THE STRUCTURE AND FUNCTION OF POLAR MARINE FOOD WEBS

by

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To my friends, colleagues, and most importantly, my family,
who have always stood by me when I was at my best and my worst.

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Abstract

To predict the consequences of anthropogenic and environmental change, understanding the structure and function of food webs is crucial to predicting their robustness and resilience to disturbance. Detailed knowledge of food web structure is particularly needed in the Arctic and Antarctic as the magnitude of environmental change in these regions will be amongst the highest on Earth and will lead to complex changes in species composition and ecosystem function. I explored the structure and function of polar food webs at various levels of resolution from broad meta-food webs, in which both species composition and interactions are integrated over space and time, to regional food webs, which included depth dependent food webs, to highly detailed analyses of the nutritional composition of microalgae. I also addressed two methodological challenges in food web theory: 1) whether predictions of trophic position based on presence-absence feeding links are accurate and 2) the problem of comparing food webs assembled using different methodologies and with varying data quality and resolution. My results show that despite differences in terrestrial-marine biome interactions in the Arctic and Antarctic, polar food webs have broadly similar topologies. However, despite having a similar overall structure, differences in node specific properties, such as species generality and vulnerability, occur between the Arctic and Antarctic and also across a depth gradient. Significant differences were also found in the proportions of major fatty acids in microalgae between high and low latitudes, suggesting that shifts will occur in the nutritional composition of microalgae as global temperatures increase. My results show that despite high structural similarity between the Arctic and Antarctic, important differences in the energy flow pathways between the two regions, and between certain habitats within each region, were identified which may alter the influence of temperature change as well as other disturbances, such as overfishing, on the ecosystems as a whole. My thesis represents a foundational understanding of the structure and function of polar marine food webs that will allow future work to explicitly explore the impacts of anthropogenic disturbances in polar regions and adds to a growing literature on the “who eats whom” structure of ecosystems, an approach that is uniquely suited for addressing complex questions about how ecosystems will change due to anthropogenic disturbance.

List of Abbreviations Used

Abbreviation		Description
%B	Percentage of Basal species	Species with predators and no prey
%Can	Percentage of Cannibals	Species which prey on their own species
%H	Percentage of Herbivores	Species who prey on primary producers
%I	Percentage of Intermediate species	Species with both predators and prey
%Omni	Percentage of Omnivores	Species which prey on primary producers and consumers
%T	Percentage of Top predator	Species with prey and not predators
|ME|		Absolute value of model error
ANOVA		Analysis of variance
BCTP	Baseline-corrected trophic position	δ15N corrected trophic position
C	Connectance	Proportion of actual trophic links to all possible links (L/S^2)
CC	Clustering Coefficient	Probability that two taxa linked to the same taxa are also linked
CC	Clustering coefficient	Average % of pairs of nodes connected to another node and connected to each other
ConDirOmni	Consumer direct omnivory	Fraction of intermediate species that feed on more than one trophic level
ConMeanTL	Mean consumer trophic position	Mean PATP of all intermediate species in the food web
DCij		Fraction of j in the diet of i
DD	Diet Discontinuity	Number of triplets of species with an "irreducible gap" (measure of intervality)
EBS	Eastern Bering Sea	
EFA	Essential fatty acid	Fatty acids which higher trophic position taxa are unable to synthesize but require (i.e. omega-3)
FA	Fatty acid	
GenSD	Generality standard deviation	The number of prey of a taxa standardized by

		L/S
L	Number of links	Number of pred/prey links for a specific species
L/S	Links/Species	Mean number of pred/prey links per species
l_{ij}		1 if species j consumes species i and 0 if not
LinkSD	Link Standard deviation	Standard deviation of the links per species
Loop	Loop	Percent of taxa in a loop (food chain where the taxa appears twice)
MANOVA	Multivariate analysis of variance	
Mean ME	Mean model error	
ME SD	Model error standard deviation	
MUFA	Monounsaturated fatty acid	
n_j		Number of prey species in the diet of species j
nMDS	Non-metric multidimensional scaling	
PATP	Prey-averaged trophic position	One plus the mean TL of all a consumer's prey
PCA	Principle component analysis	
POM	Particulate organic matter	
PUFA	Polyunsaturated fatty acid	
S	Species	
SCL	Shortest chain length	Shortest path length from consumer to basal resource
SFA	Saturated fatty acid	
SimMaxMean	Mean maximum similarity	Mean of the maximum similarity for every node
SimMean	Mean Similarity	Mean link similarity across all nodes
SimStdDev	Similarity standard deviation	Similarity standardized by L/S
SPOM	Suspended particulate organic matter	
SWTP	Short-weighted trophic	The mean of 'prey-averaged trophic position'

	position	and one plus SCL
TLMax	Trophic level max	Maximum trophic level in the food web using prey-averaged algorithm
TLMean	Trophic level mean	Average trophic level for PATP
TLSD	Trophic level standard deviation	Standard deviation of trophic level among the entire web for PATP
TopGen	Top generality	Species with the highest number of prey
TP	Binary estimate of trophic position	Trophic position estimated from presence-absence matrices
TPSD	Trophic position standard deviation	
TROPH	weighted estimate of trophic position	One plus the mean TP, weighted by relative abundance for all prey consumed by a species
TS	Trophic Species	Number of species in the food web after being converted into a trophic web
VulSd	Vulnerability standard deviation	The number of predators of a taxa standardized by L/S
WTP		fractional trophic position
$\delta^{15}N$		Nitrogen stable isotope
$\delta^{15}N$ TP		Nitrogen stable isotope estimate of trophic position

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Chapter 1 Introduction

1.1. Preface

The Arctic and Antarctic are two of the most remote regions in the world. Despite appearing similar, when looking at environmental conditions, they differ strongly geographically with large differences in the extent of marine-terrestrial habitat interactions that can have a marked effect on species composition and food web ecology (Bertness & Leonard, 1976). The Arctic Ocean is almost completely surrounded by multiple terrestrial land masses, whereas the Antarctic is its polar opposite, as it is a terrestrial biome completely surrounded by multiple oceans. Although they have been relatively untouched by humans in comparison to tropical and temperate regions, both polar regions are far from pristine and are currently experiencing a wide range of abiotic and biotic disturbances (Becker & Pollard, 2013; Coetzee & Chown, 2015). Disturbances such as overfishing, pollution, and global warming, result in habitat and biodiversity loss, altering the structure and function of the ecosystems (Garay-Narvaez et al., 2013). In the Antarctic, for example, within a twenty-year period from the 1960's to 1980's, the Wordie Ice Shelf in the Antarctic Peninsula contracted from 2000 to 700 km^2 (Daoke & Vaughan, 1991). Additionally, 4200 km^2 of the Northern Lasen Ice Shelf on the eastern side of the Peninsula collapsed and melted within a matter of days (Rott et al., 1996). Changes in sea-ice cover can have a significant effect on a species feeding ranges, foraging ability, reproduction and other aspects of their life cycle (Post et al., 2013). Low trophic position species such as the Antarctic krill, *Euphausia superba*, are dependent on the sea-ice for all stages of their life cycle (Daly, 1990; Siegel et al., 1990; Flores et al., 2012). As the vast majority of higher trophic position taxa in the Antarctic are dependent on krill for nutrients, changes in the krill population will have a large effect on the rest of the ecosystem. The impacts of habitat loss in the polar regions is also affecting top predators like the polar bear, *Ursus maritimus*, in the Arctic where declines in body condition, size, recruitment, and survival have been associated with loss of sea-ice habitat (Rode et al., 2013). These changes in biodiversity may cause a problem not only for individual species, but entire ecosystems. There is an increasing amount of evidence that biodiversity increases the stability of ecosystem functions through time (Jiang & Pu, 2009; Hector et al., 2010; Campbell et al., 2011; Cardinale et al., 2012); thus, the consequences of loss and changes in polar species can be expected to have wide-ranging impacts.

Given the dependence that humans have on many ecosystem functions, for uses such as food, energy, and clean water, changes in the structure and function of polar food webs is particularly concerning. To understand the potential impacts of various disturbances on biological systems, we must first understand their most basic structure and function. Food webs, or "who-eats-who" networks, are a widely used technique for representing ecosystems with varying levels of detail (Williams & Martinez, 2000). Food webs can range from simplified, highly aggregated networks where nodes represent functional groups of taxa (i.e., large fish) to highly detailed networks that include quantitative information on interaction strength, biomass, and population dynamics of a particular species. Through the use of food webs, we are able to explore how various ecosystems' structure differs, how that will alter energy pathways and if their responses to disturbances differ.

1.2. Thesis Overview

In this thesis I examine differences between the structure of Arctic and Antarctic food webs. By taking a hierarchical approach, starting at the ecosystem level and progressing to trophic groups and key species, I explore the structure of polar food webs providing a framework that can be used to, for example, explore how polar regions will respond to the effects of climate change. My thesis is organized into seven chapters, including the introduction (Chapter 1):

Chapter 2 (Structure and robustness to species loss in Arctic and Antarctic ice-shelf marine ecosystem web) is a comparison between Arctic and Antarctic ice-shelf associated marine meta-food webs that have been integrated over space and time. Previously published data pertaining to species feeding interactions and biodiversity in the polar regions was used to assemble the food webs. Species extinction scenarios, based on the connectance and trophic position of taxa, were simulated to explore which ecosystem was most susceptible to species loss.

Chapter 3 (Estimating trophic position in marine and estuarine food webs) is a focused analysis to validate the accuracy of binary food webs, as those used in this thesis, when predicting the trophic structure of food webs. Binary estimates of trophic position for 366 taxa across eight food webs were compared with estimates based on stable isotopes and gut-content analysis.

Chapter 4 (Arctic and Antarctic food webs) expands upon Chapter 2, extensively reviewing previously published polar food webs from 1954 to 2012, ranging from 12 to 492 taxa/nodes. In addition to a structural comparison, I conducted a hierarchical analysis of how food web properties change along a gradient of whole-web properties to node properties, to the properties of major taxonomic groups and key species. Additionally, I use a comprehensive comparability analysis to determine if variability in taxa resolution and food web assemble methodology affects the comparability of the food webs.

Chapter 5 (Changes in the structure and function of an Antarctic meta-food web across depth) presents one of the first studies on the effect of depth gradients on the structure and function of food webs. I use the largest and most resolved food web from Chapter 4, comprised of 492 taxa and 16, 330 feeding links to assemble detrital (bottom) and phytoplankton (surface) source webs. I explore these two depth dependent webs for structural differences and how they might influence the function of the food web.

Chapter 6 (Variations in microalgae fatty acid proportions across a latitudinal gradient and implications of a warming climate) is a meta-analysis using 1348 micro algae fatty acid profiles exploring the effects of latitudinal gradients on the proportion of fatty acids which represent, on average, more than 1% of the total fatty acid content in micro algae. This chapter explores the impact of changes in the microbial composition on the overall function of the polar ecosystems.

Chapter 7 (Conclusion) provides a general summary of my findings and highlights possible directions for future research pertaining not only to the structure and function of the polar ecosystems, but also to the field of food web theory.

This thesis is an exploration of questions which arose from Chapter 2, which highlighted gaps in our understanding of the structure and function of polar marine ecosystems. Two of the Chapters (Chapter 2 and 3) are published in peer-reviewed journals, the details of which can be found at the end of each chapter. The references and appendices for all chapters are in a single list at the end of the thesis.

Chapter 2 Structure and robustness to species loss in Arctic and Antarctic ice-shelf meta-ecosystem webs

2.1. Abstract

While changes in the structure and dynamics of food-webs associated with sea-ice in polar regions will be among the most pronounced ecosystem-level changes on the planet that will occur with warming temperatures, little is known about how the loss of sea-ice will affect energy flow in polar food webs or whether Arctic and Antarctic sea-ice associated food-webs will respond similarly to species loss. Sea-ice ecosystems are unique from a global warming perspective as increasing temperature will result in the reduction of actual habitat substrate in addition to the air and water warming that will affect most other ecosystems. Over the next century sea-ice declines are predicted to range from 3-67% in the northern hemisphere and 8 to 64% in the southern hemisphere. We assembled meta-ecosystem food webs for Arctic and Antarctic sea-ice ecosystems for terrestrial and marine species that are dependent on the sea-ice to compare their topological structure and structural robustness to species loss. While the Arctic and Antarctic webs generally showed similar topology, a number of differences between the webs were identified including higher trophic species richness in the Antarctic, a right shifted trophic position distribution, and greater generality. Arctic webs had higher looping, clustering, and diet discontinuity suggesting the presence of stronger sub-webs and compartmentalization. Both the Arctic and Antarctic webs showed low robustness to the loss of low trophic position species and highly connected species, with 50% species loss occurring after the removal of ~8% of species. The Arctic web was 33% less robust to deletions when ordered from lowest to highest trophic position than the Antarctic web. Our results suggest that food webs in the Arctic webs

may be more sensitive to species loss as might occur due to sea-ice declines than Antarctic food webs.

2.2. Introduction

It has been predicted that climate change, independent of other stressors, will result in the premature extinction of between 15 and 37% of extant species in the next 50 years (Thomas et al., 2004). Many of these extinctions will occur in the polar regions where the increase in temperature is expected to be more pronounced than in warmer regions, and where many species depend on sea-ice as a critical habitat. While changes in the structure and dynamics of food-webs associated with sea-ice in polar regions will be among the most pronounced ecosystem-level changes on the planet that will occur with warming temperatures (Smetacek & Nicol, 2005), little is known about how the loss of sea-ice will affect energy flow in polar food webs or whether Arctic and Antarctic sea-ice associated food-webs will respond similarly to species loss.

Two aspects of current climate change in polar regions suggest that warming will result in major changes to food web structure and dynamics. First, warming has been predicted to be more pronounced in polar regions than in temperate and tropical regions (Christensen et al., 2007; Turner et al., 2005). Second, warming in polar regions will result in reductions in sea-ice, an important habitat for many polar species, such as micro-algae, which are a major source of carbon (Lizotte, 2001; Meehl et al., 2007). Satellite data since 1978 has shown that annual average Arctic sea ice extent has decreased by 2.7% (*Range* = 2.1 - 3.3) per decade, with especially high decreases in summer of 7.4% (*Range* = 5.0 - 9.8) per decade (Serreze et al., 2003). In Antarctica, there is less confidence in the estimates for sea-ice decline; however, Curran et al. (2003) have suggested a 20% decline in sea-ice since about 1950 in west Antarctica.

Sea-ice ecosystems are unique from a global warming perspective as warming in these ecosystems will result in the reduction of actual habitat substrate in addition to the air and water warming that will affect most other global ecosystems (Anisimov et al., 2007). Sea-ice provides critical habitat and breeding grounds for marine mammals (Wiig et al., 1999; Derocher et al., 2004) and birds (Croxall et al., 2002) and also supports sea-ice algae, one of the main basal pathways of polar food-webs (Bradstreet & Cross, 1982). The strong dependence of many polar organisms on sea-ice suggests that declines in the cover of sea-ice will result in major changes to the energy-flow pathways in polar webs due to changes in abundance of different trophic compartments as well as species extinctions (Tynan & Demaster, 1997; Atkinson et al., 2004). For example, earlier melt-times for sea-ice in spring have increased the frequency of stratification in the upper water column, promoting primary production (Alexander & Niebauer, 1981). Declines in sea-ice extent and duration since 1976 have reduced the abundance of ice-algae, a critical component in the diet of krill during the winters, causing rapid declines in krill abundance from 38%–75% per decade (Atkinson et al., 2004). Krill are a keystone species in the Antarctic and are a primary food resource for many fish (Barbraud & Weimerskirch, 2001), seabirds (Barbraud et al., 2000), and marine mammals (Atkinson et al., 2004). As many species are highly dependent on krill, declines in krill abundance could have cascading effects throughout the food web (Forcada et al., 2005; Rosemond, 1993). Evidence of this has been observed during a two-year study in which the krill biomass decreased four-fold, reducing the krill content of four of the main krill dependent predators' diets by 88-90% (Croxall et al., 1999)

Sea-ice is also a critical habitat for marine mammals and the location of ice edges is extremely important to seabirds (Ainley & Jacobs, 1981). For example, in the Arctic the primary prey of polar bears, the ringed seal, have declined due to reductions in sea-ice cover, which is a critical habitat for their reproduction (Tynan & Demaster, 1997; Derocher et al., 2004; Ferguson et al., 2005). Due to the lengthening of ice-free periods on Hudson Bay, Polar bears have suffered significant population declines and reductions in body weight, which have lead to starvation (Derocher et al., 2004). The consequences of sea-ice declines have also been observed for sea-ice-dependent birds. In Antarctica, penguins (Ainley et al., 2003) and other seabirds (Croxall et al., 2002) have shown dramatic responses to changes in sea-ice extent over the past century. The sea-ice dependent adelie (*Pygoscelis adeliae)* and emperor penguins *(Aptenodytes forsteri*) have nearly disappeared from their northernmost sites around Antarctica since 1970 (Barbraud & Weimerskirch, 2001).

A major impediment to developing predictive models for the effects of warming on energy-flow patterns in polar food-webs has been the lack of similarly constructed food-webs for these ecosystems (Table 2.1) (Jordan, 2003). In the Arctic, ten food-webs have been previously compiled ranging from generalized Arctic webs, that attempt to capture major patterns of energy flow and numbers of trophic compartments (Hobson et al., 2002), to site-specific webs (e.g. Bering Sea, (Blanchard et al., 2002). The number of trophic compartments in previously published Arctic food-webs ranges from 10 (Pattern & Finn, 1979; Tomy et al., 2004) to 65 (Hobson et al., 2002; Nilsen et al., 2008), with none including both marine and terrestrial organisms. For the Antarctic, nine food-webs have been compiled ranging from generalized (i.e. Antarctica, (Mori & Butterworth, 2004)) to site-specific (e.g. Ross Shelf, (Patten and Finn, 1979)). The number of trophic compartments in previously published Antarctic food-webs ranges from 8 (Mori & Butterworth, 2004) to 490 (Jacob, 2005), with three including both marine and terrestrial organisms (Erfan & Pticher, 2005; Jacob, 2005; Cornejo-Donoso & Antezana, 2008).

