoo	0.3% of total abundance	0.7%of total abundance	3	Copepoda	4	Abramova and Tuschling 2005
Harpacticoida nauplii	O	Zoo	June (16,018*1000 ind m^{-3})	April 12 (*1000 indm^{-3})	1	Copepoda	3	Horner and Murphy 1985
Limnocalanus macrurus	O	Zoo	6.3% of total abundance	0%of total abundance	1	Copepoda	4	Abramova and Tuschling 2005
Metridia longa	O	Zoo	peaked in June (30,000 ind m^{-2})	lowest in Jul.-Dec. (<2500 ind m^{-2})	1	Copepoda	1	Ashjian et al. 2003
M. longa	O	Zoo	1.8 g C m^{-2} August	1 g C m^{-2} January	1	Copepoda	3	Forest et al. 2011
M. longa	O	Zoo	biomass typically higher in summer than winter but interannual variability high		1	Copepoda	5	Michel et al. 2006
M. longa	O	Zoo	August 0.002 g m^{-2}	April 0.035 g m^{-2}	2	Copepoda	5	Conover and Siferd 1993
Microcalanus pygmaeus	O	Zoo	40,000 ind m^{-2} in August	peaked in March (140,000 ind m^{-2})	2	Copepoda	1	Ashjian et al. 2003
M. pygmaeus	O	Zoo	0.9% of total abundance	1.4%of total abundance	2	Copepoda	4	Abramova and Tuschling 2005
Oithona similis	O	Zoo	25,000 ind m^{-2} in August	peaked in March (90,000 ind m^{-2})	2	Copepoda	1	Ashjian et al. 2003
O. similis	O	Zoo	high in Sept., peak in Nov.	lower in Jan. - April	1	Copepoda	2	Lischka and Hagen 2005
O. similis	O	Zoo	6.8% of total abundance	1.6%of total abundance	1	Copepoda	4	Abramova and Tuschling 2005
O. similis naupulii	O	Zoo	abundance peaked in July 325,000 ind m^{-2}	low in Dec. - Jan. (<25,000 ind m^{-2})	1	Copepoda	1	Ashjian et al. 2003
Pseudocalanus acuspes	O	Zoo	high in May - July and in Nov.	lower in Jan. - April	1	Copepoda	2	Lischka and Hagen 2005
P. acuspes	O	Zoo	biomass typically higher in summer than winter but interannual variability high		1	Copepoda	5	Michel et al. 2006

P. acuspes	O	Zoo	August 0.132 g m-2	April 0.782 g m-2	2	Copepoda	5	Conover and Siferd 1993
P. major	O	Zoo	9.9% of total abundance	2.2%of total abundance	1	Copepoda	4	Abramova and Tuschling 2005
P. minutus	O	Zoo	higher in August and Sept.	lower in Jan. - April	1	Copepoda	2	Lischka and Hagen 2005
Pseudocalanus sp.	O	Zoo	(CV) June (20,260 *1000 ind m^{-3})	April (CV) 26,561 (*1000 ind m^{-3})	2	Copepoda	3	Horner and Murphy 1985
Pseudocalanus sp.	O	Zoo	August 7131 mg m^{-2}	April 1070 mg m^{-2}	1	Copepoda	5	Grainger 1971
Triconia borealis	O	Zoo	0.6% of total abundance	2.2%of total abundance	2	Copepoda	4	Abramova and Tuschling 2005
Sagitta elegans	C	Zoo	lower in summer	higher in winter	2	Cheatognath	2	Soreide et al 2003
Aeginoposis laurentii	C	Zoo	June 383 (*1000 ind m^{-3})	April 173 (*1000 ind m^{-3})	1	Cnidaria	3	Horner and Murphy 1985
Aglantha digitale	C	Zoo	higher in summer	lower in winter	1	Cnidaria	2	Soreide et al. 2003
Beroe cucumis	C	Zoo	higher in summer	lower in winter	1	Cnidaria	2	Soreide et al. 2003
Euphysa flammea	C	Zoo	June 261 (*1000 ind m^{-3})	April 796 (*1000 ind m^{-3})	2	Cnidaria	3	Horner and Murphy 1985
Halitholus cirratus	C	Zoo	June 87 (*1000 ind m-3)	April 91 (*1000 ind m^{-3})	3	Cnidaria	3	Horner and Murphy 1985
Mertensia ovum	C	Zoo	1.17 mg dw in summer	0.63 mg dw winter	1	Ctenophora	5	Welch et al. 1992
Pleurobrachia pileus	C	Zoo	June 87 (*1000 ind m^{-3})	April 91 (*1000 ind m^{-3})	2	Ctenophora	3	Horner and Murphy 1985
Apherusa glacialis	DF/FF	Ben	hihger in summer (6.5 ind m-2)	lower in winter (2.1 ind m^{-2})	1	Amphipoda	2	Werner and Auel 2005
A. glacialis	DF/FF	Ben	June 267 (*1000 ind m^{-3})	April 23 (*1000 ind m^{-3})	1	Amphipoda	3	Horner and Murphy 1985
Axinopsida orbiculata	DF/FF	Ben	August (7.4 ind m^{-2})	November 133 ind m^{-2}	2	Mollusca	2	Pawlowska et al. 2011
A. orbiculata	DF/FF	Ben	summer 97 ind m^{-2}	winter 342 ind m^{-2}	2	Mollusca	2	Kedra et al. 2010
Cylichna occulta	DF/FF	Ben	April (178) August (14.8 ind m2)	November 148 ind m^{-2}	2	Mollusca	2	Pawlowska et al. 2011
Macoma calcarea	DF/FF	Ben	summer 702 ind m^{-2}	winter 129 ind m^{-2}	1	Mollusca	2	Kedra et al. 2010
Apistobranchus tullbergi	DF/FF	Ben	summer 1,844 ind m^{-2}	winter 4,840 ind m^{-2}	2	Polychaeta	2	Kedra et al. 2010
Capitella capitata	DF/FF	Ben	August (393 ind m^{-2})	November 122 ind m^{-2}	1	Polychaeta	2	Pawlowska et al. 2011
C. capitata	DF/FF	Ben	summer 884 ind m^{-2}	winter 182 ind m^{-2}	1	Polychaeta	2	Kedra et al. 2010

Chaetozone setosa	DF/FF	Ben	highest in April after phytoplankton bloom (711.1 ind m^{-2})	November 200.0 ind m^{-2}	1	Polychaeta	2	Pawlowska et al. 2011
Chone paucibranchiata	DF/FF	Ben	summer 613 ind m^{-2}	winter 4 ind m^{-2}	1	Polychaeta	2	Kedra et al. 2010
Cirratulidae	DF/FF	Ben	summer 2,591 ind m^{-2}	winter 3,067 ind m^{-2}	3	Polychaeta	2	Kedra et al. 2010
Cossura longocirrata	DF/FF	Ben	April (496 ind m^{-2})	November 230 ind m^{-2}	1	Polychaeta	2	Pawlowska et al.
Heteromastus	DF/FF	Ben	August (15 ind m^{-2})	November 119 ind m^{-2}	2	Polychaeta	2	Pawlowska et al.
Leitoscoloplos	DF/FF	Ben	summer 1,849 ind m^{-2}	winter 342 ind m^{-2}	1	Polychaeta	2	Kedra et al. 2010
Lysippe labiata	DF/FF	Ben	summer 938 ind m^{-2}	winter 449 ind m^{-2}	1	Polychaeta	2	Kedra et al. 2010
Paraonella nordica	DF/FF	Ben	summer 2,489 ind m^{-2}	winter 62.2 ind m^{-2}	1	Polychaeta	2	Kedra et al. 2010
polychaete larvae	DF/FF	Ben	June 1396 (*1000 ind m^{-3})	April 81 (*1000 ind m^{-3})	1	Polychaeta	3	Horner and Murphy 1985
polychaete larvae	DF/FF	Ben	August 404 mg/m^{-2}	April 164 mg m^{-2}	1	Polychaeta	5	Grainger 1971
Anonyx nugax	O/C/S	Ben	Jun-Aug %frequency=69	Nov-Feb %frequency=52	3	Amphipoda	2	Weslawski 1991
A. sarsi	O/C/S	Ben	Jun-Aug %frequency=94	Nov-Feb %frequency=100	3	Amphipoda	2	Weslawski 1991
Gammarus spp.	O/C/S	Ben	Jun-Aug %frequency=6	Nov-Feb %frequency=19	2	Amphipoda	2	Weslawski 1991
G. wilkitzkii	O/C/S	Ben	similar in both summer and winter (2.0 and 1.5 ind m^{-2}, respectively)		3	Amphipoda	2	Werner and Auel 2005
Halirages mixtus	O/C/S	Ben	June 2084 (*1000 ind m^{-3})	April 947 (*1000 ind m^{-3})	1	Amphipoda	3	Horner and Murphy 1985
Onisimus edwardsi	O/C/S	Ben	Jun-Aug %frequency=69	Nov-Feb %frequency=62	3	Amphipoda	2	Weslawski 1991
O. littoralis	O/C/S	Ben	Jun-Aug %frequency=50	Nov-Feb %frequency=33	1	Amphipoda	2	Weslawski 1991
O. littoralis	O/C/S	Ben	June 1456 (*1000 ind m^{-3})	April 912 (*1000ind m^{-3})	1	Amphipoda	3	Horner and Murphy 1985
Onisimus spp.	O/C/S	Ben	low in both seasons		3	Amphipoda	2	Werner and Auel 2005
Orchomene minuta	O/C/S	Ben	Jun-Aug %frequency=38	Nov-Feb %frequency=43	3	Amphipoda	2	Weslawski 1991
Eualus gaimardii	O/C/S	Ben	Jun-Aug %frequency=6	Nov-Feb %frequency=0	1	Decapoda	2	Weslawski 1991
Hyas araneus	O/C/S	Ben	Jun-Aug %frequency=0	Nov-Feb %frequency=14	2	Decapoda	2	Weslawski 1991

Pagurus pubescens	O/C/S	Ben	Jun-Aug %frequency=0	Nov-Feb %frequency=0.2	2	Decapoda	2	Weslawski 1991
Nemertea	O/C/S	Ben	summer 13 ind m^{-2}	winter 351 ind m^{-2}	2	Polychaeta	2	Kedra et al. 2010
Fulmarus glacialis	C	Con	present	1-10% of summer population	1	Aves	2	Weslawski 1991
Pagophila eburnea	C	Con	117 counted in Aug-Sept	0 in April	1	Aves	5	Karnovsky et al. 2009
P. eburnea	C	Con	52 counted in Aug-Sept	0 in April	1	Aves	5	Karnovsky et al. 2009
Rissa tridactyla	C	Con	present	1-10% of summer population	1	Aves	2	Weslawski 1991
Somateria mollissima	C	Con	present	1-10% of summer population	1	Aves	2	Weslawski 1991
Mallotus villosus	C	Con	present	not present	1	Teleostei	2	Weslawski 1991
Salvelinus alpinus	C	Con	present	not present	1	Teleostei	2	Weslawski 1991

Shelf ID (from Carmack and Wassmann 2006): 1. Bering/Chukchi Sea (shallow inflow shelf) 2. Barents Sea (deep inflow shelf) 3. Beaufort Sea (narrow interior shelf) 4. Kara/Laptev/Siberian Seas (wide interior shelf) 5. Canadian archipelago (network outflow shelf) 6. East Greenland (longitudinal outflow)

Table S6.5. Changes in diet between summer and winter of arctic zooplankton (Zoo), benthos (Ben) and upper trophic level fish, marine mammal and seabird consumers (Con). Putative diet or feeding mode is reported (H: herbivore, O: omniovore, C: carnivore, DF/FF: deposit/filter feeder, O/C/S: omnivorous, carnivorous and/or scavenging). Change in diet was categorized as a switch from feeding in summer to reliance on internal reserves in winter (1), switch to a higher trophic position in winter (2), switch to a greater reliance on benthic/macroalgae-derived carbon in winter (3) or no change (4).

Species	Diet	Fun. Group	Summer	Winter	Change	Taxon	ID	Reference
C. finmarchicus	H	Zoo	feeding on phytoplankton	overwintering driven by stored lipids	1	Calanoida	*	Hopkins et al. 1984
C. finmarchicus	H	Zoo	δ13C=-22.8±0.3, δ15N=7.2	-22.4±0.8, δ15N=7.9	1	Calanoida	2	Sato et al. 2002
C. finmarchicus	H	Zoo	δ13C=-23.8±1.9, δ15N=7.4±0.4	δ13C=-20.0±0.4, and δ15N 9.7±0.3	1	Calanoida	2	Soreide et al. 2006
C. finmarchicus	H	Zoo	feeds on phytoplankton	overwinters relying on lipids	1	Calanoida	*	Sargent and Falk-Petersen 1988
C. finmarchicus	H	Zoo	primarily herbivorous in August/summer	likely in diapause, might have been opportunistically feeding in December	1	Calanoida	2	Soreide et al. 2009
C. glacialis	H	Zoo	May CVI δ15N=8.1	January CVI δ15N=9.5	1	Calanoida	2	Sato et al. 2002
C. glacialis	H	Zoo	δ13C -23.6±0.2, δ15N 7.1±0.3	δ13C -21.7±0.7, δ15N 9.7±0.2	1	Calanoida	2	Soreide et al. 2006
C. glacialis	H	Zoo	primarily omnivorous in August/summer	likely in diapause (not feeding) but some opportunistically feeding in December based on d15N	1	Calanoida	2	Soreide et al. 2009
C. glacialis	H	Zoo	δ13C=-24.10, δ15N=12.41	δ13C=-21.57, δ15N=10.92	1	Calanoida	3	Forest et al. 2011
C. hyperboreus	H	Zoo	δ13C=-23.0±0.2, δ15N=7.5±0.4	δ13C=-21.9±0.8, δ15N=9.3±0.2	1	Calanoida	2	Soreide et al. 2006