As a first step towards assembling highly resolved food-webs for the Arctic and Antarctic we compiled Arctic and Antarctic food-webs for ice-associated taxa that included both marine and terrestrial organisms. Our objectives were: 1) to assemble equally resolved and similarly constructed food-webs for the Arctic and Antarctic focusing on higher trophic level taxa (e.g. fish, marine mammals, birds), 2) to compare the topological structure of ice-associated food-webs for the Arctic and Antarctic and 3) to determine if the structural differences between the webs lead to differences in robustness, the number of secondary extinctions that occur, resulting from primary species loss.

2.3. Methods

2.3.1. Meta-ecosystem web assembly

We assembled cumulative meta-ecosystem food webs for each region. In a cumulative food web, feeding relationships are integrated over space and time such that the focus is on detailing energetic links among taxa that co-occur in at least part of the landscape or over some time period (Maschner et al. 2009), such as would be observed in highly seasonal systems such as the Polar regions. The webs differ from local food webs in that they are meta-ecosystem webs, defined as sets of feeding relationships connected by spatial flows of energy and organisms across ecosystem boundaries (Loreau et al., 2003). While the Arctic and Antarctic webs assembled here are composed of multiple regional and habitat specific sub-systems such as the Antarctic Peninsula, the Antarctic in particular has been previously identified as a single functional unit with transfer of energy between regional and habitat subsystems (Cornejo-Donoso & Antezana, 2008).

The study of the topological properties of food webs across larger spatial and temporal scales has become a recent focus in food web ecology. Examples include the Sanak intertidal web, which was assembled using co-occurring species across 5,000 years (Maschner et al., 2009) and the deep-time paleowebs of the Cambrian (Dunne et al., 2008), Late Permian, and Neogene (Roopnarine, 2009). Meta-ecosystem webs differ from local habitat specific food webs as they explicitly incorporate energy flow across spatial boundaries and through time, thus their topological properties are not strictly comparable with local site-specific food webs; however, like all food-webs they focus on energetic links in a system. The assembly rules for constructing both webs were identical, thus the topological structure of the webs can be rigorously compared. Species were chosen to be incorporated in our webs based on the following: 1) taxa were included in the web if they were listed in FishBase.org or Sealifebase.org as being present in polar regions and they are associated with sea-ice (above, in, or under the ice, in the water column under the ice, in benthic habitats that receive detrital input from sea-ice, or present along ice-shelf margins) and there was at least one record of an energetic link between the taxa in the literature, 2) for fish, birds and marine mammals we used additional published sources to identify polar species (see Appendices B Supplement S1). Two exceptions were made to these criteria to deal with migratory and keystone prey species. First, species were included in the web if they resided outside of the polar regions but were dependent on prey that were designated as a polar species (e.g., whales that migrate into polar regions to feed on seasonal krill; Kasamatsu & Joyce, 1995). Second, prey species that are a main dietary component of sea-ice dependent species were included as individual nodes.

2.3.1.1. The Arctic Ice-Shelf Ecosystem

The spatial extent of the marine Arctic was defined as the Arctic Ocean, including the deep Eurasian and Canadian Basins, the surrounding continental shelf seas (Barents, White, Kara, Laptev, East Siberian, Chukchi, and Beaufort Seas), the Canadian Archipelago, and the transitional regions to the South through which exchanges between temperate and Arctic waters occur (Figure 2.1A). These transitional regions include the Bering Sea in the Pacific Ocean and large parts of the northern North Atlantic Ocean, including the Arctic sections of the Nordic, Iceland, Labrador Seas, and Baffin Bay.

2.3.1.2. The Antarctic Ice-Shelf Ecosystem

The spatial extent of the Antarctic web was defined as the Antarctic Ocean and its surrounding waters including the Southern Ocean, Weddell Sea, Amundsen Sea, Ross Sea, South Pacific Ocean, South Indian Ocean, and Scotia Sea (Figure 2.1B). Also included are the island chains of Bouvet Island, Scott Island, and the South Shetland Islands in the Southern Ocean.

2.3.2. Resolution of the meta-ecosystem webs

Food-webs were assembled for coastal marine sea-ice shelf ecosystems for both the Arctic and the Antarctic focusing specifically on ice-associated taxa. Ice-associated taxa were defined as species or basal nodes (such as detritus) that are found on, within, or under the ice (i.e. in the water column or marine benthos) or species that interact in a consumer-resource link with an ice-associated species. The resulting sea-ice webs included a wide variety of taxa with both marine and terrestrial associations including marine mammals, sea-birds, fish, terrestrial vertebrates such as foxes and deer, terrestrial vegetation that grows on ice shelves, marine pelagic and benthic fish, and invertebrates (see Appendices B Supplement S2).

Species lists and binary (presence-absence) feeding links for Arctic and Antarctic taxa were compiled using online databases, including FishBase.org (Froese & Pauly, 2016), Sealifebase.org (Palomares & Pauly, 2016), the primary literature, and technical reports (see Appendices B Supplement S1 for complete reference list). In total, we identified 161 nodes for the Arctic web and 239 for the Antarctic web. Because the diets of many polar species, particularly invertebrates, are incompletely described, the resolution of our webs was not even across trophic levels or taxa. Fish, birds, and marine mammals were resolved to species level, while invertebrates and basal sources were aggregated into functional taxonomic groups. For example, benthic crabs and shrimps, which make up a substantial proportion of the diet of bearded, harp, and ringed seals, were aggregated as “benthic crustaceans”. Such functional taxonomic groups were used for invertebrates and other lower trophic position species to ensure comparable topology between the regions. In a few cases no published dietary information was available. In these cases, which occurred primarily for skates and rays, we used morphological characteristics (i.e. such as jaw structure) and information on species ranges, body size, and diets of conspecifics to assign feeding links. Basal resources were highly aggregated and included detritus, phytoplankton, ice algae, suspended particulate organic matter (SPOM), and plants.

Although the number of species and feeding links would have increased substantially (a recent estimate of biodiversity in the marine Canadian Arctic suggests between 8124 and 58547 species throughout the tree of life; Archambault et al., 2010, and a recent study on the biodiversity of Antarctica includes a taxonomic list for all marine species compiled to form the Register of Antarctic Marine Species, and currently includes over 8200 species; Griffiths, 2010) with the inclusion of basal and low trophic position taxa identified to species, our focus was on constructing food webs based on functionally different taxa.

Trophic compartments were resolved to the highest level resolution at which data on feeding links could be reliably established for both of the webs to facilitate between web comparisons. Specifically, compartment resolution was standardized such that if a compartment could be more highly resolved for one web but not the other, the lower level of resolution was used in both webs. In the Arctic web, 144 nodes (~89%) were resolved to species-level. The 17 nodes not resolved to species-level include invertebrates (n = 12), basal sources (n = 5), and "other juvenile and adult fish". In the Antarctic web, 206 nodes (~87%) were resolved to species-level. The 33 nodes not resolved to species-level include invertebrates (n = 28), basal sources (n = 5), and "other juvenile and adult fish".

2.3.3. Validation

To validate our link data, we compared our binary estimates of trophic position with those calculated using stable isotopes of nitrogen δ^{15}N for 88 Arctic species and 108 Antarctic species (see Appendices B Supplement S2). δ^{15}N values were collected from primary literature for species included in the webs and which resided within the boundaries previously stated. If multiple δ^{15}N values were available, we used the mean across all reported values (see Appendices B Supplement S2 for a full list of all literature sources and the dataset). Because δ^{15}N values alone cannot be used as an absolute measure of trophic position due to variation in δ^{15}N at the base of food-webs among ecosystems, we corrected δ^{15}N values according to the average δ^{15}N values for primary consumers (e.g. species with a binary trophic position of 2) in each web according to Vander Zanden & Rasmussen (1999) as:

$$\delta^{15}\mathrm{NbaselinecorrectedTP} = \frac{\delta^{15}\mathrm{N}_{\mathrm{Consumer}} - \delta^{15}\mathrm{N}_{\mathrm{PrimaryConsumer}}}{3.4} + 2 (\mathrm{Eq.}\,1)$$

To establish the primary consumer baseline, we used every species with a trophic level (*TL)* =2 in the binary matrices that we could find a location-specific (species was sampled in the areas defined above) δ^{15}N value for. The species/taxa used for δ^{15}N baselines are listed in Appendices B Supplement S2. We determined the correlation (Pearson correlation coefficient) for both prey-averaged trophic position (*PATP*) and short-weighted trophic position (*SWTP*) to determine which measure of trophic position best reflected δ^{15}N for baseline corrected *TP* (*BCTP*) as well as between δ^{15}N and *PATP* and *SWTP*. Short-weighted trophic position (*SWTP*) is the average of 'prey-averaged trophic position' (*PATP*) (one plus the mean trophic position of all the taxon's trophic resources) and 'shortest trophic position' (one plus the shortest chain length from the consumer taxon to a basal taxon; Williams & Martinez, 2004). The distributions of δ^{15}N values for both webs were compared by grouping species into ten broad categories including: detritus, phytoplankton, ice algae, zooplankton, benthic invertebrates, pelagic invertebrates, benthic fish, pelagic fish, mammals and birds. For each group the mean δ^{15}N value was calculated along with its standard deviation and standard error (Figure 2.2).

2.3.4. Assessing comparability

We used two methods to ensure that the food webs were constructed similarly. First, we performed a sequential aggregation procedure in which nodes were aggregated according to minimum similarity in feeding links ranging from 100% to 50% (Figure A.1). If the food webs are comparable, changes in food web properties with increasing aggregation should be roughly equivalent in the two webs. We compared the change in eight food-web properties to assess comparability during aggregation, including: number of species, connectance, links per species, fraction of top, and intermediate species, generality standard deviation, vulnerability standard deviation, and mean clustering coefficient (see Table 2.2 for definitions; Figure A.1).

Second, in order to determine the sensitivity of global food web properties, and in particular the relative difference in the value of a food web property between the Arctic and the Antarctic, to the inclusion of species that would not have been present in some of the regional or habitat subsystems or at some temporal periods, we sequentially removed 50% of the nodes from each web randomly. If the difference between both webs structural properties remains relatively consistent, then the structural properties are insensitive to inclusion of nodes and links that would not always be present in the system. We compared the difference between seven structural properties during node removals including; fraction of top and intermediate species, connectance, links per species, generality standard deviation, vulnerability standard deviation and mean clustering coefficient (see Table 2.2 for definitions; Figure A.2).

2.3.5. Food-web topology

All nodes with 100% similarity in predator and prey links were aggregated prior to calculating food-web properties as our interest was in comparing the functional (energetic) structure of the webs. Aggregating nodes or taxa (S) into trophic species (TS) is a standard method used in comparative studies of food-web topology that partially accounts for differences in completeness and resolution across different webs (Dunn et al., 2002a, 2002b). Furthermore, in static non-weighted food webs, species which depend on the same resources and preyed upon by the same predator are energetically identical.

For each food web, we calculated 17 structural properties (Table 2.2). Two standard measures of food-web trophic interaction richness are reported: links per species (L/S), which equals the mean number of species' predators plus prey, also referred to as link density; and connectance (C), where $C = L/S^2$, the proportion of all possible trophic links (S^2) that are actually realized (L), also referred to as 'directed connectance.' Six properties give fractions of types of species in a food web: top (*T*) (taxa that lack any predators or parasites), intermediate (*I*); cannibals (*Can*); omnivores (*Omn*) (taxa with food chains of different lengths, where a food chain is a linked path from a non-basal to a basal species); herbivores plus detritivores (*Herb*); and species involved in looping (*Loop*) by appearing in a food chain twice. Fraction of basal species (*B*), taxa that lack any prey items, were not considered due to the high level of aggregation at the basal level. Short-weighted trophic position (*SWTP*) is the average of 'prey-averaged trophic position' (*PATP*) (one plus the mean trophic position of all the taxon's trophic resources) and 'shortest trophic position' (one plus the shortest chain length from the consumer taxon to a basal taxon; (Williams & Martinez, 2004)). We report three related measures, the maximum trophic level (*TLMax*), the mean trophic level (*TLMean*) and the trophic level standard deviation (*TLSD*), all based on short-weighted trophic position. The standard deviation of mean generality (*GenSD*), describes how many prey items a species has, and vulnerability (*VulSD*), how many predators a species has. These two measures quantify the variabilities of species' normalized predator and prey counts (Schoener, 1989). We used diet discontinuity (*DietDis*) defined as the number of triplets of species with an "irreducible gap", i.e. a gap in a consumer's diet that cannot be made contiguous because of the constraints imposed by other consumers' diets, divided by the number of possible triplets (Stouffer et al., 2006) as a measure of intervality. We also report one measure of 'small-world' network structure (Watts & Strogatz, 1998), the clustering coefficient (*Clust*), which is the mean fraction of species pairs connected to the same species that are connected to each other (Camacho et al., 2002; Dunne et al., 2002a; Montoya & Sole, 2002; Williams et al., 2002).

Cumulative degree distributions (Dunne et al., 2002a; Williams, 2009) were used for both the predator and prey in order to more rigorously explore differences in generality and vulnerability (Figure 2.3). Cumulative degree distributions show the fraction of trophic species *P (k)* which have *k* or more trophic links (for both predator and prey; Dunne et al., 2002a). When comparing between the Arctic and Antarctic, the degree distributions were compared based on the maximum degree (i.e. maximum number of predator and prey species) and the degree of the exponential decay.

2.3.6. Species loss simulations

Species loss simulations were conducted as in Dunne et al. (2002b, 2004), Srinivasan et al. (2007), and Coll et al. (2008). The structural robustness (R_{50}) of food webs to species removal was calculated as the fraction of primary removals needed to collapse the webs to 50% of their original size. To relate the degree of food web robustness with extinction, we explored the potential effects of different types and magnitudes of species removals to trigger cascades of secondary extinctions. Secondary extinctions result when a consumer species loses all of its prey items or when a cannibalistic species loses all of its prey items except itself.

Species loss was simulated in both Arctic and Antarctic webs using a sequential deletion protocol (Dunne et al., 2002b, 2004; Memmott et al., 2004; Srinivasan et al., 2007; Dunne & Williams, 2009) using five different scenarios: (1) the most-connected (*MC*) species were removed sequentially; (2) the least-connected (*LC)* species were removed sequentially; (3) 1000 sequential random removal sequences (*R*); (4) species with the highest trophic position (*H-L*) were removed first; (5) species with the lowest trophic position (*L-H*) were removed first.

Because primary producers in polar regions are highly vulnerable to extinction due to sea-ice decline, all deletion sequences, except for the random sequences, were run including and excluding basal species. The basal species were not protected in the removal of random species because the percent of basal species in the webs were not high enough to show differences between simulation with and without basal species, in the average of the 1000 iterations. While it is generally acknowledged that including basal species in deletions can lead to large losses and not particularly informative results (Dunne et al., 2002b), we included basal species in the deletion sequences due to the critical role of sea-ice algae in these systems.

2.4. Results

2.4.1. Comparability

Sequential node aggregation from 100% to 50% showed similar trends in change in the eight food web properties analyzed. Detailed results for each property can be found in Figure A.1. Random removal of nodes resulted in only marginal changes to the differences between web properties in the Arctic and Antarctic and the relative magnitude of differences in food web properties were preserved throughout the removal sequence, suggesting that the webs are not sensitive to any methodological error associated with the inclusion of nodes that would not be present in specific subsystems or during defined temporal periods (Figure A.2). Combined, these analyses show high comparability between the Arctic and Antarctic webs and low sensitivity to the inclusion of nodes that might differ in subsystems.

2.4.2. Direct Comparison of Food Webs

A complete set of food web properties can be found in Table 2.2 for both the Arctic and Antarctic. Taxa richness was 161 in the Arctic and 239 in the Antarctic. When aggregated into nodes with 100% similarity in predators and prey, trophic richness (*TS*) was 46% greater in the Antarctic than the Arctic ($TS_{Arctic} = 152$, $TS_{Antarctic} = 224$). Connectance (*C*) was ~ 30% higher in the Arctic ($C_{Arctic} = 3.9\%$, $C_{Antarctic} = 3\%$). The number of links per species (*L/S*) was lower on average by almost one less link per species in the Arctic ($L/S_{Arctic} = 5.99$, $L/S_{Antarctic} = 6.74$).

Mean short-weighted trophic position was similar for the Antarctic and Arctic ($Mean\ SWTP_{Arctic}$ = 3.42, $Mean\ SWTP_{Antarctic}$ = 3.38), however the distribution of prey-averaged trophic position (*PATP*) was left-shifted in the Arctic, specifically for species with a trophic position above 4 (Figure 2.4). The average minimum food chain length was the same in both the Arctic and Antarctic (FCL_{Arctic} = 2.78**,** $FCL_{Antarctic}$ = 2.78).

The fraction of top predators in the Antarctic was 42.5% greater than in the Arctic *(*$\%T_{Arctic}$ = 7.8, $\%T_{Antarctic}$ = 11.1). The fraction of intermediate species was similar in both the Antarctic and Arctic *(*$\%I_{Arctic}$ = 88.8, $\%I_{Antarctic}$ = 86.6). Diet discontinuity was roughly twice as high in the Arctic as in the Antarctic ($DietDis_{Arctic}$ = 0.36, $DietDis_{Antarctic}$ = 0.2). The clustering coefficient was 30% higher in the Arctic than the Antarctic (CC_{Arctic} =0.23, $CC_{Antarctic}$ = 0.17) and looping was over twice as high in the Arctic ($\%Loop_{Arctic}$ = 17, $\%Loop_{Antarctic}$ = 8). Standard deviations of vulnerability ($VulSD_{Arctic}$ = 2.2, $VulSD_{Antarctic}$ = 2.11), generality ($GenSD_{Arctic}$ = 1.00, $GenSD_{Antarctic}$ = 1.08), and fraction of cannibals was similar between the webs *(*$\%Can_{Arctic}$ = 11.1, $\%Can_{Antarctic}$ = 10.2).