C. hyperboreus	H	Zoo	primarily herbivorous in August/summer	did not feed based on δ15N	1	Calanoida	2	Soreide et al. 2009
C. hyperboreus	H	Zoo	δ13C=-23.47, δ15N=11.23	δ13C=-21.59, δ15N=7.94	1	Calanoida	3	Forest et al. 2011
C. hyperboreus	H	Zoo	phytoplankton diet in summer	overwintering driven by stored lipids	1	Calanoida	5	Lee 1974
Metridia longa	O	Zoo	feeding on phytoplankton	likely takes non-phytoplankton food in winter	2	Calanoida	*	Hopkins et al. 1984
M. longa	O	Zoo	CVI δ15N=8.2	CVI δ15N=9.6	2	Calanoida	2	Sato et al. 2002
M. longa	O	Zoo	feeds on phytoplankton	feeds on Calanus copepods	2	Calanoida	*	Sargent and Falk-Petersen 1988
Pseudocalanus minutus	O	Zoo	ate flagellate/dinoflagellate diet in summer	omnivorous in winter	2	Calanoida	2	Lischka and Hagen 2007
Thysanoessa raschii	O	Zoo	feeding on phytoplankton	likely takes non phytoplankton food	1	Euphausiacea	*	Hopkins et al. 1984
T. raschii	O	Zoo	feeding on phytoplankton	likely takes non phytoplankton food (e.g. small copepods) in winter	2	Euphausiacea	*	Sargent and Falk-Petersen 1981& Falk-Petersen et al. 1981
Thysanoessa inermis	O	Zoo	feeding on phytoplankton	likely takes non phytoplankton food (e.g. small copepods) in winter	2	Euphausiacea	*	Sargent and Falk-Petersen 1981& Falk-Petersen et al. 1981
T. inermis	O	Zoo	feeding on phytoplankton	overwintering and gonad maturation driven by lipids stored during spring/summer	1	Euphausiacea	*	Hopkins et al. 1984
T. inermis	O	Zoo	δ13C=-21.6±0.3, δ15N=8.2±0.6 (size 10-19mm)	δ13C=-21.9±0.2, δ15N=9.4±0.1 (size 17-19mm)	4	Euphausiacea	2	Soreide et al 2006
Mysis litoralis	O	Zoo	δ13C=-21.2±0.3 (29% reliance on macroalgae)	δ13C=-19.4±0.3 (48% reliance on macroalgae)	3	Mysida	3	Dunton and Schell 1987
Paraeuchaeta norvegica	C	Zoo	sδ13C=-20.6, δ15N=9.8	δ13C=-20.7±0.7, δ15N=10.5±0.3	4	Calanoida	2	Soreide et al. 2006

Sagitta elegans	C	Zoo	δ13C=-19.3±0.8, δ15N=11.9±0.2	δ13C=-20.8±0.3, δ15N=12.2±0.1	4	Chaetognatha	2	Soreide et al 2006
Aglantha digitale	C	Zoo	δ13C=-21.0±0.4, δ15N=10.4±0.1	δ13C=-19.7±0.6, δ15N=9.6±0.4	4	Cnidaria	2	Soreide et al 2006
Lucernaria infundibulum	C	Zoo	δ13C=-20.5	δ13C=-19.0±0.8 (increased reliance of prey on macroalgae)	3	Cnidaria	3	Dunton and Schell 1987
Beroe cucumis	C	Zoo	δ13C=-20.9±0.5, δ15N 11.2±0.2	δ13C=-20.8±0.3, δ15N=10.3±0.3	4	Ctenophora	2	Soreide et al 2006
Mertensia ovum	C	Zoo	δ13C=-23.0±0.6, δ15N=9.7±0.4	δ13C=-23.2±0.8, δ15N 8.2±0.2	4	Ctenophora	2	Soreide et al 2006
Thysanoessa libellula	C	Zoo	δ13C=-22.7±0.3, δ15N=10.7±0.2	δ13C=-22.8±0.7, δ15N=9.8±0.5	4	Euphausiacea	2	Soreide et al 2006
T. longicaudata	C	Zoo	δ13C=-20.8±0.5, δ15N=9.2±0.1	δ13C=-22.1±0.3, δ15N=9.2±0.2	4	Euphausiacea	2	Soreide et al 2006
Meganyctiphanes norvegica	C	Zoo	accumulates lipids all year likely feeding on copepods		4	Euphausiacea	*	Sargent and Falk-Petersen 1981& Falk-Petersen et al. 1981
Apherusa glacialis	DF/FF	Ben	ice algae during productive period	internal reserves	1	Amphipoda	2	Werner and Auel 2005
Ctenodiscus crispatus	DF/FF	Ben	δ13C=-18.4±0.2, δ15N=11.2±0.9	δ13C=-17.8, δ15N=11.4	4	Echinodermata	2	Renaud et al. 2011
Ophiacantha bidentata	DF/FF	Ben	δ13C=-18.0, δ15N=15.1	δ13C=-17.8, δ15N=12.8	4	Echinodermata	2	Renaud et al. 2011
Ophiopholis aculeata	DF/FF	Ben	δ13C=-18.3±0.3, δ15N=8.6±0.4	δ13C=-17.4, δ15N=11.9	4	Echinodermata	2	Renaud et al. 2011
Ophiopholis sarsi	DF/FF	Ben	δ13C=-19.3, δ15N=8.0	δ13C=-19.1±0.2, δ15N=9.6±0.3	4	Echinodermata	2	Renaud et al. 2011
Strongylocentrotus sp.	DF/FF	Ben	δ13C=-17.9, δ15N=9.9	δ13C=-16.8±0.3, δ15N=9.5±0.5	4	Echinodermata	2	Renaud et al. 2011
Macoma clcarea	DF/FF	Ben	consumed similar foods that did not vary in quality		4	Mollusca	1	Lovvorn et al. 2005
Nucula belloti	DF/FF	Ben	consumed similar foods that did not vary in quality		4	Mollusca	1	Lovvorn et al. 2005
Nuculana radiata	DF/FF	Ben	consumed similar foods that did not vary in quality		4	Mollusca	1	Lovvorn et al. 2005
Polyplacophora	DF/FF	Ben	δ13C=-17.5, δ15N=10.1	δ13C=-17.8, δ15N=10.6	4	Mollusca	2	Renaud et al.

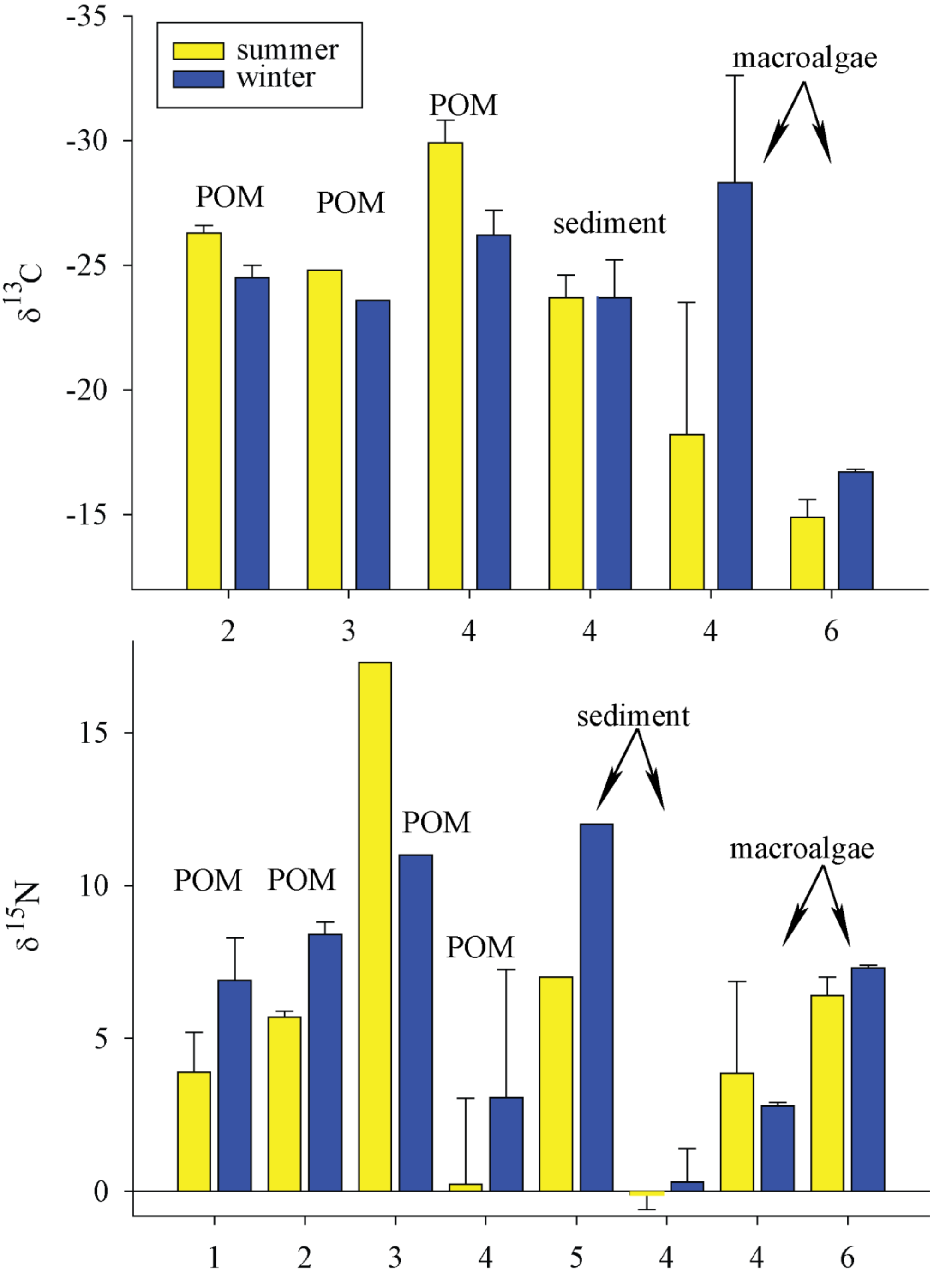
								2011
Flabelligera affinis	DF/FF	Ben	δ13C=-20.8	δ13C=-19 (increased reliance on macroalgae)	3	Polychaeta	3	Dunton and Schell 1987
Ophelina acuminata	DF/FF	Ben	δ13C=-18.8, δ15N=9.2	δ13C=-19.2, δ15N=9.0	4	Polychaeta	2	Renaud et al. 2011
Anonyx nugax	O/C/S	Ben	δ13C=-22.26, δ15N=11.10	δ13C=-21.58, δ15N=10.51	4	Amphipoda	2	Legenzynska et al. 2012
A. sarsi	O/C/S	Ben	δ13C=-22.2	δ13C=-20.2±0.1 (increased reliance onmacroalgae)	3	Amphipoda	3	Dunton and Schell 1987
A. sarsi	O/C/S	Ben	δ13C=-20.3, δ15N=9.65	δ13C=-20.62, δ15N=10.37	4	Amphipoda	2	Legenzynska et al. 2012
Arrhis phyllonyx	O/C/S	Ben	δ13C=-20.85, δ15N=10.44	δ13C=-20.32, δ15N=10.07	4	Amphipoda	2	Legenzynska et al. 2012
Gammarus wilkitzkii	O/C/S	Ben	ice algae during productive period	ice fauna and zooplankton (some internal reserves)	2	Amphipoda	2	Werner and Auel 2005
Hyperia galba	O/C/S	Ben	δ13C=-21.2±0.4, δ15N=9.9±0.5	δ13C=-22.4±0.2, δ15N=10.5±0.2	4	Amphipoda	2	Soreide et al 2006
Onisimus affinis	O/C/S	Ben	similar protein, lipid and carbohydrate in August and February, suggests no lipid accumulation and constant feeding all year		4	Amphipoda	5	Percy 1979
Onisimus caricus	O/C/S	Ben	δ13C=-22.14, δ15N=10.86	δ13C=-21.97, δ15N=10.86	4	Amphipoda	2	Legenzynska et al. 2012
Onisimus edwardsi	O/C/S	Ben	δ13C=-21.10, δ15N=8.84±1.83	δ13C=-20.9, δ15N=9.27	4	Amphipoda	2	Legenzynska et al. 2012
Onisimus glacialis	O/C/S	Ben	herbivory (algae)	carnivory (e.g. zooplankton)	2	Amphipoda	2	Werner and Auel 2005
Onisimus litoralis	O/C/S	Ben	diatoms in June	crustaceans in April	2	Amphipoda	3	Cary and Boudrias 1987
Onisimus nanseni	O/C/S	Ben	similar diet in both seasons - opportunistic on zooplankton, etc.		4	Amphipoda	2	Werner and Auel 2005
Onisimus similus	O/C/S	Ben	year round omnivorous/carnivorous feeding on flagellates/dinoflagellates		4	Amphipoda	2	Lischka and Hagen 2007
Paroediceros lynceus	O/C/S	Ben	generally similar fatty acid profiles during summer and winter		4	Amphipoda	2	Legenzynska et al. 2012
Pontoporeia femorata	O/C/S	Ben	generally similar fatty acid profiles during summer and winter		4	Amphipoda	2	Legenzynska et al. 2012
Themisto libellula	O/C/S	Ben	δ13C=-22.7±0.1, δ15N=8.7±0.2	δ13C=-22.8±0.7, δ15N=9.8±0.5	4	Amphipoda	2	Soreide et al. 2006
Pandalus borealis	O/C/S	Ben	δ13C=-19.2±0.4, δ15N=12.5±0.4	δ13C=-19.1±0.1, δ15N=12.0±0.9	4	Decapoda	2	Renaud et al. 2011