The Arctic and the Antarctic differed in the cumulative degree distributions for the number of prey per species, with the Arctic having a 40% fewer maximum number of prey links than the Antarctic ($Max\ Prey_{Arctic}$ = 40, $Max\ Prey_{Antarctic}$ = 56). In contrast, the cumulative degree distribution for the number of predators per species did not differ between the webs. Both the cumulative degree distributions for the number of prey and predators per species showed an exponential distribution (Figure 2.3).

2.4.3. Marine Mammals, Birds, and Fish

The species with the highest trophic position in the Arctic was the polar bear, *Ursus maritimus* ($\mathrm{PA}TP_{Max}$ = 5.88). In the Antarctic, the species with the highest trophic position was the killer whale, *Orcinus orca* ($\mathrm{PA}TP_{Max}$ = 5.48). The killer whale had three times as many prey species as the polar bear ($No.\ Prey_{Polar\ Bear}$ = 5, $No.\ Prey_{Killer\ Whale}$ = 15). Arctic whales had a higher number of prey than Antarctic whales ($No.\ Whales_{Arctic}$ = 10, $No.\ Prey_{Arctic}$ = 7.4, $No.\ Whales_{Antarctic}$ = 6, $No.\ Prey_{Antarctic}$ = 6.8). The number of prey for seals and walrus were similar between the webs ($No.\ Prey_{Arctic}$ = 23.5, $No.\ Prey_{Antarctic}$ = 24.6). Antarctic marine birds had a slightly higher mean trophic position compared to Arctic marine birds (TL_{Arctic} = 4.40, $TL_{Antarctic}$ = 4.53). Mean prey count for birds was higher in the Arctic ($No.\ Prey_{Arctic}$ = 9.6, $No.\ Prey_{Antarctic}$ = 7.1) despite the higher species richness of fish in the Antarctic ($No.\ Taxa_{Arctic}$ = 109, $No.\ Taxa_{Antarctic}$ = 161). Mean trophic position differed slightly for fish between the Arctic and Antarctic, though Antarctic fish had a greater number of prey species (TL_{Arctic} = 3.65, $No.\ Prey_{Arctic}$ = 5.5, $TL_{Antarctic}$ =3.59, $No.\ Prey_{Antarctic}$ = 6.6).

2.4.4. Species Removal

The Arctic and Antarctic webs showed very low robustness to deletions when basal species were included in the deletion scenarios and highly similar R_{50}. When the most connected (*MC*) and lowest to highest (*L-H*) trophic position species were removed, both webs collapsed to 50% of their original size after a maximum of 8% of the species were removed (*MC* $R_{50Arctic}$ = 0.079, *MC* $R_{50Antarctic}$ = 0.08, *L-H* $R_{50Arctic}$ = 0.04, *L-H* $R_{50Antarctic}$ =0.054; Figure 2.5A,C). Both webs showed high robustness when species were removed randomly when basal species were included in the deletions ($R_{50Arctic}$ = 0.5, $R_{50Antarctic}$ =0.5).

The Arctic and Antarctic also showed low and similar robustness to species loss when the basal species were protected (i.e., not allowed to be removed in the simulations) for the deletions of the most connected species ($MC\ R_{50Arctic} = 0.079$, $MC\ R_{50Antarctic} = 0.085$; Figure 2.5A). When species were removed in the order of highest to lowest (*H-L*) trophic position no secondary extinctions occurred ($H\text{-}L\ R_{50Arctic} = 0.5$, $H\text{-}L\ R_{50Antarctic} = 0.5$). The primary difference in robustness between webs occurred for the deletion sequence of lowest to highest (*L-H*) ($L\text{-}H\ R_{50Arctic} = 0.1$, $L\text{-}H\ R_{50Antarctic} = 0.15$; Figure 2.5C), with the Antarctic webs showing a 33% higher structural robustness than the Arctic webs.

2.4.5. Validation

We were able to compare $\delta^{15}N$ values for 88 Arctic and 108 Antarctic species. Prey-averaged binary trophic position was highly correlated with $\delta^{15}N$ in the Arctic ($R = 0.74$, $p < 0.001$) and the Antarctic ($R = 0.7$, $p < 0.001$). Short-weighted trophic position showed a similar correlation with $\delta^{15}N$ in the Arctic ($R = 0.72$, $p < 0.001$) and the Antarctic ($R = 0.68$, $p < 0.001$). When prey-averaged trophic position and short-weighted binary trophic positions were compared against the baseline corrected $\delta^{15}N$ trophic position, the Arctic and Antarctic showed slightly different patterns. In the Antarctic, *PATP* and *SWTP* were underestimated for all species. In contrast, in the Arctic *PATP* was underestimated for species with a trophic position above 3.25 and *SWTP* overestimated for all species (Figure 2.6). When the prey-averaged trophic position for the top predators in both webs were compared to average baseline corrected $\delta^{15}N$ trophic position, the polar bear and killer whale differed by 0.02 and 0.49 of a trophic position, respectively.

2.5. Discussion

The webs reported here are unevenly resolved, with higher taxa resolution for higher trophic levels. Despite this, the validation analysis between $\delta^{15}N$ estimates of trophic position and short-weighted and prey-averaged trophic position for 88 taxa in the Arctic and 108 in the Antarctic showed that both webs had a high concordance in trophic position estimates with an R of 0.74 ($p < 0.001$) and 0.72 ($p < 0.001$) in the Arctic and an R of 0.7 (p < 0.001) and 0.68 (p < 0.001) in the Antarctic for prey averaged and short weighted trophic positions respectively. Despite the strong and similar correlations, binary estimates of trophic position were more accurate predictors of baseline corrected $\delta^{15}N$ estimates for the Arctic than the Antarctic. Mean binary estimates of trophic position differed from baseline corrected estimates by 0.3 (*SWTP*) and 0.34 (*PATP*) of a trophic level in the Arctic and by 0.34 (*SWTP*) and 0.91 (*PATP*) of a trophic level in the Antarctic. Prey-averaged binary estimates for the top predators were within 0.02 and 0.49 trophic levels for the Arctic and Antarctic, respectively.

Why our binary estimates performed more accurately for the Arctic than the Antarctic is of interest. Recorded $\delta^{15}N$ values ranged from 0.9 (ice algae) to 21.1 (polar bear) and 0.57 (phytoplankton) to 18.7(killer whale), respectively. Despite the similarity in ranges, the Arctic had a mean $\delta^{15}N$ (12.62), which was 3.2‰ higher than in the Antarctic (9.43). This lower $\delta^{15}N$ average in the Antarctic was driven by a number of trophic groups that had significantly lower $\delta^{15}N$ in the Antarctic than in the Arctic. For example, in the Antarctic seabirds had a mean $\delta^{15}N$ of 9.12 (SD = 1.65) while krill had a mean $\delta^{15}N$ of 4.2 (SD = 0.89). In the Arctic, seabirds had a mean $\delta^{15}N$ of 13.35 and zooplankton had a mean $\delta^{15}N$ of 12.5. The lower $\delta^{15}N$ observed for some trophic groups in the Antarctic relative to the Arctic has been noted previously (Wada & Shibata, 1981) and may be due to differences in environmental factors such as light, differences in growth (Wada & Shibata, 1981; Lajtha & Michener, 1994), or depletion in $\delta^{15}N$ in atmospheric in atmospheric and oceanic sources. The lack of expected fractionation of 3.4‰ from primary producers to herbivores (Minagawa & Wada, 1984) that we observe in the Antarctic (Figure 2.2B) is also interesting. We observed a very wide range in $\delta^{15}N$ for primary producers in the Antarctic such as ice-algae ($\delta^{15}N = 1.8 - 17.9$) and phytoplankton ($\delta^{15}N = 0.57 - 13.79$), with the range in $\delta^{15}N$ for herbivores such as krill ($\delta^{15}N = 3.6 - 5.5$) and bryozoa ($\delta^{15}N = 3.1 - 6.34$) included in the range for primary producers. As a result of the lower $\delta^{15}N$ values in the Antarctic, $\delta^{15}N$ estimates of trophic positions were 0.91 (*PATP*) of a trophic level lower in the Antarctic than expected based on the binary webs. Given the high concordance between our binary estimates of *TP* for the Arctic, which for *SWTP* and *PATP* predicted baseline corrected $\delta^{15}N$ *TP* to within 0.3 and 0.34 of a trophic level, we suggest that that the lack of concordance between our estimates of *PATP* in the Antarctic are due to a combination of environmental differences and potentially differences in trophic fractionation in Antarctic organisms (Figure 2.2B; McCutchan et al., 2003).

Our comparative analysis identified several differences between Arctic and Antarctic webs that are of significant interest. We focus our discussion on differences between the webs in topology and robustness rather than on absolute values of topology as meta-ecosystem webs differ somewhat from site-specific local webs. Firstly, trophic species richness was 46% higher in the Antarctic than in the Arctic and connectance was 30% lower in the Antarctic, consistent with a greater number of nodes in the Antarctic (Riede et al., 2010). Secondly, differences in the topological properties of the Arctic web, including a higher clustering coefficient, higher fraction of species in loops, and higher diet discontinuity, suggest that the Arctic has more distinct sub-webs or trophic pathways. Furthermore, the Antarctic showed a higher number of high trophic position consumers and increased diet generality in comparison to the Arctic. Thirdly, despite these differences, both webs showed a low and similar robustness to species deletions with ~50% of species lost after ~8% of primary removals on average for the most connected sequential deletions. The only major difference in robustness observed between the webs was that Antarctic webs had a 33% higher structural robustness than Arctic webs when the deletion sequence did not include basal species and was ordered from lowest to highest trophic position. Below we discuss each of these results and compare structural properties and robustness to species loss to other polar food-webs and other marine webs.

Trophic species richness was 46% greater in the Antarctic than in the Arctic. The higher trophic species richness in the Antarctic was primarily due to higher fish species richness in the Antarctic ($No.\ of\ Fish_{Antarctic}$ = 161) relative to the Arctic ($No.\ of\ Fish_{Arctic}$ =109), which is likely a function of the physical differences between the regions. For example, despite similar surface areas (i.e. ~ 11 million km^2; NSIDC), the Antarctic is on average five times deeper than the Arctic (Smith & Sandwell, 1997) resulting in more vertical habitat zones and greater niche diversity in the Antarctic (Ekau, 1990).

Connectance was 30% higher in the Arctic than the Antarctic (C_{Arctic} = 3.9%, $C_{Antarctic}$ = 3%) consistent with the lower trophic richness in the Arctic (Riede et al., 2010). While these values of connectance are low compared to other marine food webs (Dunne et al., 2004) they are similar to marine webs with similar numbers of species and resolution skewed towards intermediate and upper trophic level species such as Caribbean Reef web, which has 245 trophic species and C=0.05 (Dunne et al., 2004). Our values for connectance are also within the range reported for more equally resolved food-webs (e.g. 3-32%, Dunne et al., 2004). However, we caution that food web properties calculated for meta-ecosystem webs are not strictly comparable to local site specific food webs. Ice-shelf webs receive subsidies from both terrestrial and marine sources and are composed of a number of relatively independent habitat zones (e.g. above, below, and within the ice). The most evenly resolved and high richness food-webs assembled to date, the Weddell Sea web (Jacob, 2005) and Lough Hyne (O'Gorman et al., 2010), have 491 and 345 nodes and a connectance values of 0.067and 0.042 respectively. The higher connectance of the Weddell Sea web (O'Gorman et al., 2010) relative to the generalized Antarctic web analyzed here is likely due to the restricted spatial extent for the Weddell Sea web.

In addition to differences in trophic species richness and connectance, the Arctic and Antarctic webs differed in a number of additional topological properties suggestive of different and more distinct sub-webs or trophic paths (i.e. detrital versus phytoplankton) in the Arctic relative to the Antarctic. Specifically, the Arctic web had 40% fewer top species (species with no predators), 35% more clustering, over two times the fraction of species involved in loops, and was less interval (i.e. 80% greater diet discontinuity) than the Antarctic web. These differences are suggestive of a food-web with more distinct energy-flow pathways or sub-webs as well as higher compartmentalization. One other major set of differences that we observed between the Arctic and Antarctic food-webs was for cumulative degree distributions of the number of prey per species, which had a maximum value that was 40% higher in the Antarctic. Differences in the frequency distributions of trophic positions were also left shifted in the Arctic. These differences suggest a structural difference between the Arctic and the Antarctic that is not simply related to higher *S* in the Antarctic. In general, these differences in feeding links suggest that Antarctic consumers have higher trophic positions and are more generalized in their diets than Arctic consumers.

Because many topological properties are strongly correlated with *S* and *C*, food webs models are typically used to correct for differences in S and C when comparing properties across webs (e.g. Williams & Martinez, 2000). We did not use this approach here as we were interested in the actual empirical differences between the webs and not in how well the webs were described by models such as the niche model. Thus, it is important to determine whether the topological differences we observed were simply due to co-variation with differences in *S* and *C*. A number of the differences in food-web properties that we observed suggest that they were not simply due to differences in *S* and *C*. For example, Vermaat et al. (2009) have shown that *S* is strongly positively correlated with *L/S*, chain length, chain number, while *C* is positively correlated with *Clust*, *%Int*, *%Can*, *%Omn*, *%Loop*, and mean *TL*, and negatively with *Path*, *VulSD*, *%Top*, and *LinkSD*. Based on these patterns we should have observed positive associations between *C* and both *CC* and *%Loop*. For *CC*, the magnitude of the difference in clustering (35% difference) was similar to the difference in *C* (30%) suggesting that clustering was only slightly higher in the Arctic than the Antarctic. In contrast, we observed over a 200% increase in looping in the Arctic versus the Antarctic. The higher fraction of loops in the Arctic is thus unlikely to be simply an artefact of *C* differing from 3 to 3.9% in the Antarctic relative to the Arctic. Diet discontinuity has not yet been addressed in the literature in relation to variation in *S* and *C*, however the 80% greater diet discontinuity in the Arctic argues against this being a spurious result of associations between *S*, *C* and other food-web properties.

Both the Arctic and the Antarctic experienced a large number of secondary extinctions when the most connected species were removed sequentially and when deletions were ordered from lowest to highest trophic position, with the webs collapsing to less than 50% of their initial trophic richness after only ~8% of primary removals. In polar webs, lower trophic position species are almost completely dependent on the sea-ice for survival (Garrison, 1991; Arrigo and Thomas, 2004). Figure 2.7 shows that although low trophic position species are directly dependent on sea-ice, a large portion of the remaining species in the food web, including top species, can be linked to low trophic position species within three feeding links. For example, krill, which are a major food source for more than 25% of the species in the Antarctic food web, are highly dependent on sea-ice microalgae as prey (Huang et al., 2006; Dauby et al., 2001). A decline in krill abundances could result in a cascading effect up the food-web, affecting species such as penguins (Boyd, 2002), seals (Boyd, 2002), many fish species (Takahashi & Iwami, 1997), and other large marine mammals (Pauly et al., 1998), all of which can be linked to the krill within three feeding links.

It has previously been shown that marine food webs are more structurally robust to species loss compared to other food webs from other habitat types (e.g. freshwater, terrestrial; Dunne, 2004). The high robustness of marine food webs relative to other webs is generally thought to be related to their greater connectance, a property that is generally linked to higher structural robustness (Dunne et al., 2002b, 2004). The polar webs described here had very low connectance, thus the low robustness to species loss was expected. The only major difference in robustness observed between the webs was that Antarctic webs had a 33% higher robustness than Arctic webs when the deletion sequence did not include basal species and was ordered from lowest to highest trophic position. The 42% greater trophic species richness observed in the Antarctic web may have partially accounted for its higher robustness to the deletions of most-connected and sequential deletions of lower to higher trophic position species. Our results for robustness suggest that Arctic webs may experience a greater magnitude of secondary extinctions if lower trophic level species are adversely affected by warming than Antarctic webs.

Our comparative analysis of the topology and structural robustness of Arctic and Antarctic meta-ecosystem food webs for ice-associated species suggest that despite broad similarities in topology, there are a number of potentially important topological differences between Arctic and Antarctic regions. First, Arctic webs are more connected, clustered, have higher looping, and greater diet discontinuity than Antarctic webs. These properties suggest that Arctic webs contain more distinct pathways of energy flow such that they might contain more distinct sub-webs and are more compartmentalized than Antarctic webs. While these features are potentially associated with a greater robustness to perturbation (Stouffer & Bascompte, 2011), sequential species removals showed that when most connected species are removed or when species are removed from lowest to highest trophic position, Arctic webs were less robust to species loss, with 33% lower robustness than Antarctic webs. The higher robustness of the Antarctic webs can be related to a number of aspects of the topology including higher species richness, higher fraction of top predators, and more generalized diets of species in the Antarctic. While the patterns of species loss or change in biomass will likely differ substantially in Arctic and Antarctic regions due to habitat differences related to the nature of the ice-cover, which is floating in the Arctic and land-associated in the Antarctic, our comparative analysis of food-web topology and robustness suggests that even without these broad habitat differences, the nature of the changes that will occur with sea-ice reduction in Polar regions may differ somewhat, with Arctic webs being more sensitive to cascading extinctions following species loss than Antarctic webs.