Clione limacina	O/C/S	Ben	δ13C=-22.8±0.6 and δ15N=10.1±0.3	δ13C=-22.5±0.6, δ15N=9.4±0.2	4	Mollusca	2	Soreide et al 2006
Eubranchus sp.	O/C/S	Ben	δ13C=-18.5	δ13C=-21.2±0.7	3	Mollusca	3	Dunton and Schell 1987
Eunoe oerstedi	O/C/S	Ben	δ13C=-18.4, δ15N=13.1	δ13C=-18.1, δ15N=11.9	4	Polychaeta	2	Renaud et al. 2011
Lumbrineris sp.	O/C/S	Ben	δ13C=-18.6, δ15N=10.8	δ13C=-18.2, δ15N=11.0	4	Polychaeta	2	Renaud et al. 2011
Nephtys sp.	O/C/S	Ben	δ13C=-19.2±0.5, δ15N=12.6±0.3	δ13C=-18.9, δ15N=12.0	4	Polychaeta	2	Renaud et al. 2011
Gadus morhua	C	Con	δ13C=-19.4±0.3, δ15N=12.3±0.5	δ13C=-18.4±0.5, δ15N=12.8±0.3	4	Teleostei	2	Renaud et al. 2011
Boreogadus saida	C	Con	copepods, mysis	copepods, mysis, fish	2	Teleostei	1	Craig et al. 1982
Gymnocanthus tricuspis	C	Con	δ13C=-17.4±0.3, δ15N=14.2±0.4	δ13C=-18.2±0.7, δ15N=14.3±0.9	4	Teleostei	2	Renaud et al. 2011
Myoxocephalus scorpius	C	Con	δ13C=-17.7±0.8, δ15N=14.2±1.0	δ13C=-17.8±0.8, δ15N=14.2±0.7	4	Teleostei	2	Renaud et al. 2011
Alle alle	C	Con	consumed herbivorous copepods in spring and summer	switched to higher trophic level in fall feeding on amphipods and fish	2	Aves	5	Karnovsky et al. 2008
A. alle	C	Con	Calanus copepods in summer	feeding at higher trophic level in winter	2	Aves	2	Fort et al. 2010
A. alle	C	Con	Calanus copepods in summer	likely feeding on copepods in winter	4	Aves	6	Fort et al. 2010
Fulmarus glacialis	C	Con	cephalopods, polychaets, crustaceans	switch to higher tropihc position in winter	2	Aves	5	Mallory et al. 2010
Rissa tridactlya	C	Con	fed all year on carnivorous amphipods and fish		4	Aves	5	Karnovsky et al. 2008
Somateria mollissima	C	Con	δ13C=-18.7±0.3, δ15N=11±0.7	δ13C=-17.9±0.5, δ15N=10.9±0.8	3	Aves	2	Renaud et al. 2011
Uria lomvia	C	Con	fed all year on carnivorous amphipods and fish		4	Aves	5	Karnovsky et al. 2008
Cystophora cristata	C	Con	squid, polar cod	squid, capelin	4	Mammalia	6	Haug et al. 2005
Monodon monodon	C	Con	arctic cod, polar cod, squid	Greenland halibut and squid	2	Mammalia	5	Laidre et al. 2005
Phoca groenlandica	C	Con	Parathemisto	added krill and capelin	2	Mammalia	6	Haug et al. 2005
Pusa hispida	C	Con	rely heavily on pelagic prey	consume benthic prey	3	Mammalia	2	Weslawski et al

								1994
P. hispida	C	Con	invertebrates and fish	fish	2	Mammalia	5	Smith 1987
P. hispida	C	Con	saffron cod	arctic cod	4	Mammalia	1	Lowry 1980
P. hispida	C	Con	saffron cod and shrimp	arctic cod	2	Mammalia	1	Lowry 1980
P. hispida	C	Con	shrimp	arctic cod	2	Mammalia	1	Lowry 1980
P. hispida	C	Con	amphipods	arctic cod	2	Mammalia	3	Lowry 1980

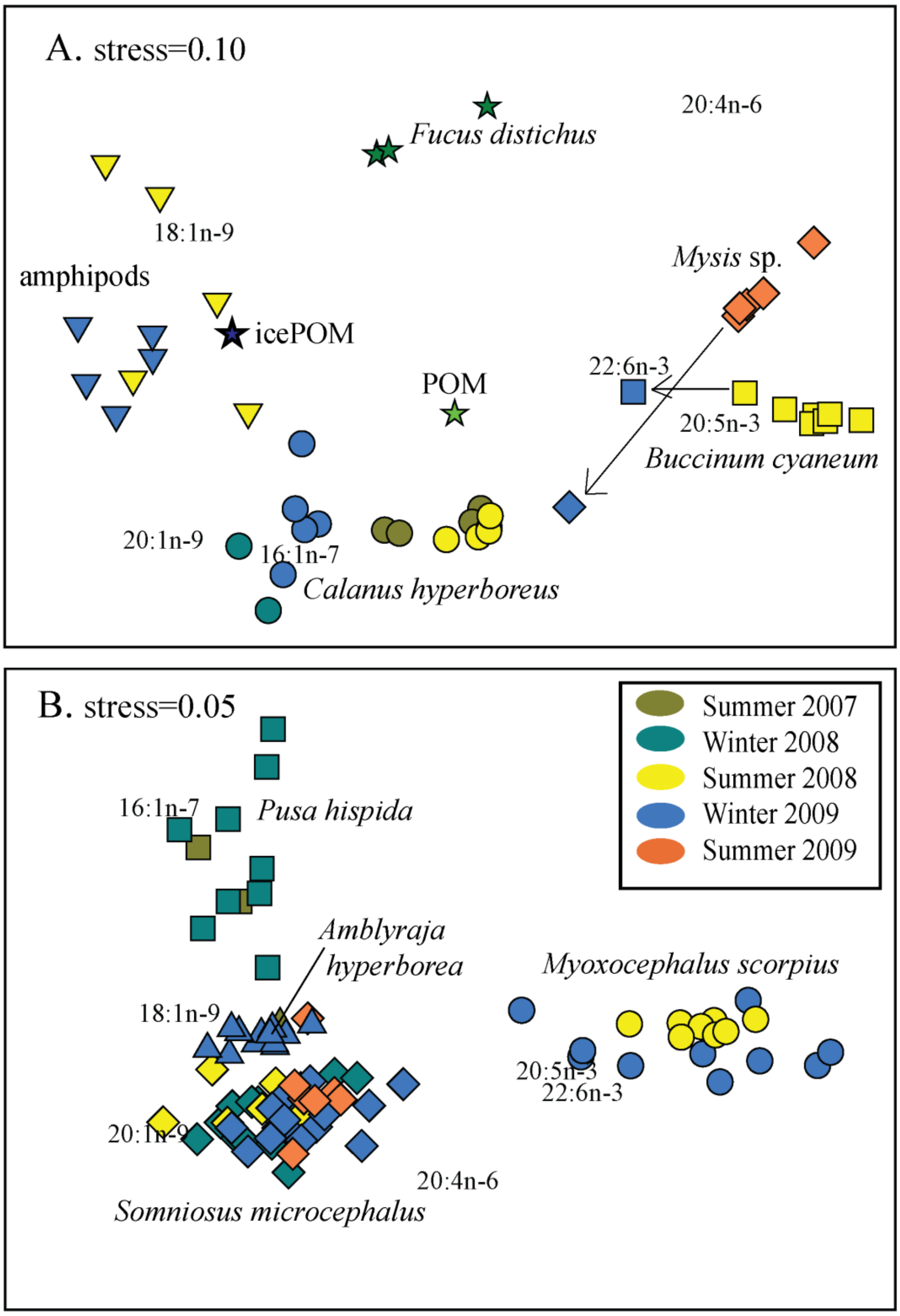
Shelf ID (from Carmack and Wassmann 2006): 1. Bering/Chukchi Sea (shallow inflow shelf) 2. Barents Sea (deep inflow shelf) 3. Beaufort Sea (narrow interior shelf) 4. Kara/Laptev/Siberian Seas (wide interior shelf) 5. Canadian archipelago (network outflow shelf) 6. East Greenland (longitudinal outflow), * Balsfjorden, northern Norway

Fig. S6.1. Mean ± SD of δ^{13}C and δ^{15}N (‰) for basal resources sampled from various arctic regions (references indicated by numbers on x axis) during summer and winter.



Resources: particulate organic matter (POM), POM detritus (detritus), sedimenting particles (Sed.Part.), sediment, macroalgae; References (location): 1. Sato et al. 2002 (Svalbard), 2. Søreide et al. 2008 (Svalbard), 3. Lovvorn et al. 2005 (Bering Sea), 4. Legenzynska et al. 2012 (Svalbard), 5. Baerfind et al. 1997 (east Greenland), 6. this study (eastern Baffin Island)

Fig. S6.2. Non metric multidimensional scaling performed on A. primary producers, zooplankton and benthos and B. fish and marine mammal consumers sampled from Cumberland Sound, Nunavut during summer (August) and winter (April).



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CHAPTER 7

GENERAL DISCUSSION

FINDINGS

Theoretical and empirical studies have revealed that resource variability (Polis and Strong 1996; McCann and Rooney 2009), consumer coupling of these resources in space (Rooney et al. 2006) and perhaps in time (Polis et al. 1996; McCann et al. 2005), as well as intra-specific diet variability (i.e. individual specialization (IS), Bolnick et al. 2003; Araújo et al. 2011), are common structures in real food webs (Fig. 1.1-1.3). Beyond being common, however, these structures are associated with the ability of food webs to persist through time by providing a steady resource base to consumers (McCann et al. 2005; Rooney et al. 2006) and decreasing intra-specific competition at the level of individuals (Bolnick et al. 2003; Svanbäck and Bolnick 2005). The goal of this dissertation was to unite the current understanding of energy flow in arctic marine food webs with recent predictions from theory by asking: do predicted structures (i.e. resource coupling and individual specialization (IS), Fig. 1.1-1.3) arise in systems that experience high degrees of temporal environmental variability and abiotic-driven resource fluctuation?

The findings of this dissertation contribute to science in two broad areas: 1) by identifying structures in arctic food webs that are potentially important for their persistence and 2) by revealing the ubiquity of the aforementioned structures in natural systems. Arctic food webs were predicted to be structured differently than previously observed food webs due to lower diversity and biomass in arctic vs temperate, tropical and Antarctic seas (Grebmeier and Barry 1991; Hillebrand 2004; Piepenburg et al. 2011), as well as the long separation between periods of primary production with which arctic animals must contend (Weslawski et al. 1991). Specifically, arctic food webs were predicted to exhibit: 1) low resource coupling in space during the open-water period, due to the dominance of phytoplankton as a resource to both benthic and pelagic consumers (Graeve et al. 1997; Søreide et al. 2006; Renaud et al. 2011), 2) low individual specialization, due to the expectation that arctic consumers will feed as generalists (MacArthur 1955; Rooney et al. 2006) and 3) low temporal resource coupling between summer and winter, due to the likelihood of consumers feeding on similar prey all year and not switching their diet with season (Werner and Auel 2005; Legezynska et al. 2012). Results of this dissertation both agree with and deviate from the above predictions. However, in general, the arctic food webs studied here were structured such that resources varied asynchronously in space (Chapter 3) and time (Chapter 6) and that some, but not all, consumers coupled these resources (Chapter 3 and 6) through generalist feeding behaviour (Chapter 5), which agrees with theoretical predictions for Chapter 3 and 6 (i.e. Figs. 1.1 and 1.3). Conclusions drawn in the present dissertation have several implications, which are discussed below in light of their contributions to science.

CONTRIBUTIONS TO SCIENCE

Food web ecology

Agreement between empirical observations and predicted patterns in Chapter 3 indicates that the coupling of different resources in space by consumers imparts a flexible nature to food webs, and increases their persistence (Rooney et al. 2006). Further, the recognition that not all consumers acted as spatial resource couplers, which has been discussed previously in the literature (Araújo et al. 2011; Matich et al. 2011), has special relevance in the arctic given the nature of these 'non-coupling' consumers. Species like capelin and herring that did not couple phytoplankton and macroalgae resource compartments (Chapter 3), have already increased their presence in arctic seas and shifted arctic food webs towards more pelagic-dominated food chains (Grebmeier et al. 2006). In the context of food web theory, as food webs become increasingly dominated by the 'fast' phytoplankton resource compartment, there will be less of a 'slow' resource base (i.e. benthic/detrital consuming prey) to support consumers when seasonal phytoplankton production ceases.

No arctic ecologist will be surprised by the empirical observations summarized in Chapter 6, notably that zooplankton have different times of peak abundance and that some consumers switch their diet between summer and winter. However, this is the first time that these patterns have been 1) compiled from across the arctic, 2) investigated across an entire food web in both benthic and pelagic animals, and 3) united with predictions from food web theory. The agreement between observed patterns and theoretical predication in Chapter 6 makes a crucial but yet unmade connection between structure and potential function. Similar to the conclusions drawn for space (see preceding paragraph), temporal resource asynchrony and coupling by consumers of this resource variability through time are likely important for the persistence of arctic food webs. By viewing species in arctic food webs in light of their *role*, with regards to acting as a resource coupler or as a resource for upper trophic levels (i.e. by viewing arctic food webs through the lens of food web theory, Fig. 6.7), one has an increased ability to interpret predicted changes associated with a warming climate (e.g. in species composition or biomass) in regards to the potential effects on food web persistence.