The work in Chapter 2 also appears in: Carscallen, W.M.A., Romanuk, T.N. 2012. Structure and robustness to species loss in Arctic and Antarctic ice-shelf meta-ecosystem webs. Ecological Modelling. 245: 208-218.

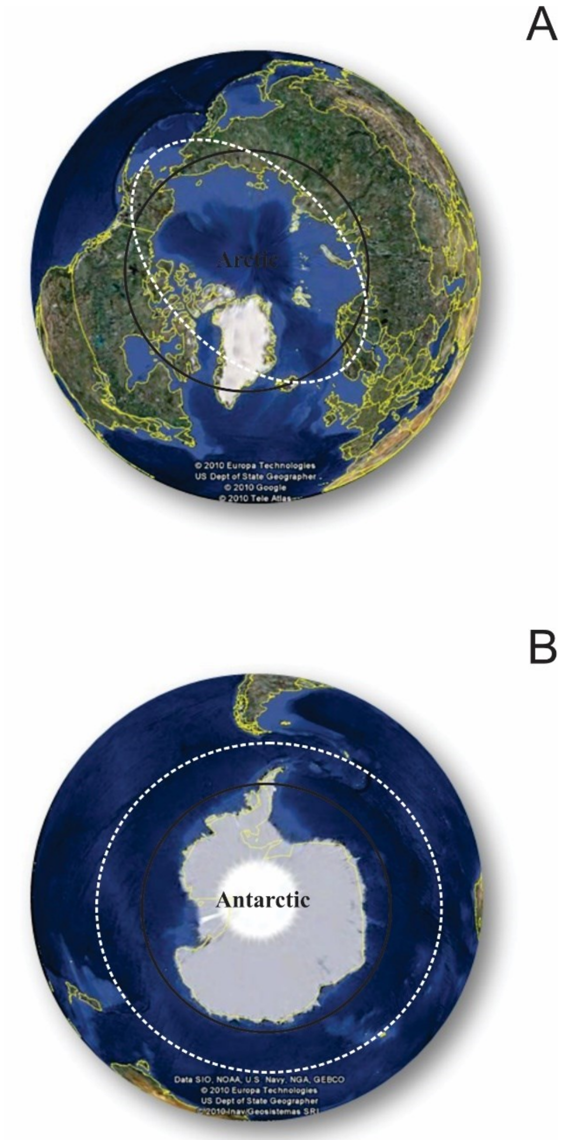


Figure 2.1: Geographical image of the Arctic (A) and the Antarctic (B) sea-ice habitats. Black circles represent the Arctic and Antarctic circles and the area which the majority of the species in the food webs reside. The white dotted area represents an extended range for species included in the web which did not primarily reside within the polar circles, but which had a high interaction strength with ice-associated species.

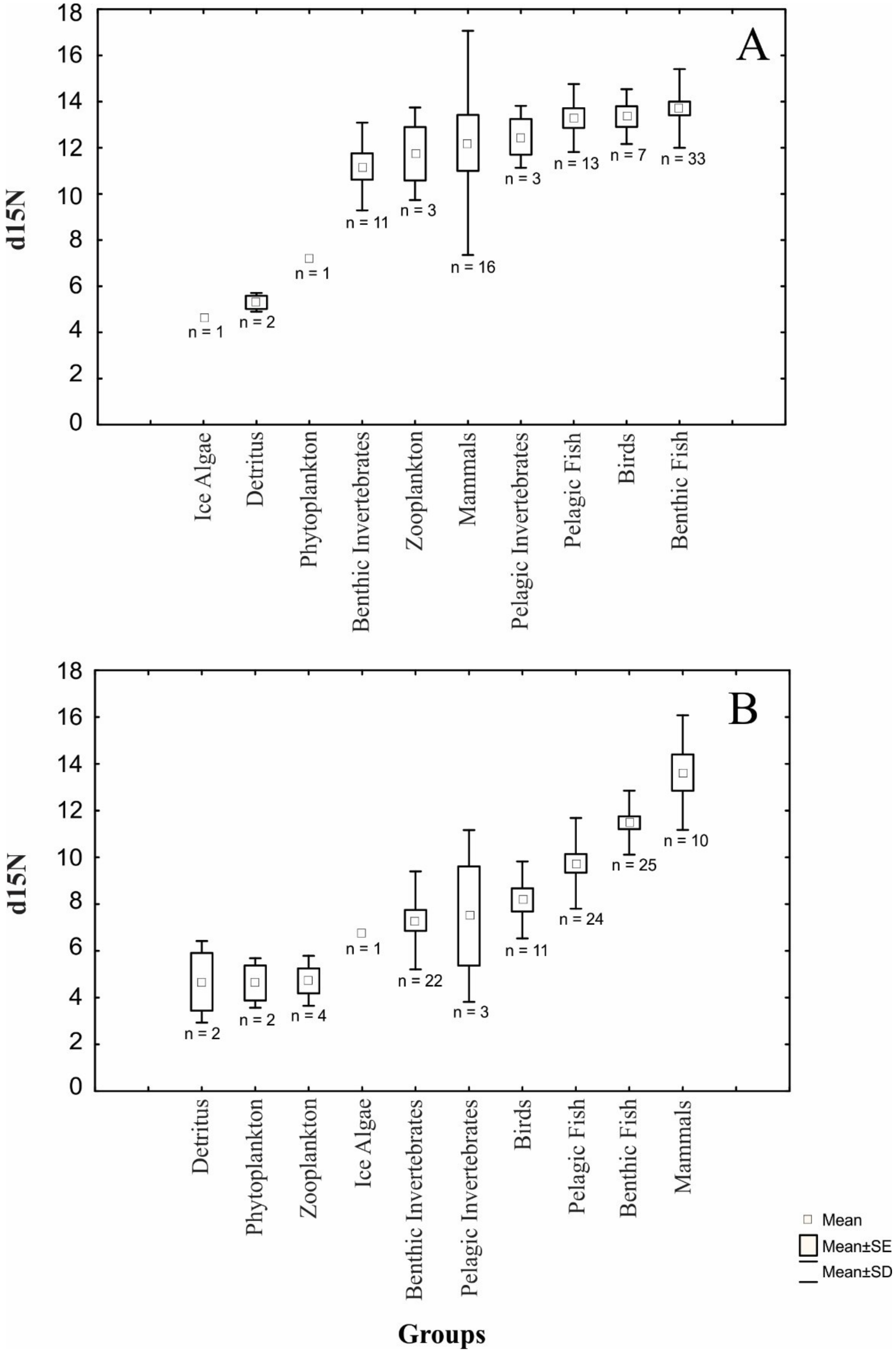


Figure 2.2: Mean δ^{15}N distribution for the Arctic (A) and Antarctic (B) after species had been consolidated into 10 groups ordered from lowest to highest mean δ^{15}N levels. ‘n’ represents the number of species or trophic compartments in each group.

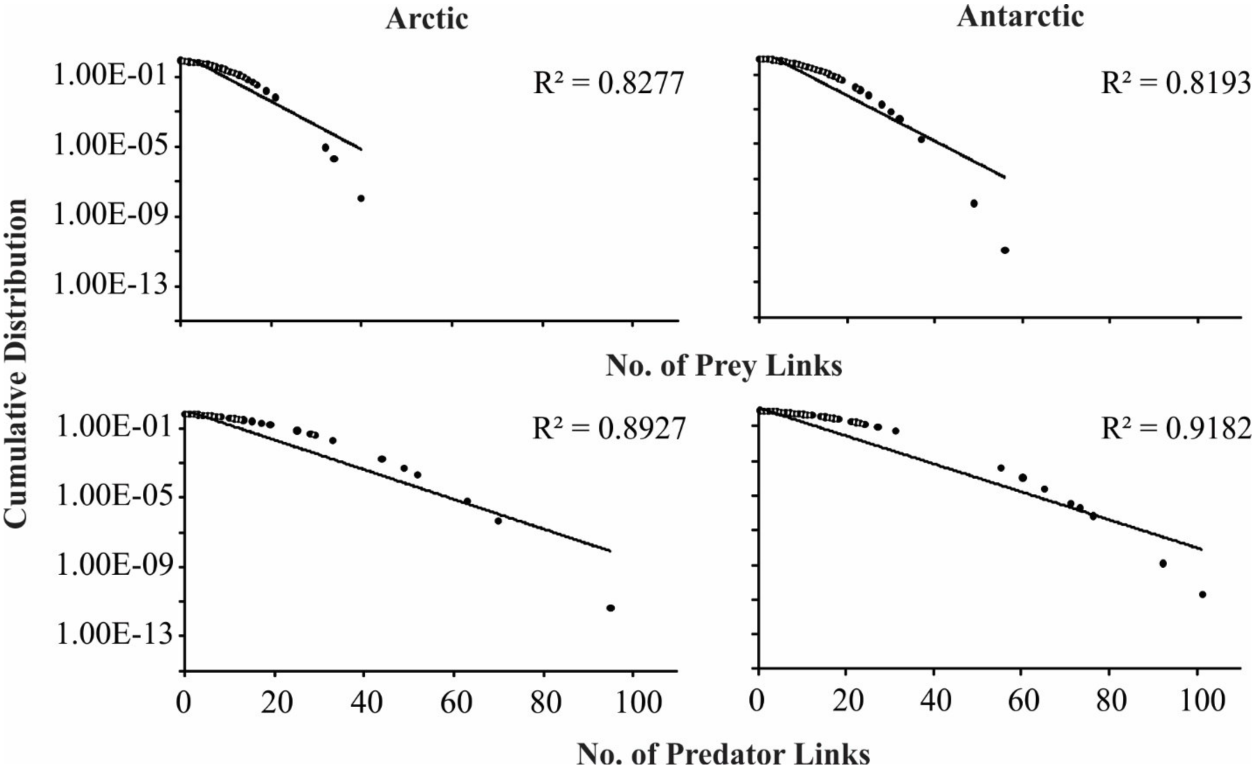


Figure 2.3: Log plots of the cumulative distribution for both the number of predators and prey per species in the Arctic (A) and Antarctic (B). Both ecosystems show a exponential decay behaviour. The distribution of the number of prey links is a representation of the generality of the species. The distribution of the number of predator links is a representation of the vulnerability of the species.

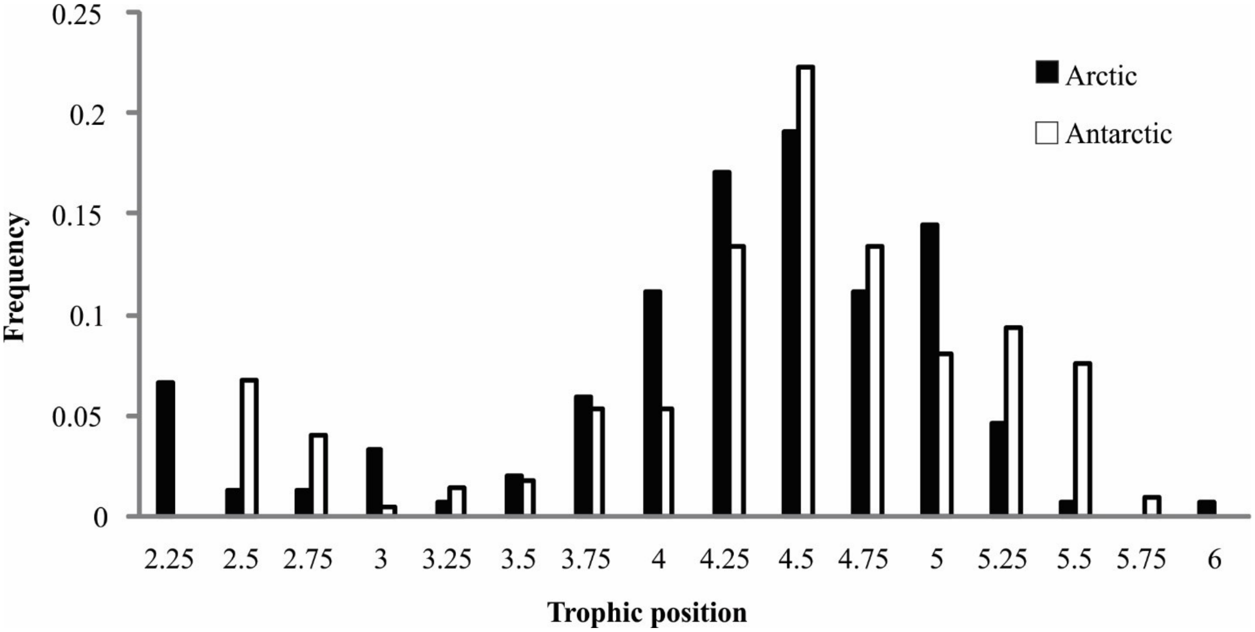


Figure 2.4: Distribution of trophic positions for both the Arctic (black) and Antarctic (white). Basal species were removed to eliminate any zero bins between a trophic position of 1 and 2.

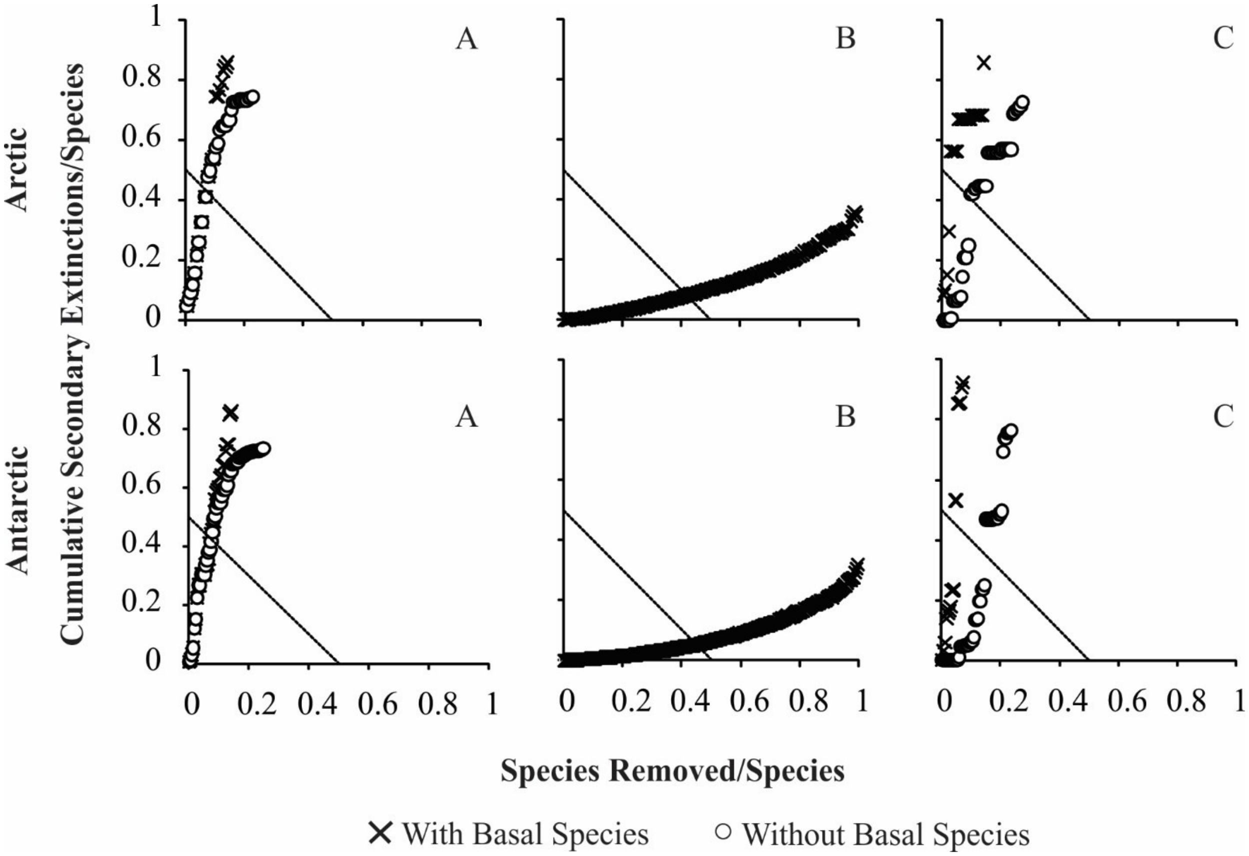


Figure 2.5: Cumulative secondary extinctions due to primary species loss in Arctic (Top) and Antarctic (Bottom) food webs. Each graph corresponds to a specific species removal scenario, where S corresponds to the initial number of species in the web. A – Most connected species, B – Random species averaged over 1000 iterations, C – Lowest to Highest trophic species. The dotted lines indicate when 50% of the species have been lost through primary and secondary extinctions.

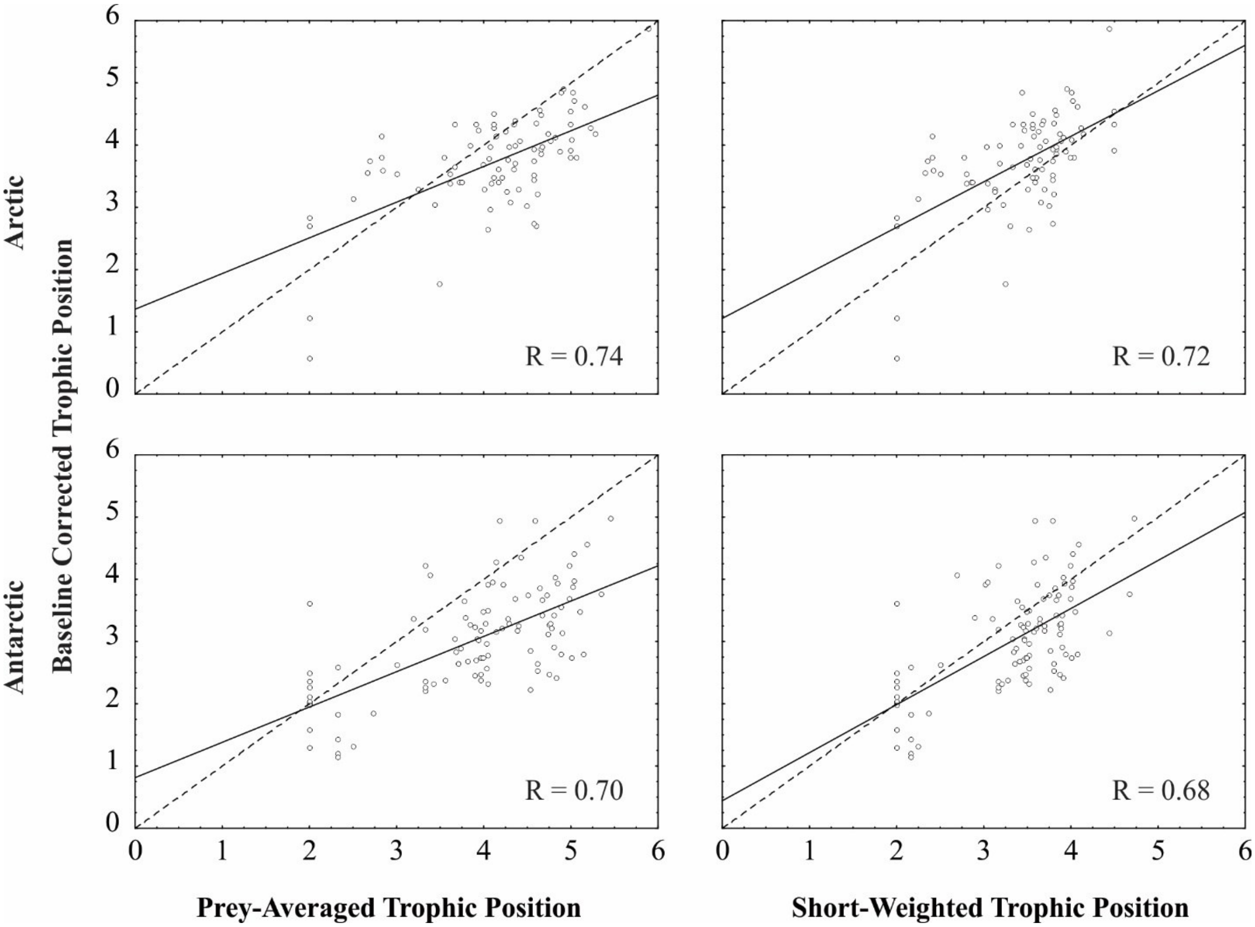


Figure 2.6: δ^{15}N estimated trophic positions vs. prey-averaged and short-weighted trophic positions. Dotted black line represents 100% correlation. Solid black line represents the line of best fit.

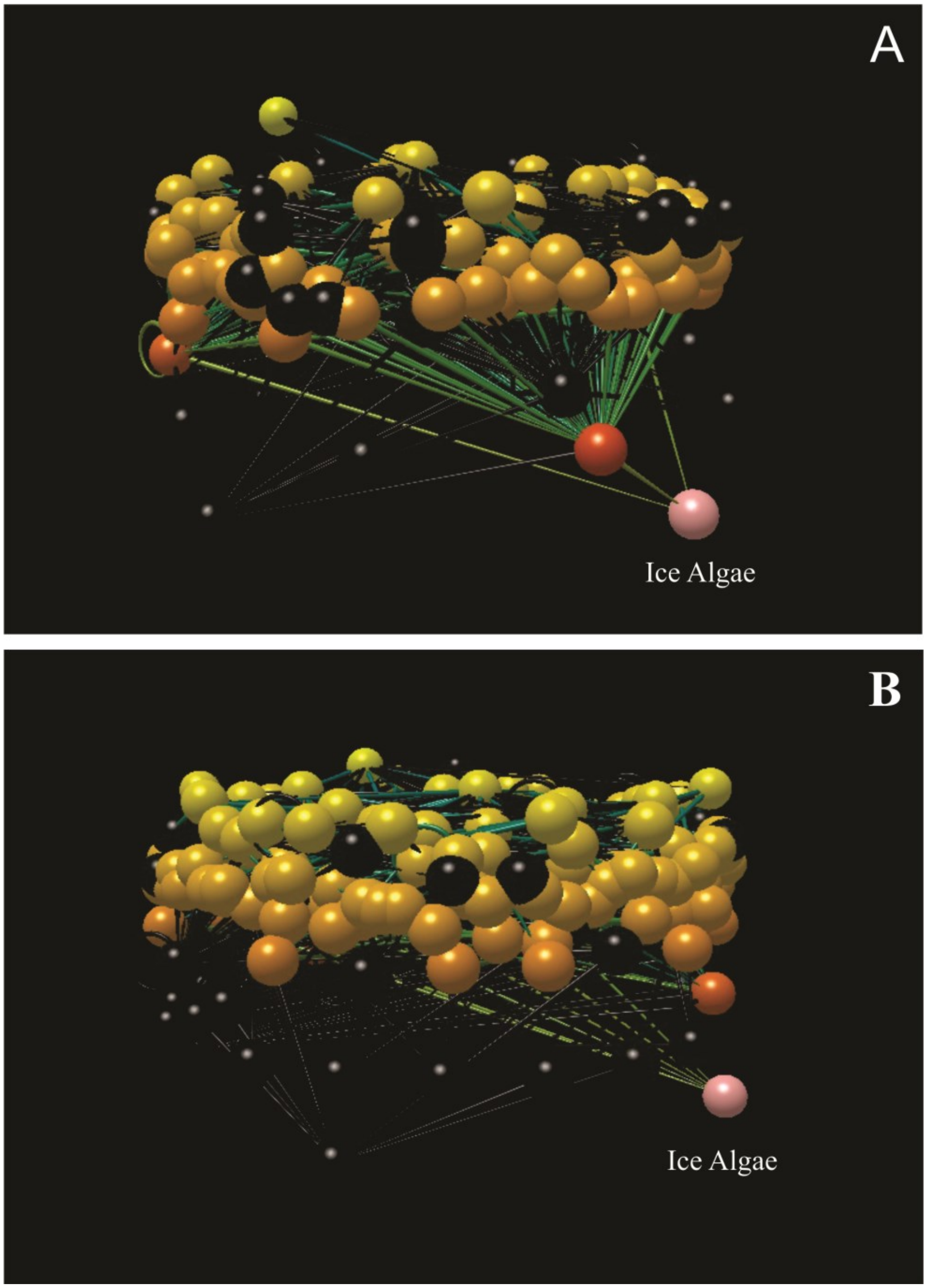


Figure 2.7: Feeding links for Sea ice algae in the Arctic (A) and Antarctic (B), with a maximum shown chain length of three. The highlighted nodes represent the predators for each connecting node below itself. The height of the nodes represents the trophic position. The blacked out nodes represent species which are not connected, within three feeding links, to sea-ice algae.

Table 2.1: List of previously published binary and quantitative food webs for the Arctic and Antarctic

	Region	S	Binary or Quantitative	Marine or Terrestrial	Reference
Arctic	Arctic (North Norway)	65	Quantitative	Marine	Nilsen et al. 2008
	Arctic Seas	22	Binary	Marine	Dunbar. 1954
	Barents Sea	41	Quantitative	Marine	Blanchard et al. 2002
	Barents Sea	30	Quantitative	Marine	Dommasnes et al. 2001
	Canadian Arctic	24	Quantitative	Terrestrial	Krebs et al. 2003
	Eastern Arctic	10	Quantitative	Marine	Tomy. 2004
	Eastern Bering Sea	29	Quantitative	Marine	Trites et al. 2004
	Bering Sea	41	Quantitative	Marine	Ciannelli et al. 2004
	High Arctic	65	Quantitative	Marine	Hobson et al. 2002
Antarctic	Falkland islands	44	Quantitative	Marine	Cheung & Pitcher. 2005
	Antarctic Pack ice zone	19	Binary	Both	Knox. 1970
	Ross Sea	10	Binary	Marine	Patten & Finn. 1979
	Antarctic Seas	14	Binary	Marine	Mackintosh. 1964
	Antarctic Peninsula	28	Quantitative	Both	Cornejo-Donoso & Antezana. 2008.
	Western Antarctic Peninsula	35	Quantitative	Marine	Daniels et al. 2006
	Antarctic Shelf	490	Quantitative	Both	Jacob. 2005
	Antarctic Peninsula	39	Quantitative	Both	Erfan & Pitcher. 2005
	Antarctica	8	Quantitative	Marine	Mori & Butterworth. 2004

Table 2.2: Arctic and Antarctic structural trophic food web properties

Food- Web Properties		**Arctic**	**Antarctic**	**Description**
Species	*TS*	152	224	Number of species in the food web after being converted into a trophic web
Links/Species	*L/S*	5.99	6.74	Number of pred/prey links per species
Link Standard deviation	*LinkSD*	1.17	1.14	Standard deviation of the links per species
Clustering Coefficient	*CC*	0.23	0.17	Probability that two taxa linked to the same taxa are also linked
Connectance	*C*	0.039	0.03	Proportion of actual trophic links to all possible links (L/S^2)
Percentage of Top predators	*%T*	7.8	11.1	Species with prey and not predators
Percentage of Intermediate species	*%I*	88.8	86.6	Species with both predators and prey
Percentage of Basal species	*%B*	3.2	2.2	Species with predators and no prey
Percentage of Herbivores	*%H*	3.2	4.4	Species who prey on primary producers
Percentage of Cannibals	*%Can*	11.1	10.2	Species which prey on their own species
Trophic level max	*TLMax*	5.88	5.48	Maximum trophic level in the food web using prey-averaged algorithm
Trophic level mean	*TLMean*	4.07	3.98	Average trophic level for PATP
Trophic level standard deviation	*TLSD*	0.9	0.89	Standard deviation of trophic level among the entire web for PATP
Diet Discontinuity	*DietDis*	0.36	0.2	Number of triplets of species with an "irreducible gap" (measure of intervality)
Generality standard deviation	*GenSD*	1	1.08	The number of prey of a taxa standardized by L/S
Vulnerability standard deviation	*VulSd*	2.2	2.11	The number of predators of a taxa standardized by L/S
Loop	*Loop*	0.17	0.08	Percent of taxa in a loop (food chain where the taxa appears twice)

Chapter 3 Estimating trophic position in marine and estuarine food webs

3.1. Abstract

Structural or binary approaches, based on presence-absence of feeding links, are the most common method of assembling food-webs and form the basis of the most well explored food-web models. Binary approaches to assembling feeding links are often criticized as being less powerful and accurate than flow-based methods. To test this assumption, we compared binary estimates of trophic position with estimates based on stable isotope values of nitrogen ($\delta^{15}N$). For 366 species from eight marine and estuarine food-webs, we compared trophic position estimates based on binary (presence-absence) feeding links with estimates based on the stable isotope of nitrogen ($\delta^{15}N$). For a sub-set of 127 fish species in four of the webs, we further compared trophic position estimates based on gut-content analysis using a flow-based algorithm using data from FishBase.org with binary and $\delta^{15}N$ estimates. Across all species and webs, binary estimates of trophic position were strongly correlated ($R = 0.644$) with $\delta^{15}N$ estimates. On average binary estimates differed from baseline corrected $\delta^{15}N$ estimates by 2.33% for mean trophic position and 6.57% for maximum trophic position. On average the difference between binary $\delta^{15}N$ estimates was 0.14 of a trophic level. For the sub-set of 127 fish species binary estimates performed similarly or more accurately in predicting $\delta^{15}N$ values than the flow-based estimates. Binary approaches to assembling feeding links are often criticized as being less powerful and accurate than flow-based methods. Our results show a high concordance between binary and $\delta^{15}N$ estimates of trophic position as well as showing that in some cases binary estimates are better predictors of $\delta^{15}N$ than flow-based estimates, reaffirming the robustness of the structural approach to assembling food-webs. Additional cross-validation studies in other

ecosystems are necessary to determine whether our results can be generalized to terrestrial and freshwater ecosystems.

3.2. Introduction

A species' trophic position, which represents a quantitative measure of its energetic interactions, is one of the most widely used descriptors of the role of species in ecological communities. Trophic position is correlated with variation in body size (Jennings et al., 2001; Bode et al., 2006; Arim et al., 2007, Arim et al., 2010, Romanuk et al., 2010), consumer-resource size ratios (Brose et al. 2006), species ranges (Mace et al., 1983, McLoughlin & Ferguson, 2000), interaction strengths (Wood et al., 2010) and the distributions of energy flow in food webs (Scotti et al., 2009). The maximum trophic position in an ecosystem, or food-chain length, has been shown to be related to aspects of community structure and dynamics, ecosystem processes, and bioaccumulation (Post, 2002). Trophic position is determined by consumer-resource links between species and the distribution of these links provides the basis for determining the topological structure of food-webs (Dunne, 2006). As such, trophic position is correlated with many other key food-web properties, including connectance and variations in the fractions of species with different trophic roles (Vermat et al., 2009).

Changes in food-chain length and trophic position are becoming widely used as indicators of ecosystem degradation (Pauly & Watson, 2005), to assess the impact of fisheries exploitation (Pauly et al., 1998, Pauly & Watson, 2005), habitat fragmentation (Layman et al., 2007), and species invasions (Vander Zanden et al., 1999). Resolving differences in trophic position are also important in studies of niche differentiation and competition (Schneider et al., 2004; Romanuk & Levings ,2005), and for predicting the strength of trophic cascades (Thompson et al. 2007).

Despite the ubiquity of the use of trophic position as a variable in ecological research, few studies have attempted to cross-validate estimates of trophic position based on binary or flow-based methods or between different flow-based estimates such as between gut content analysis and stable isotope analysis. When cross-validation has been conducted between flow-based and stable isotope based estimates of trophic position, the number of comparisons typically only includes a small fraction of the species in an ecosystem and while good concordance is found is some cases (see Vander Zanden et al., 1997; Harvey & Kitchell, 2000; Schimdt et al., 2009), in other cases no, weak, or inconsistent relations are observed (Ribczynski et al., 2008; Franssen & Gido, 2006; Dame & Christian, 2008).

Flow-based methods are also time consuming, expensive, and methodologically involved. Thus, highly and evenly resolved flow-based or isotope based food-webs are still exceedingly rare due to the massive effort involved in assembling these types of quantitative food-webs. This leads to binary (presence-absence) food-webs being the most prominent type of food-web in the literature, forming the basis for the majority of published comparative analyses, theoretical models, and characterizations of food-web structure (Cohen, 1978; Cohen et al., 1990; Williams and Martinez, 2000; Dunne, 2006; Cattin et al., 2004; Vermat et al., 2009). Still, the degree to which binary links reflect actual energy flow patterns in food-webs is poorly understood.

The major criticism levied against binary food-webs is that their presence or absence designation to trophic links inadequately describes the huge variability of flows among links. In the only large-scale comparative study conducted to date, spanning four highly resolved terrestrial and marine webs, binary estimates of trophic position were shown to differ by a quarter of a trophic level on average from empirically derived (e.g. gut content, observation) flow-based estimates (Williams & Martinez, 2004). Thus, in general there appears to be a strong concordance between flow-based estimates of trophic position based on gut content analysis or observation and binary estimates. However, because gut content analysis and observation can bias estimates of trophic position due to limited spatial and temporal extent and the over-representation of non-assimilated materials in diet descriptions (Vander Zanden et al., 1999), a more effective test of the ability of binary webs to reflect actual trophic position is to compare binary estimates with stable isotope estimates (Williams & Martinez, 2004).

Stable isotope estimates represent a temporally and spatially averaged measure of carbon and nitrogen that is actually assimilated by organisms (Schmidt et al., 2007) and thus resolve some of the methodological issues associated with the analyses of relatively episodic gut contents. Early studies on fractionation of nitrogen across trophic levels suggested an average enrichment of 3.4‰ with each trophic level (DeNiro & Epstein, 1981; Minagawa & Wada, 1984). This is a result of the preferential excretion of the lighter isotope during protein synthesis (Kling et al., 1992) which enriches the $\delta\,^{15}N$ of the consumer relative to its diet. Estimating trophic position based on $\delta^{15}N$ is complicated, however by trophic and taxonomic differences in fractionation between resources and consumers (McCutchan et al., 2003), wide variability in $\delta^{15}N$ for basal resources across different ecosystems (Solomon et al., 2008) that requires the establishment of relevant basal baselines (Vander-Zanden & Rasmussen, 1999), and tissue specific fractionation (Hobson & Clark, 1993). Despite these issues, $\delta^{15}N$ estimates of trophic position are widely considered the most rigorous method of determining trophic position.

In this paper, we present the results of a comparison of binary estimates of trophic position and trophic position estimates using $\delta^{15}N$ values for eight marine and estuarine ecosystems compiled from the primary literature. To determine whether flow-based (but non-isotope) links led to higher correlations with $\delta^{15}N$ estimates than binary estimates we compiled weighted estimates of trophic position from fishbase.org for four of the food-webs for which flow-based location-specific data was available.

3.3. Methods

We analyzed five marine food-webs: North Eastern U.S. Shelf, Benguela Current, Adriatic Sea, Arctic sea-ice, and Antarctic sea-ice and three estuarine food-webs: Chesapeake Bay, St. Marks Estuary, and Ythan Estuary. The eight webs were compiled from previously published sources (Baird & Ulanowicz, 1989; Huxham et al., 1996; Yodzis, 1998; Christian & Luczkovich; 1999, Link 2002; Coll et al. 2008; Carscallen & Romanuk, 2012) and six have been used previously in structural analysis and tests of food-web theory (Williams and Martinez, 2000; Dunne et al., 2004; Coll et al., 2008; Vermaat et al., 2009). The food webs include between 29 and 239 species (Table 3.1). Additional details on the webs can be found in Vermaat et al. (2009), Coll et al. (2008), and Carscallen & Romanuk (2012).