Intra-specific trait variation in seasonal environments

Individual specialization is being increasingly reported in a variety of species (Bolnick et al. 2003; Araújo et al. 2011), which runs counter to the notion that generalists are common and important in food webs (MacArthur 1955; Polis and Strong 1996; Polis et al. 1996). Based on results from Chapter 5, even though high IS might be predicted in Greenland sharks, due to potentially high intra-specific competition, the extent of IS was variable through time and is therefore unlikely to remain high in Greenland sharks. Findings of Chapter 5 indicate that Cumberland Sound Greenland sharks feed as generalists, but are able to exploit a small subset of resources for a given time, feeding as 'short term specialists' using the terminology of Bolnick et al. (2003). This result raises the important considerations that studies should make some attempt, not only to document the extent of IS, but to categorize its variability through time. Chapter 5 contributed to science by answering several of the questions raised by Bolnick et al. (2003), including whether populations can be composed of both individual specialists and individual generalists (this was the case in Greenland sharks) and whether IS varies or remains constant through time (it did not in the Greenland shark).

Results of Chapter 5 support the alternate hypothesis for this dissertation, that observed patterns would deviate from theoretical predictions (Fig. 1.2). Unfortunately, data do not exist to quantify the strength of intra-specific competition in Cumberland Sound Greenland sharks, and it cannot be ruled out that low intra-specific competition gave rise to low IS (i.e. and that the theoretical prediction should therefore have been *low* IS). Regardless, Chapter 5 still provides important contributions to science, notably by indicating that populations of apparent generalists, like the Greenland shark, can be composed of individual generalists and that IS can vary through time in an arctic consumer. Clearly, there is a need to further address the extent of IS in other arctic marine consumers, but results from Chapter 5 support the conclusions of Chapters 3 and 6 that flexible feeding behaviour is likely an important strategy for arctic consumers.

Application of stable isotopes and fatty acids

The combined application of stable isotopes and fatty acids to explore consumer feeding behaviour in the arctic is not new (Søreide et al. 2008; Falk-Petersen et al. 2000). This dissertation, however, is the first attempt to apply both chemical tracers to test hypotheses about arctic food web structure generated from recent theory (Rooney et al. 2006; Bolnick et al. 2011). Further, very few studies have attempted to calculate trophic positions of (from $\delta^{15}N$) or relative carbon source use by (from $\delta^{13}C$) species sampled in the winter using stable isotopes (but see Søreide et al. 2008). Several challenges arise when attempting the aforementioned task, including: 1) sampling appropriate baselines during winter and 2) sampling appropriate tissues to capture a diet switch between summer and winter if one exists. Choosing baselines for the open-water food web (Chapter 3), *C. hyperboreus* and the limpet (*T. testudinalis*), was straightforward because these species were known to consume phytoplankton (Søreide et al. 2008) and macroalgae (Fredriksen 2003), respectively. Fatty acids were useful for supporting these designations due to high phytoplankton biomarkers (e.g. 16:1n-7) in the former and macroalgae biomarkers (e.g. 20:4n-6) in the latter (Chapter 3). However, sampling appropriate baselines was more difficult in the winter because *C. hyperboreus* does not feed (Søreide et al. 2008). The fact that the benthic filter-feeding clam (*M. eideri*) had significantly higher $\delta^{15}N$ in winter and that the deposit-feeding polychaete (*C. granulata*) had lower $\delta^{13}C$ (but not significantly so) indicates that these species were incorporating the signature of more degraded material in the winter. Thus, these species were appropriate choices for winter baselines.

Another obvious challenge was whether or not the turnover time of stable isotopes and fatty acids would be rapid enough to allow the detection of a seasonal diet switch if one existed (Chapter 6). To account for this issue, faster turnover tissues like liver (MacNeil et al. 2005) and plasma (Käkelä et al. 2009) were sampled. However, it is important to note that sampling different tissues from different consumers prevented direct comparisons of calculated trophic positions and % reliance on pelagic carbon between species (Chapter 6). The methodology employed in Chapter 6 will be useful for future studies focused on investigating winter food web structure.

In addition to overcoming challenges associated with stable isotopes, this dissertation provides two novel fatty acids data sets that explore: 1) the seasonal lipid strategy of *C. hyperboreus* over two consecutive years (Chapter 2) and 2) the extent that dietary fatty acids are modified by a shark (Chapter 4). Lipids are a hugely important 'currency' in the arctic, and one that is threatened by warming climates due to decreased phytoplankton quality (Falk-Petersen et al. 2007). The results of Chapter 2 revealed that several fatty acids (e.g. 18:1n-9, 20:1n-9) were not consistently depleted in *C. hyperboreus* sampled during late winter vs. summer, suggesting that these fatty acids may actually be retained during the winter for other purposes. One intriguing possibility is that MUFA like 18:1n-9 are important for membrane competency (see discussion in Chapter 2). The data presented in Chapter 2 will be important for future monitoring of *C. hyperboreus* and were important in the context of this dissertation by revealing how variable the seasonal cycle of fatty acids was from year-to-year in this key herbivore from Cumberland Sound.

Chapter 4 revealed that Greenland sharks accumulate higher MUFA in their liver than obtained in their prey, and subsequently, that liver did in fact differ the most from prey fatty acids, as predicted. This information is crucial for future studies focused on fatty acids in sharks and will increase the ability of researchers to more accurately interpret their fatty acid data. Further, results obtained in Chapter 4 were a necessary first step to establish which fatty acid may be appropriate for exploring individual-level resource use by Greenland sharks (Chapter 5). By applying stable isotopes and fatty acids to test predictions from theoretical work, and to study fatty acid metabolism in a lower and upper trophic level arctic consumer, contributions of this dissertation have both theoretical and applied implications.

FUTURE WORK

Findings of this dissertation reveal that arctic food webs do exhibit food web structures similar to those observed in temperate environments and predicted from theoretical models (McCann et al. 2005; Rooney et al. 2006), in spite of their low diversity and high seasonality. Individual specialization, when it did arise, was not stable through time, such that Greenland sharks can be considered generalists or only 'short term specialists' (Bolnick et al. 2003). The next step is to add in detail about when and where these structures differ among arctic areas, and subsequently, where the stabilizing mechanisms of spatial and temporal coupling, as well as the extent of IS, could be differentially important throughout the arctic. Exploring these unknowns will increase our ability to link structure and function in a variety of ecosystems, and to better understand how systems will respond to change. I pose two questions here as directions for future work.

1) What factors drive differences in structure and the strength of different mechanisms among arctic food webs?

Because arctic seas differ in their properties (e.g. benthic-pelagic coupling and productivity, reviewed by Carmack and Wassmann 2006), it is important to now explore in more detail: 1) when and where does the relative *strength* of spatial and temporal coupling, for food web persistence, vary among arctic areas? and 2) what mechanisms generate and maintain these structures? Quantifying the extent of coupling by consumers among different arctic seasons not studied here (e.g. spring, fall) and in different arctic areas would help answer these questions.

Intriguing insight into how the strength of spatial resource coupling by consumers may vary throughout the arctic is provided by work conducted along gradients in the Chukchi and Beaufort seas. Dunton et al. (2006) found that consumers sampled in the Chukchi Sea (including both zooplankton and benthos) used carbon primarily of marine origin ($\delta^{13}C$ ranged from ~ -18 to -21‰), indicating tight benthic-pelagic coupling, whereas conspecifics from the Eastern Beaufort Sea used both terrestrial and marine carbon ($\delta^{13}C$ range ~ -18 to -26‰), indicating weaker benthic-pelagic coupling. A similar situation was indentified within the benthic communities of the Anadyr Water (western Chukchi Sea) and the Alaska Coastal Water (eastern Chukchi Sea) (Iken et al. 2010). Higher benthic-pelagic coupling was concluded to occur in the more productive Anadyr Water (benthic consumers $\delta^{13}C$ range=4.6‰) than in the less productive, more terrestrially influenced Alaska Coastal Water (δ^{13}C range=6‰) (Iken et al. 2010). Iken et al. (2010) found that food chain length did not differ between these two locations, and therefore, the authors found no evidence to support the productivity hypothesis. However, the authors make the important observation that the allocation of biomass to different trophic levels did differ, with benthic biomass being higher and dominated by suspension and surface-deposit feeding clams in the Anadyr Water, and omnivorous/ carnivorous polychaetes dominating infaunal biomass in the Alaska Coastal Water (Iken et al. 2010).

Spatial differences also exist throughout the arctic in what resources drive entire food webs. For example, food webs of the Beaufort Sea area are dependent on microbial-processed terrestrial carbon (Dunton et al. 2012). The requirement of terrestrial carbon to be degraded by microbes prior to incorporation by consumers (Dunton et al. 2012) indicates that these food webs are dominated by 'slow' resource compartments (sensu Rooney et al. 2006). In contrast, food webs in the Canadian arctic, including Cumberland Sound (Chapter 3 and 6), and in the Barents Sea, in Svalbard seas, for example (Renaud et al. 2011), are driven by 'fast' phytoplankton production in the summer, which supports both benthic and pelagic food chains. However, results of the present dissertation reveal that the Cumberland Sound food web was also supplemented by 'slow' energy channels like macroalgae (Chapter 3) similar to the situation in the Beaufort Sea (Dunton and Schell 1987).

Clearly, spatial differences in the availability of basal resources (e.g. phytoplankton, terrestrial carbon) among different arctic areas can give rise to differences in the feeding behaviour of consumers (Dunton et al. 2006; Iken et al. 2010), the community composition with regards to biomass at a given trophic level (Iken et al.

2010) and the energy channel that ultimately contributes to the food web as a whole (Chapter 3, Dunton et al. 2012). Such spatial differences are important because they could provide insight into the relative strength of the stabilizing effects that arise from the food web structures identified in this dissertation. For example, how does the importance of spatial and temporal coupling vary among arctic locations and between arctic and southerly latitudes? Further, there is a need to explore how *much* removal of resource heterogeneity and/or resource coupling by consumers will have a negative effect on persistence?

2) What is the relative effect of resource coupling and individual specialization, within and among predator populations, on food web stability?

There is a need to consolidate the views that both resource coupling by generalist consumers (Rooney et al. 2006) and populations composed of individual specialists (Bolnick et al. 2011) increase food web persistence. Investigating their relative occurrence in food webs is a good place to begin. For example, based on results from the present dissertation (Chapter 4) and previous work (Rosenblatt and Heithaus 2011), a population can be composed of both individual specialists and individual generalists. Further, 'couplers' (i.e. species that feed as generalists on multiple resources in space) and 'non-couplers' (i.e. species that feed as specialists or on only resource channel) can both exist in the same food web (Chapter 3, Matich et al. 2011). Prudent questions to ask are, within a given food web, how many consumers act as couplers and how many consumer populations exhibit IS? How many consumers need to act as resource couplers (sensu Rooney et al. 2006) in a given food web to elicit a stabilizing response? How many populations within a food web need to be composed of individual specialists to effectively increase interactions and decrease interaction strength to elicit a stabilizing response (sensu Bolnick et al. 2011)? What is the relative importance of resource coupling vs IS on food web stability?

Based on results from Cumberland Sound, 57% of consumers sampled for Chapter 3 coupled phytoplankton and macroalgae resources in space (i.e. % reliance on pelagic carbon 10-90%) and 50% of consumers sampled for Chapter 6 coupled resources in time by switching their diet between summer and winter. How do these percentages compare with other arctic habitats and with temperate and tropical food webs? Answers to these questions could lend insight into the relative importance of the structures studied in this dissertation (resource coupling in space and time and IS) for food web persistence.

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From: mcmeans@uwindsor.ca
Sent: Monday, 19 March, 2012 6:57 PM
To: Roos, Paul, Springer SBM NL
Subject: permission to include Marine Biology paper in Dissertation

Hello,

I apologize if you are not the appropriate contact for this question. If not, perhaps you could pass it along to the correct person?

I am writing to request permission to include our paper, which was recently published in Marine Biology, titled Seasonal patterns in fatty acids of Calanus hyperboreus (Copepoda, Calanoida) from Cumberland Sound, Baffin Island, Nunavut DOI 10.1007/s00227-012-1889-6 as a Chapter in my PhD dissertation at the University of Windsor, Canada. Is there any problem with this?

Thank you in advance,
Bailey McMeans

From: Roos, Paul, Springer
Sent: Tuesday March 20, 2012 02:52AM
To: mcmeans@uwindsor.ca
Bcc: Bailey McMeans
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Sent: 17 May 2012 13:11
To: oxfordcopyrights (ELS)
Subject: permission-second request

Hello,

I emailed last week to request written permission to include our revised manuscript currently under review at the Journal of Experimental Marine Biology and Ecology (Ref. No.: JEMBE-D-12-00056, Title: Similarity between predator and prey fatty acid profiles is tissue dependent in Greenland sharks (Somniosus microcephalus): implications for diet reconstruction) in my PhD dissertation. I am defending my dissertation on May 24th and I would greatly appreciate receiving a response as soon as possible.

Please contact me with any questions, or if I should direct my inquiry elsewhere.

Sincerely,

Bailey McMeans
PhD candidate
Great Lakes Institute for Environmental Research
University of Windsor
(519) 253 - 3000, ext. 4246

To: "Bailey C McMeans" <mcmeans@uwindsor.ca>
From: "Parker, Kerry (ELS-OXF)" <Kerry.Parker@elsevier.com>
Date: 05/29/2012 06:40AM
Subject: RE: RE: permission-second request

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