We calculated four measures of trophic position (*TP*). Trophic position is a continuous measure of the relative trophic height of a species and is distinct from trophic level which describes categories of trophic modes based on integer values (e.g. herbivores have a trophic level of 2). For all eight webs we calculated two estimates of binary trophic position based on binary feeding matrices: prey-averaged trophic position (*PATP*) and short-weighted trophic position (*SWTP*; Williams & Martinez, 2004) and compiled δ^{15}N estimates of trophic position for as many species from the webs as we could find data for (see below for further details). For NE Shelf, Benguela Current, Arctic sea-ice, and Antarctic sea-ice we also calculated a non-isotope weighted measure of trophic position based on data from fishbase.org (see below for further details).

Prey-averaged *TP* is equal to 1 + the mean *TP* of all the consumer's trophic resources:

$$\text{Prey-averaged TP}_j = 1 + \sum_{i=1}^{s} l_{ij} \frac{TL_i}{n_j} \qquad \text{(Eq.1)}$$

where n_j is the number of prey species in the diet of species (Williams & Martinez, 2004). Short-weighted trophic position was calculated as the average of the shortest *TP* for the species and prey-averaged *TP* (Williams & Martinez, 2004).

$\delta^{15}N$ values were used to determine an isotope measure of trophic position. To compile the isotope database, we conducted an extensive literature review (see Appendices B Supplement S3 for values and sources). Either location-specific $\delta^{15}N$ values from the literature were used or, if none were available, values from nearby similar ecosystems. All previously published studies that report $\delta^{15}N$ for the species within the food web of interest were included. If more than one value was reported an average was used. The spatial extent of the food webs differed with some webs such as Ythan, St. Marks, and Chesapeake being more spatially restricted to a well-defined location while other webs were more regional (e.g. Adriatic, Arctic, Antarctic). For NE Shelf and Benguela, location-specific $\delta^{15}N$ values were available. For Ythan, Chesapeake, Adriatic and St. Marks, $\delta^{15}N$ values were collected from studies in either the exact location or nearby similar ecosystems. For example, for Ythan we included values $\delta^{15}N$ reported for the North Sea. For the Arctic and Antarctic webs, $\delta^{15}N$ values were included throughout the Arctic and Antarctic oceans.

Because $\delta^{15}N$ values alone cannot be used as an absolute measure of trophic position due to variation in $\delta^{15}N$ at the base of food-webs among ecosystems (Post, 2002) we corrected $\delta^{15}N$ values according to the average $\delta^{15}N$ values for primary consumers (e.g., species with a binary trophic position of 2) in each web according to Vander Zanden & Rasmussen (2001) as:

$$\delta^{15}\text{NbaselinecorrectedTP} = \frac{\delta^{15}\text{N}_{\text{Consumer}} \;\; -\delta^{15}\text{N}_{\text{PrimaryConsumer}}}{3.4} + 2(\text{Eq. }1)$$

Primary consumers were used as baseline organisms because their δ^{15}N is more representative of average trends in assimilated nitrogen from primary producers (Post, 2002) due to larger body size and lifespan which contributes to decreased seasonal variability (Vander Zanden & Rasmussen, 1999). In order to find the most accurate baseline value for δ^{15}N in an ecosystem, Vander Zanden & Rasmussen (1999) suggest using a wide range of organisms. To establish the primary consumer baseline we used every species with a *SWTP* = 2 in the binary matrices that we could find an accompanying δ^{15}N value for. The species/taxa used for δ^{15}N baselines are listed in Appendices B Supplement S3.

In order to further explore differences in baseline-corrected δ^{15}N and *SWTP* estimates, frequency distributions were analyzed across all species for each of eight webs as well as for four broad trophic groups: invertebrates, fish, birds and mammals across all eight webs (Figure 3.1, Figure 3.2).

To determine whether a non-isotope but weighted estimate of trophic position using the *TROPH* algorithm from FishBase.org provided a better fit to δ^{15}N estimates than binary *TP* estimates, we used four of the eight food-webs for which location-specific trophic position information was available for fish on FishBase.org: Benguela, Arctic, Antarctic and NE Shelf. In FishBase, *TROPH* is calculated by adding one to the mean trophic position, weighted by relative abundance of all food items consumed by a species (Froese & Pauly 2010). For a consumer species *i*, weighted trophic position (*TROPH*) is defined as:

$$\text{TROPH}_i = 1 + \sum_{j}^{s} DC_{ij} * WTP_j \qquad \text{(Eq. 3)}$$

where WTP_j is the fractional trophic position of prey j, DC_{ij} represents the fraction of j in the diet of i, and S is the total number of prey species. Calculations of trophic position are based on diet information and food items in FishBase, which are assigned discrete trophic positions (Froese & Pauly 2010). Prey items include organisms that have been found in stomach contents or are otherwise known to be ingested by a given species. More than 800 citations have been used to support the diet information in FishBase, in addition to the verification of over 16,000 records. In FishBase, primary producers and detritus (including associated bacteria) are assigned a definitional trophic position of 1. Primary consumers (herbivores), which consume mainly plants or detritus, are assigned trophic positions between 2 and 2.19 (WTP = 2 - 2.19). Omnivores, which consume plants or detritus as well as animals, have trophic positions between 2.2 and 2.79 ($2.2 < WTP > 2.79$); secondary ($WTP > 2.8$) and tertiary ($WTP > 4$) consumers (carnivores) are assigned trophic positions greater than 2.8 (see www.fishbase.org).

3.3.1. Statistical analysis

Pearson's correlation coefficients were used to assess the correlation between different estimates of trophic position. Dependent t-tests were used to determine whether there were significant differences between binary estimates of trophic position and baseline corrected δ^{15}N estimates (see above). Two sets of analyses were conducted. First, we assessed the correlation between binary and δ^{15}N estimates across all species and webs (n = 366) as well as for each of the eight webs separately. Dependent t-tests were used to determine whether there were significant differences between binary and baseline corrected δ^{15}N estimates. For baseline corrected analyses δ^{15}N estimates were limited to consumer species with a $TP > 2$ as primary consumers ($TP = 2$) were used as the baseline taxa to estimate δ^{15}N TP. Second, we compared estimates of

TP calculated as *TROPH*, binary TP, and δ^{15}N for 127 fish species for four of the marine webs (Shelf, Arctic, Antarctic, and Benguela).

Binary feeding matrices were also used to calculate food-web properties that may have affected or confounded the relation between binary estimates of trophic position and δ^{15}N estimates of trophic position including: number of species (*S*), connectance (L/S^2, number of links/number of species^2), number of links per species (*L/S*), and fractions of top, intermediate, basal, and omnivore species (Table 3.2). To determine if differences in the fraction of species that we were able to find δ^{15}N values for might have accounted for differences in the strength of the correlations between binary and δ^{15}N *TP*, we determined whether there was a correlation between the fraction of species in the webs that δ^{15}N values were available for (i.e. completeness) and the correlation coefficients for the binary *TP* v. δ^{15}N relations for each web. To determine whether the strength of the correlation between different estimates were correlated with food-web properties we assessed the correlation between the correlation coefficients of the binary TP- δ^{15}N estimates and the number of species (*S*), number of links/species (*L/S*), connectance (C = links/species^2), and fractions of top (%*T*), intermediate (%*I*), basal (%*B*), and omnivore species (%*Omn*).

3.4. Results

The total number of species or nodes in the eight webs was 676. We were able to find δ^{15}N values for 366 or 54% of the species. We were able to find corresponding δ^{15}N values for more than 50% of the species in each web for all webs except for Ythan ($S = 45$) and Antarctic for which only 35% and 45% of corresponding nitrogen isotope values were. Shelf was the most complete web, with corresponding δ^{15}N values for 74% of species (S = 79; Table 3.1). Across all webs and species, the correlation for short-weighted *TP* and δ^{15}N was R = 0.644 ($p < 0.0001$)

and for prey-averaged TP and δ^{15}N was R = 0.645 ($p < 0.001$, n = 171; Figure 3.3A, B). As there was no significant difference between the explained variability in δ^{15}N by short-weighed and prey-averaged trophic position and as short-weighted *TP* has previously been shown to more accurately reflect trophic position estimates based on gut-content analysis (Williams & Martinez, 2004) we used short-weighted trophic position as our measure of binary *TP* in all further analyses.

3.4.1. Comparison of binary and isotope analysis estimates of trophic position

The average correlation between binary *TP* and δ^{15}N across all eight webs was R = 0.644 (Figure 3.3A). Significant correlations between binary *TP* and δ^{15}N were observed in all webs ranging from R = 0.594 in Chesapeake ($p = 0.007$) to R = 0.83 in Benguela ($p < 0.0001$, Figure 3.4).

Mean binary *TP* differed from baseline corrected δ^{15}N *TP* by 2.33% across all webs and species with a $TP > 2$, ranging from 0.1% in St. Marks to 18.11% in Benguela (Table 3.3; Figure A.3). Mean binary TP differed significantly from baseline corrected δ^{15}N *TP* in Shelf ($p < 0.0001$), Benguela ($p < 0.0001$), and Antarctic ($p < 0.0001$; Figure A.4). In the other five webs (Arctic, Adriatic, Ythan, St. Marks and Chesapeake) there was no significant difference between mean binary *TP* and mean baseline corrected δ^{15}N *TP* ($p > 0.05$; Figure A.4). Maximum binary *TP* differed from baseline corrected δ^{15}N *TP* by 5% on average, ranging from 0.58% in Ythan to 17.5% in Adriatic (Table 3.3).

3.4.2. Comparison of binary TP and baseline corrected TP by taxonomic group

Across all webs no significant difference was observed for mean binary *TP* and baseline corrected δ^{15}N *TP* for invertebrates ($p = 0.161$), mammals ($p = 0.782$), or fish ($p = 0.055$); however, the latter was only marginally insignificant (fish binary $TP = 3.53$, baseline corrected

δ^{15}N *TP* = 3.43). In contrast, mean binary trophic position was significantly greater for birds than the δ^{15}N estimate (binary *TP* = 3.71, baseline corrected δ^{15}N *TP* = 3.25; *p* = 0.002). Maximum binary *TP* was also higher for birds (maximum binary *TP* = 4.7, baseline corrected maximum δ^{15}N *TP* = 4.35) whereas for invertebrates and fish, maximum baseline corrected δ^{15}N was slightly higher than maximum binary *TP* (fish maximum binary *TP* = 4.57, baseline corrected δ^{15}N *TP* = 4.89; invertebrates' maximum binary *TP* = 4.01, baseline corrected δ^{15}N *TP* = 4.14). The difference between maximum binary *TP* and baseline corrected δ^{15}N *TP* was particularly strong for mammals with maximum binary *TP* lower by more than a full trophic level than the baseline corrected estimate (maximum binary *TP* = 4.74, baseline corrected δ^{15}N *TP* = 5.86).

Analysis of the variance, skewness, and kurtosis of frequency distributions for the four taxonomic groups also showed a number of trends. Across all four groups variance in *TP* was higher for baseline corrected δ^{15}N *TP* and distributions were more peaked for binary *TP* (Figure 3.4). Relative to baseline corrected δ^{15}N *TP*, binary *TP* was more positively skewed for birds and invertebrates and more negatively skewed for fish and mammals. These results suggest that while there are some taxonomic differences in the distributions of binary *TP* and δ^{15}N *TP* related to skewness, on average binary *TP* leads to lower estimates of maximum *TP* than δ^{15}N *TP*, and has a more truncated range, and a flatter distribution than baseline corrected δ^{15}N *TP*.

3.4.3. Comparing trophic position estimates for fish

For the 127 fish species that we were able to compile *TROPH* (weighted estimates of *TP* based on gut-contents) values for the correlation between binary *TP* and δ^{15}N was R = 0.259 (*p* = 0.003; Figure A.5A). A similar correlation was seen between *TROPH* and δ^{15}N with an R = 0.285 (*p* = 0.001; Figure A.5B). Binary *TP* and *TROPH* were correlated with an R = 0.462 (*p* < 0.0001; Figure A.5C). Arctic and Benguela were the only webs to show a significant correlation between binary *TP* and δ^{15}N ($p = 0.024$, $p = 0.022$, Figure 3.5A). No significant correlation was observed between *TROPH* and δ^{15}N estimates for any of the webs. Correlations between *TROPH* and binary *TP* ranged from R = 0.324 in the Arctic ($p = 0.032$) to R = 0.893 in Benguela ($p = 0.001$, Figure 3.5C). In the Benguela and Arctic webs, the correlation between binary *TP* and δ^{15}N was significant (R = 0.736, $p = 0.024$, R = 0.344, $p = 0.022$, Figure 3.5A) whereas the correlation between *TROPH* and δ^{15}N TP was not ($p = 0.111$, $p = 0.641$ Figure 3.5B).

3.4.4. Effects of sampling effort and food web properties

The fraction of species in each web for which δ^{15}N values were reported in the literature differed across webs (Table 3.1). For example, for Shelf we were able to match 74% of the species in the binary web to δ^{15}N values from the literature, while for Ythan we were only able to match 35% of the species in the binary web with corresponding δ^{15}N values from the literature. To determine if differences in the fraction of species that we were able to find δ^{15}N values for might have accounted for differences in the strength of the relations between binary and δ^{15}N we determined the correlation between the fraction of species in the webs that δ^{15}N values were reported for with the correlation coefficients for the binary *TP* vs. δ^{15}N relations for each web. Completeness, in terms of the proportion of species in the webs for which δ^{15}N values were available, was unrelated to the correlation between binary and δ^{15}N estimates of *TP* ($p = 0.805$).

To determine whether aspects of the structure of the food-webs affected relations between binary *TP* and δ^{15}N we compared the correlation coefficients of the binary *TP* vs. δ^{15}N relation with a number of key food-web properties including species richness, number of links per species, connectance (links/species^2), and fractions of top, intermediate, basal species, and omnivores. Because we had only eight webs we would have needed an R value of 0.706 for a relation to be significant at $p < 0.05$. None of the food-web properties analyzed were significantly correlated with the strength of the binary *TP* versus δ^{15}N relation. The two highest correlations were for fraction of basal species (R = -0.576, *p* = 0.13) and connectance (R = 0.58, *p* = 0.13).

3.5. Discussion

Since Odum & Herald (1975) expanded the trophic level concept of Elton (1927) and Lindeman (1942) from a qualitative to a quantitative metric, the use of trophic position as a key descriptor of the functional role of species and the state of ecosystems has become firmly established (Pauly & Watson, 2005). With the recent adoption of trophic position as a marine resource indictor to assess the state and sustainability of fisheries resources (Pauly & Watson, 2005), its importance and use as a relevant metric of ecosystem degradation will only increase. While in some cases the value is relatively important, such as for the reduction in mean trophic position of landings over time (Pauly & Watson, 2005), the accuracy of trophic position estimates remains highly contentious and is deeply intertwined with the utility of structural approaches to food-web descriptions.

Although few studies have attempted to track changes in food-web properties other than trophic position to quantify ecosystem degradation (but see Coll et al., 2008), a food-web approach may be one of the more powerful ecological methods to describe how ecosystem structure changes as disturbance increases, and thus in predicting the consequences of disturbance to the functioning of ecosystems. A major impediment in using changes in food-web structure to quantify disturbance is the inherent difficulties in assembling highly resolved flow-based food-webs, which require massive time and financial investments (Williams & Martinez, 2004). If structural approaches to assembling food-webs can be shown to be as accurate or at least an acceptable representation of food-web structure, structural analyses of ecosystem change can advance at a much faster pace.

The ability of structural approaches to accurately depict feeding interactions as opposed to flow-based methods, such as gut content and stable isotope analysis, has been a contentious issue in food-web ecology for decades. Previous comparative analyses have shown that using the short-weighted trophic position algorithm, which uses prey-averaged trophic position and the shortest trophic position to calculate effective trophic position, binary links come within a quarter of a trophic level to quantitative values predicted from gut content analysis (Williams & Martinez, 2004). Due to the inherent problems with gut content analysis, such as limited spatial and temporal extent and inclusion of non-assimilated material in diet data (Vander Zanden et al., 1999), it has been suggested that a more robust test of the ability of structural approaches should involve cross-validation of binary estimates of trophic position with stable isotope estimates based on nitrogen (Williams & Martinez, 2004).

Our analysis of 366 species in eight marine and estuarine webs shows that trophic position estimates using binary (presence-absence) is strongly correlated with $\delta^{15}N$ estimates. Across all species and webs the correlation between binary and $\delta^{15}N$ was $R = 0.644$ ranging from 0.594 to 0.83 for the different webs (Figure 3.4). Binary estimates of mean trophic position differed by only 2.33% and maximum trophic position differed by only 6.57% from estimates based on baseline corrected $\delta^{15}N$ (Table 3.3). This high concordance between binary and $\delta^{15}N$ estimates clearly shows that a structural approach to constructing food-webs can be highly effective in estimating trophic position. Our results also show that using binary links to construct a food-web can be more accurate when compared to isotope estimates of trophic position using $\delta^{15}N$ than flow-based estimates based on gut content analysis. Our comparisons between different flow-based methods (i.e. *TROPH* versus $\delta^{15}N$) and binary methods for 127 species of fish showed that binary estimates were either equivalent to flow-based estimates, which utilize gut-content analysis to estimate trophic position, or performed better than *TROPH* estimates. Below we discuss the use of stable isotopes and gut content analysis in food-web assembly in more detail, as well as the variation around the above averages for the eight different food-webs.

3.5.1. Issues with using nitrogen isotopes to estimate trophic position

The use of stable isotope analysis to track energy flow between consumers and their resources has been an important technical advancement in determining the trophic ecology of species (Post, 2002). Early studies on fractionation of nitrogen across trophic levels suggested an average enrichment of 3.4% with each trophic level (DeNiro & Epstein, 1981; Minagawa & Wada, 1984). This value of 3.4% became somewhat of a sacred cow in isotope ecology as it could be used to infer the trophic position of consumers and their prey. While a 3.4% increase in $\delta^{15}N$ is still considered as a standard, more recent analyses have shown extensive variability in the average fractionation between resources and consumers. For example, McCutchan et al. (2003) analyzed trophic fractionation across a wide range of organisms and found that consumers with a high-protein diet were more enriched relative to their resources than consumers that were herbivorous or consumers that fed primarily on invertebrates, with an average enrichment of 2.0% ± 0.2 S.E. Thus, in contrast to the global value of 3.4% with each increase in trophic level (DeNiro & Epstein 1981; Minagawa & Wada, 1984), the actual magnitude of enrichment depends strongly on the feeding habits of the consumer, with strict carnivores having a higher $\delta^{15}N$ relative to omnivores, which in turn show greater enrichment than herbivores (Kling et al., 1992). While this more detailed understanding of trophic fractionation has increased the accuracy of prediction of trophic position based on stable isotope values of nitrogen, it has also presented ecologists who use this method with a problem, as it is not possible to accurately predict the trophic position of all species in a community using 3.4‰ as a standard fractionation value.

The accuracy of using fractionation of $\delta^{15}N$ to estimate trophic position is further complicated by the wide variability that occurs in $\delta^{15}N$ in primary producers even in highly similar and spatially adjacent habitats (Solomon et al., 2008). Differences in the $\delta^{15}N$ of primary producers occurs as physical and chemical processes produce measurable differences in the stable isotope ratios of different classes of plants as they are assimilated into the tissues of higher-order consumers (Keegan & DeNiro, 1988; Vander Zanden & Rasmussen, 1999). The consequence of this is that $\delta^{15}N$ values only represent a valid estimate of trophic position when compared to other species in the same system whose feeding pathway leads to the same basal compartments (i.e. phytoplankton versus aquatic plants). Thus, to use $\delta^{15}N$ values as estimates of trophic position it is necessary to establish an accurate baseline. Primary consumers (trophic position = 2) are most often used as they do not differ as much spatially and temporally as primary producers (Vander Zanden & Rasmussen, 1999). The algorithm, however, which is used to estimate trophic position, is still based on a 3.4% fractionation increase with each trophic level, thus introducing an additional source of methodological error into the estimate of trophic position even when an accurate baseline has been established. The use of isotope methods to estimate trophic position itself are also subject to potential errors due to methodological issues including differences in tissue specific fractionation (Hobson & Clark, 1993; Buchheister & Latour, 2010) and effects of sample storage and preparation (Arrington, 1992; Schmidt et al., 2009).

3.5.2. Comparing binary and $\delta^{15}N$ estimates of trophic position

Given the above cautions regarding the interpretation of $\delta^{15}N$ estimates of trophic position, stable isotope analysis of nitrogen is still widely considered to be the most accurate method of estimating trophic position, particularly in experimental settings. The assembly of structural food-webs is fraught with many of the same potential errors as flow-based methods based on isotopes including the decisions involved in determining spatial and temporal extent, node resolution, and the inclusion or exclusion of detail for changes in diet sources during ontogeny, among others. Despite these caveats, our analysis shows that structural approaches are not only highly accurate in estimating trophic position based on $\delta^{15}N$ but also that the deviations in predicted trophic position are relatively minor given differences between webs in spatial and temporal extent and resolution.

Differences in binary versus $\delta^{15}N$ estimates averaged 2.33% for mean trophic position and 6.57% for maximum trophic position across all 366 species and ranged from 0.1% to 18.11% for mean trophic position and from 2.49% to 15.9% for maximum trophic position across webs (Table 3.3). On average the difference between binary and $\delta^{15}N$ estimates was 0.14 of trophic level. This difference is smaller than the mean difference of 0.25 of a trophic level in an earlier comparison of binary and flow-based estimates based on gut content analysis (Williams & Martinez, 2004) suggesting that the earlier analysis underestimated the accuracy of binary measures of trophic position.

The correlation between binary and $\delta^{15}N$ estimates was highest in Benguela with an R = 0.83 and was lowest in Chesapeake with an R = 0.594 (Figure 3.4). It is important to note that we found no significant relations between any of the food-web properties and the strength of the correlation between binary and $\delta^{15}N$ estimates. However, given that we only used eight webs in these analyses, the lack of any significant correlation with food-web properties should be approached with caution.

It was initially expected that the correlation between binary and $\delta^{15}N$ estimates would be lowest in estuarine webs due to multiple source pathways of primary producers that differed strongly in $\delta^{15}N$ (e.g. aquatic plants, phytoplankton, macroalgae). There was no consistent effect of broad habitat types such as marine versus estuarine on the strength of the relation. Additional studies spanning more habitat types are necessary to determine whether structural approaches show higher correlations with isotope estimates in different habitat types and whether multiple source pathways such as those in estuaries might result in less concordant results between different estimates of trophic position.

Only minor differences were observed for binary *TP* and baseline corrected $\delta^{15}N$ *TP* among invertebrates, fish, birds, and mammals. In general, binary *TP* under-predicts maximum *TP* relative to $\delta^{15}N$ *TP*, has a more truncated range, and a flatter distribution than baseline corrected $\delta^{15}N$ *TP*. Under-prediction of maximum trophic position was observed for fish, mammals, and invertebrates while binary *TP* over-predicted maximum trophic position for birds relative to baseline corrected $\delta^{15}N$ *TP*. This under-prediction is due in part to the short-weighted trophic level algorithm which calculates *TP* as the average of the shortest *TP* for the species and prey-averaged *TP*, which tends to have a bias towards shorter chain lengths, thus reducing the probability of species being given a higher trophic position estimate (Williams & Martinez, 2004). Under-prediction of maximum values may also be due to the lack of inclusion of species in webs that have relatively high trophic positions but are lumped together into trophic groups that on average have lower trophic positions. For example, predatory invertebrates such as jellyfish are listed in many marine food webs as trophic level = 2 (e.g. Adriatic food web). Likewise, the exclusion of parasites from binary food webs, particularly for highly parasitized species such as fish, would lower the trophic position of fish predators. It is likely that the reduction in the range of binary *TP* values relative to baseline corrected values is also partially due to the lack of high resolution of invertebrates. Binary *TP* values also showed more peakedness than baseline corrected values, indicating a bias toward average values.

The primary taxonomic difference observed was for skewness, with binary *TP* estimates being more positively skewed for birds and invertebrates and more negatively skewed for fish and mammals, relative to baseline corrected δ^{15}N *TP*. These differences in skewness could be due to a number of methodological issues. First, δ^{15}N for birds and invertebrates' likely captures a greater range of food resources than binary links. In particular, heterotrophic bacteria are generally not included in binary food webs and when they are, they are often treated as a autotrophic basal node. Similarly, birds often prey on parasites, and the exclusion of parasites from binary webs likely lowers the trophic position estimates for birds. For fish and mammals in contrast, binary *TP* was more negatively skewed relative to baseline corrected δ^{15}N *TP*. As organisms typically receive more energy from lower trophic levels than higher trophic levels, binary *TP* may over-predict trophic position, particularly for omnivores.

Perhaps the most fundamental issue concerning feeding and δ^{15}N estimates of *TP* is the definition of a feeding interaction and the distinction between the effect of the consumer on its resources and the effect of the resources on the consumer. For example, the former may have little to do with what the consumer assimilates. The resource mortality, inflicted by the consumer, is most directly related to the biomass or number of individuals lost in the act of feeding. However, how much the consumer grows or reproduces due to feeding is more directly related to how much of the resource species is assimilated. While this distinction may only alter *TP* estimates a small fraction of a level in most cases analyzed here, other cases may lead to a discrepancy of more than a full trophic level, with ruminants being the clearest example. While ruminants typically consume plant matter, the rich and multi-trophic position microbial gut flora that feeds directly and indirectly on the moist and masticated vegetation forms a substantial and protein enriched fraction of the ruminant's diet (Callewaert & Michiels, 2010). Similarly, when a decomposer consumes dead plant matter, the communities of bacteria and fungi growing on that plant matter can also form a substantial diet fraction (Callewaert & Michiels, 2010). While we only touch on these issues here, future work may do well to reconsider the definition of feeding and distinguish consumption *TP* from assimilation *TP* rather than conflating them as is standard in discussions and analyses of *TP*.

3.5.3. Comparisons between gut content, binary, and $\delta^{15}N$ estimates of trophic position

In contrast to the lack of cross-validation studies focusing on structural versus $\delta^{15}N$ estimates of trophic position, a number of studies have attempted to cross-validate flow-based estimates based on gut content analysis with isotope estimates of trophic position. Vander Zanden et al. (1997) found an $r^2 = 0.78$ between gut content and $\delta^{15}N$ estimates for eight pelagic fish species in 36 lakes in Ontario and Quebec, and Nilson et al. (2008) reported an $r^2 = 0.72$ for 65 taxa in Sorfjord, a high-latitude fjord. Correlations between flow-based and isotope-based estimates of trophic position are not, however, always as high or as consistent as is in the above studies. For example, in salt marsh ponds, Dame & Christian (2008) reported differences in mean trophic positions ranging from 0.12 to 0.53 for four different ponds with one of the four ponds showing no significant relation between flow-based and isotope estimates despite the same model specification. In stream fish, Ribczynski et al. (2008) reported high concordance between gut content and $\delta^{15}N$ estimates for omnivorous fish but large differences between gut content (*TP* range = 3.5 - 3.7) and $\delta^{15}N$ estimates (*TP* range = 2.5 - 4.1) for predatory fish. Likewise, Franssen and Gido (2006) found only weak relations between gut content and $\delta^{15}N$ estimates for stream fish in Kansas and no significant differences in $\delta^{15}N$ estimates across algivore/detritivore, omnivore, and insectivore functional groups.

Estimates of trophic position in FishBase using the *TROPH* routine have been previously shown to correlate closely with estimates based on stable isotope ratios (Kline & Pauly 1998). For example, Kline & Pauly (1998) showed an R = 0.986 for flow-based and $\delta^{15}N$ estimates for seven functional groups in Prince William Sound, Alaska. We were able to cross-validate estimates of trophic position using *TROPH*, binary TP, and $\delta^{15}N$ estimates for 127 fish in the Benguela (n = 9), Shelf (n = 26), Arctic (n = 44) and Antarctic (n = 48). In our direct comparisons of gut content, binary, and $\delta^{15}N$ estimates, binary estimates showed similar concordance with $\delta^{15}N$ estimates as gut content based estimates (Figure A.5A-B). In the Benguela and Arctic webs, the correlation between binary *TP* and $\delta^{15}N$ was significant while the correlation between *TROPH* and $\delta^{15}N$ *TP* was not (Figure 3.5A-B). Thus, in contrast to the generally accepted view that flow-based methods such as gut content analysis should be more accurate at predicting $\delta^{15}N$ estimates of trophic position than binary approaches, our results actually suggest the opposite may be correct in some cases.

There are a number of possible explanations for the greater concordance of binary and $\delta^{15}N$ estimates than between gut content and $\delta^{15}N$ estimates. In one of the most comprehensive explorations of seasonal effects on trophic level in fishes, Karachle and Stergiou (2008) have shown that trophic level of 59 fishes differed by 0.45 ± 0.04 S.E. of a trophic level on average seasonally ranging from no change to a change of 1.48. The fraction of species that changed more than one functional trophic group seasonally ranged from 27.3 to 38.9% depending on the number of seasons included in the analysis, and 8.5% of the species changed by more than one functional group. The seasonal changes in trophic position due to seasonal diet variability observed by Karachle & Stergiou (2008) were greater than the differences in trophic position we observed between binary and $\delta^{15}N$ estimates, suggesting that snapshot gut content analysis can significantly bias estimates of trophic position. Thus, while it seems counterintuitive, flow-based methods such as gut content analysis may actually be more inaccurate due to restricted temporal and spatial sampling as well as errors in species identification and counting than binary methods which typically focus on assembling spatially and temporally averaged meta-webs for ecosystems (Dunne, 2006).

3.6. Conclusion

More stable isotope data is needed to determine how broadly our results can be extrapolated. There was often less data available for primary producers and invertebrates than for vertebrates, thus having representative samples across taxonomic and functional groups is needed to determine whether there are differences in the ability of binary estimates to predict $\delta^{15}N$ estimates across specific taxonomic and functional groups. The availability of isotope data for marine and estuarine species was also much greater than for freshwater or terrestrial species, which is why we limited our analysis to marine and estuarine webs. Despite these caveats, our analysis represents a robust comparison of binary, other flow-based, and isotope estimates of trophic position for marine and estuarine ecosystems. Our results clearly show that binary estimates of trophic position show high concordance to isotope based methods and most surprisingly are more accurate than flow-based method such as gut content analysis.

The work in Chapter 3 also appears in: Carscallen, W.M.A., Vandenberg, K., Lawson, J.M., Martinez, N.D., Romanuk, T.N. 2012. Estimating trophic position in marine and estuarine food webs. Ecosphere. 3(3):25. http://dx.doi.org/10.1890/ES11-00224.1

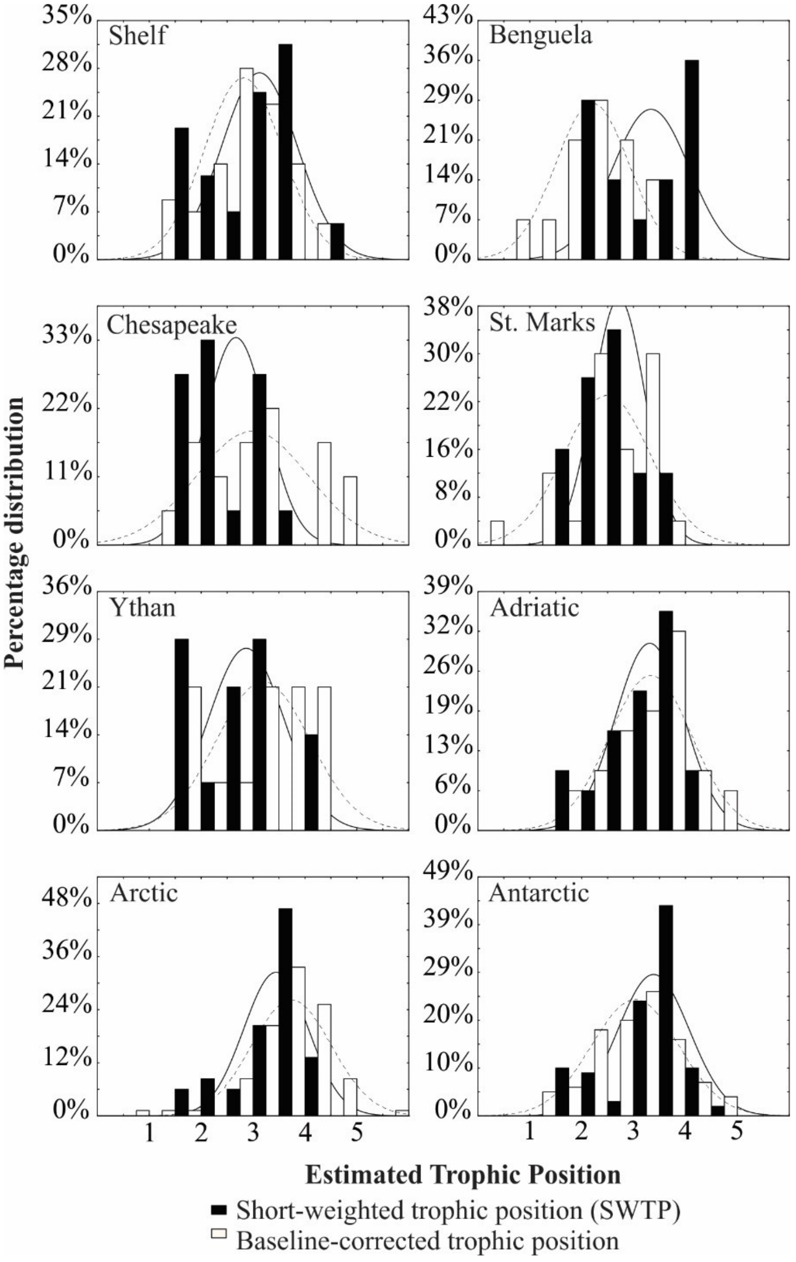


Figure 3.1 Frequency distributions of binary (SWTP) and baseline corrected trophic position estimates for all eight webs: St. Marks estuary, Ythan estuary, NE shelf, Benguela current, Adriatic sea, Chesapeake bay, Arctic sea-ice, and Antarctic sea-ice. Normal distribution curves are represented by the solid black line (binary estimates) and dotted line (baseline corrected).

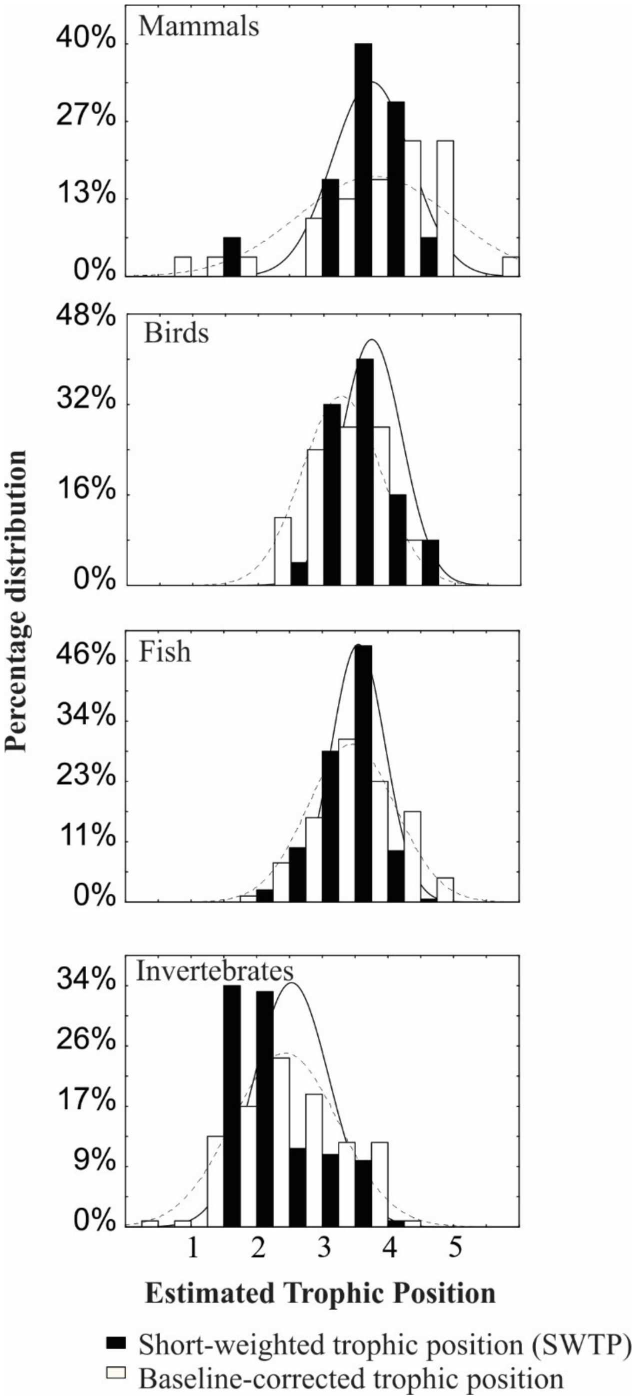


Figure 3.2: Frequency distributions of binary (SWTP) and baseline corrected trophic position estimates of four broad taxanomic groups, including mammals, birds, fish, and invertebrates, across all eight webs. Normal distribution curves are represented by the solid black line (binary estimates) and dotted line (baseline corrected).

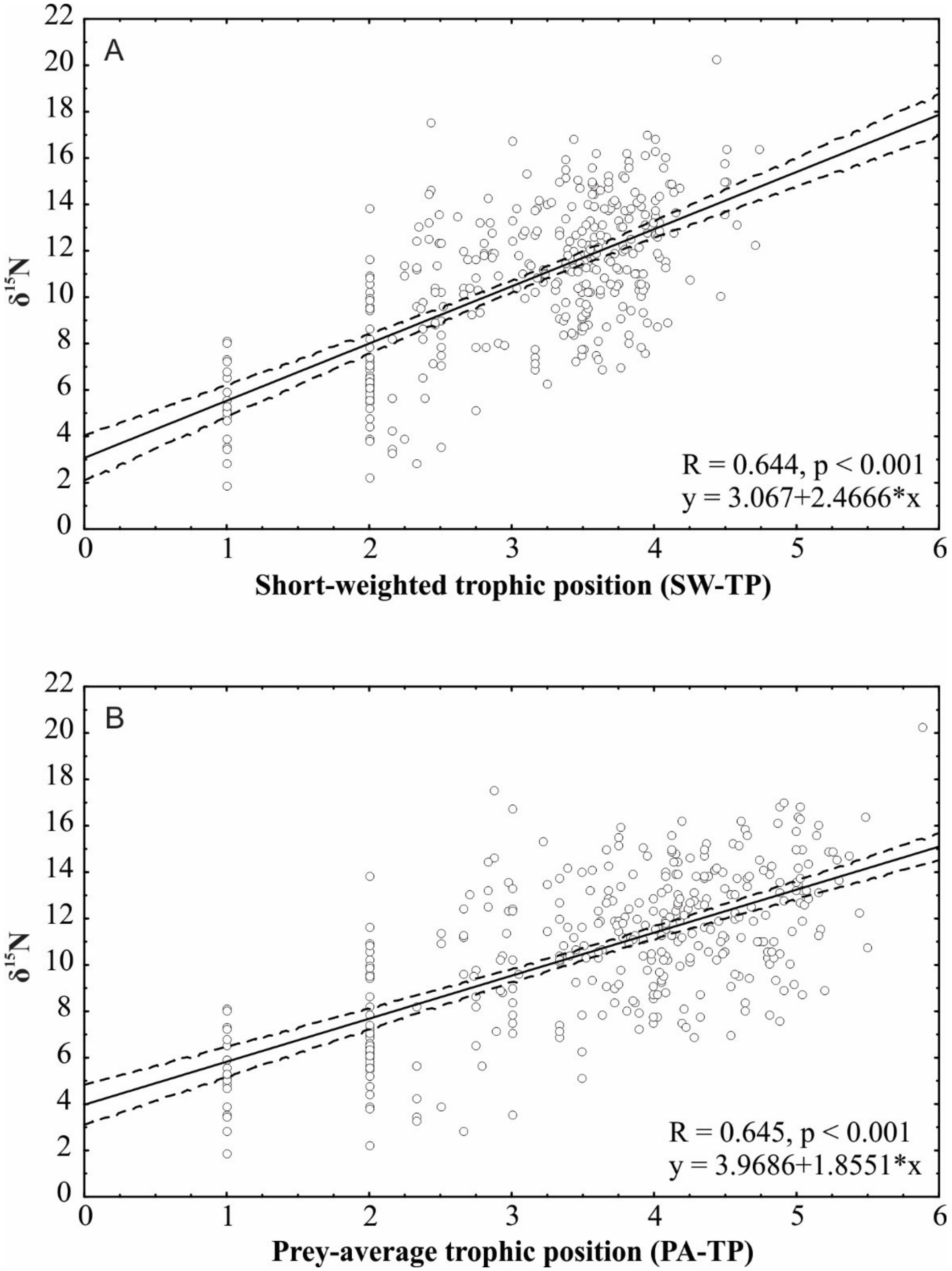


Figure 3.3: $\delta^{15}N$ values versus binary trophic position estimates based on a) short-weighted trophic position (*SWTP*) and b) prey-averaged trophic position (*PATP*) for across all webs and species (n=366) in eight marine and estuarine food-webs. Shown are the CI (± 0.95) and line of best fit (black).

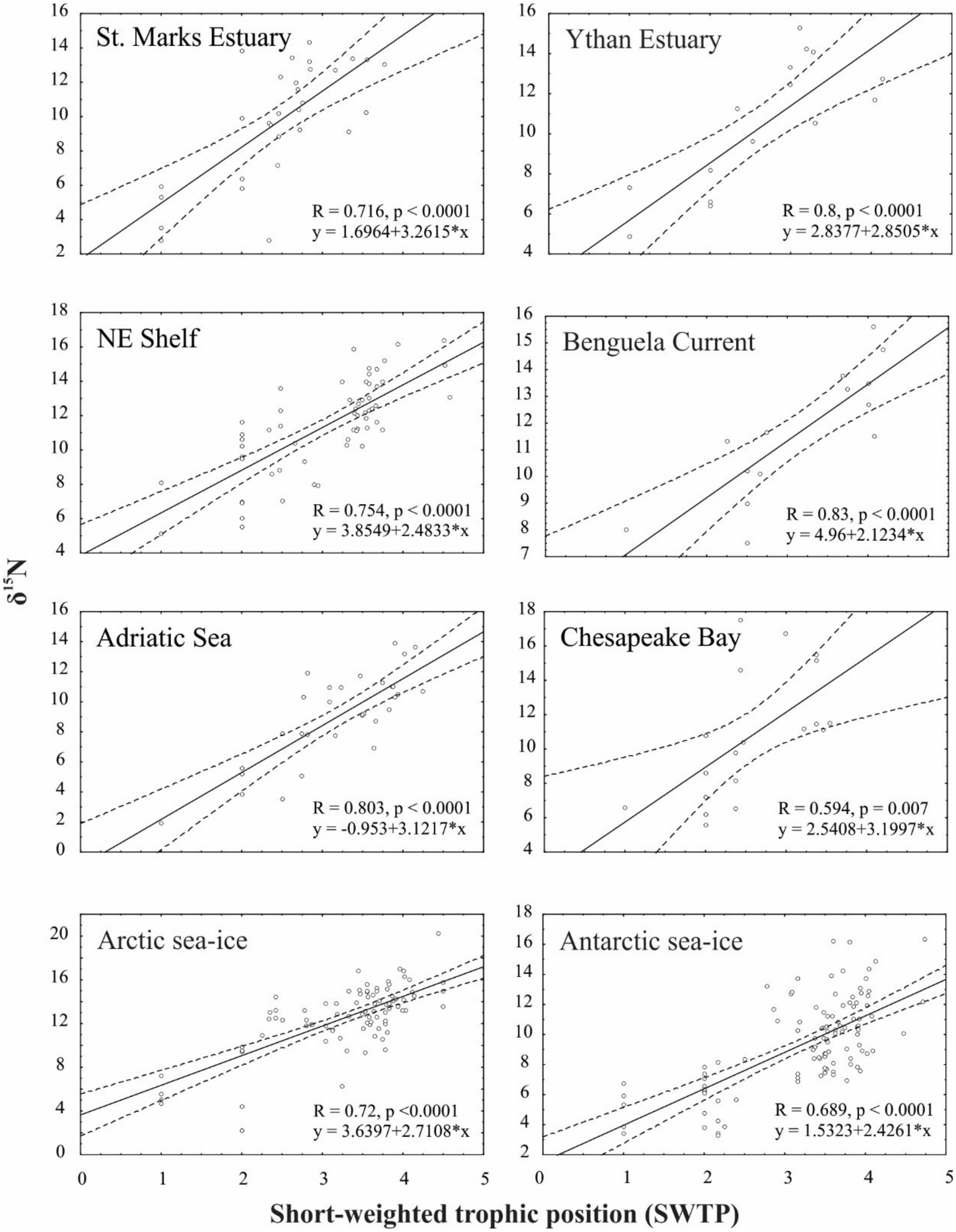


Figure 3.4: δ^{15}N values versus binary trophic position estimates (based on the short-weighted trophic level algorithm) for all eight webs: St. Marks estuary, Ythan estuary, NE shelf, Benguela current, Adriatic sea, Chesapeake bay, Arctic sea-ice, and Antarctic sea-ice. Shown are the CI (± 0.95) and line of best fit (black).

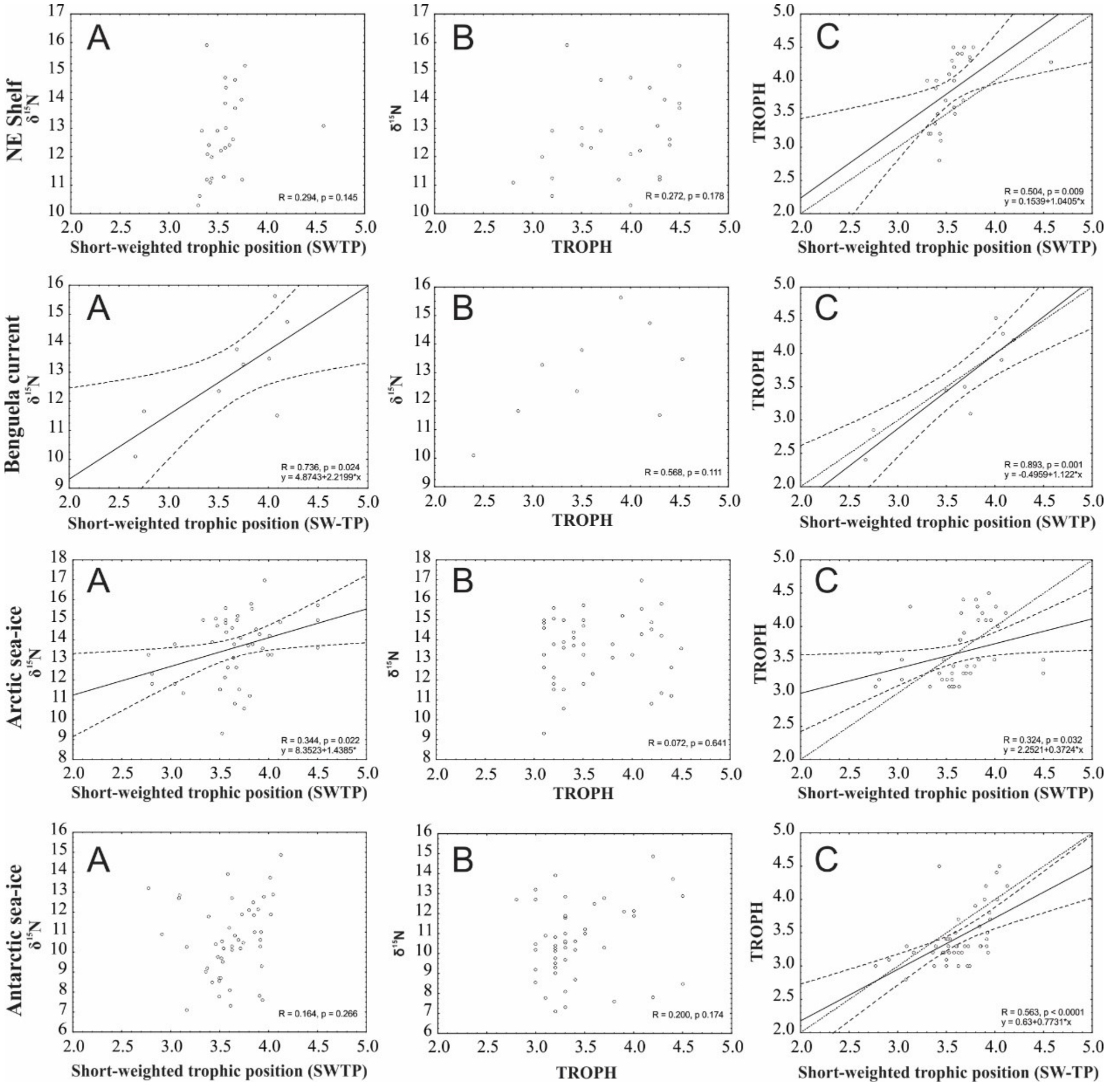


Figure 3.5: Comparison of flow-based and binary estimates of trophic position. a) $\delta^{15}N$ values versus binary trophic position (*SWTP*) estimates for 127 species of fish in Shelf, Benguela, Arctic and Antarctic. b) $\delta^{15}N$ values versus *TROPH* estimates from FishBase.org. c) relation between *TROPH* and binary trophic position estimates (*SWTP*). Shown are the CI (± 0.95) and line of best fit (black). Fine black dotted line represents a perfect correspondance between SWTP and TROPH estimates of trophic position. Data points above the line have a higher TROPH estimate of trophic position in comparison to SWTP, whereas species below the line have a higher SWTP estimate of trophic position in comparison to TROPH.

Table 3.1: Summary of characteristics of each of the eight marine and estuarine webs. A) Name of web, reference, habitat (marine or estuarine), number of species/taxa in the web, number of location specific δ^{15}N values, completeness (fraction of species/taxa for which δ^{15}N values were available, R, and p-value.

Food-web characteristics and correlations (SWTP vs. δ^{15}N)

Web	**Habitat**	***S***	**No. of δ^{15}N values**	**% Completeness**	**R**	**p-value**
Benguela	Marine	29	15	51%	0.83	<0.0001
Chesapeake	Estuarine	31	19	61%	0.594	0.007
Shelf	Marine	79	59	74%	0.754	<0.0001
St Marks	Estuarine	48	30	62.5%	0.716	<0.0001
Ythan	Estuarine	45	16	35%	0.8	<0.0001
Adriatic	Marine	44	32	72%	0.803	<0.0001
Arctic sea-ice	Marine	161	88	55%	0.72	<0.0001
Antarctic sea-ice	Marine	239	107	45%	0.689	<0.0001

Table 3.2: Food web properties calculated based on binary feeding links for each web showing number of links/species (L/S), connectance (link/species^2), fraction of top, intermediate, basal, and omnivores.

Food-web Properties						
Web	***L/S***	***C***	**% Top**	**% Intermediate**	**% Basal**	**% Omnivores**
Benguela	7	0.24	0%	97%	3%	79%
Chesapeake	2.19	0.07	32%	52%	16%	55%
Shelf	17.76	0.22	4%	94%	3%	78%
St Marks	4.60	0.1	19%	69%	13%	73%
Ythan	4.76	0.06	37%	57%	6%	55%
Adriatic	7.36	0.17	16%	77%	7%	84%
Arctic sea-ice	6	0.037	11%	86%	3%	84%
Antarctic sea-ice	6.5	0.027	11%	87%	2%	84%

Table 3.3: Differences in trophic position based on $\delta^{15}N$ values and binary trophic position (*SWTP*) estimates across all webs and species with TP>2 and for each of the eight marine and estuarine webs. Shown are means, maximum, S.D.'s, and percent (%) difference.

Web	**Property**	**SWTP**	**$\delta^{15}N$ TP**	**% Difference**
All	Mean	3.1	2.959	2.33%
	Max	4.742	5.410	6.57%
	S.D.	0.849	0.881	
Shelf	Mean	3.036	2.799	4.1%
	Max	4.578	4.221	4.1%
	S.D.	0.811	0.747	
Benguela	Mean	3.164	2.196	18.11%
	Max	4.188	3.367	10.77%
	S.D.	0.931	0.711	
Chesapeake	Mean	2.569	2.974	7.3%
	Max	3.542	4.888	15.9%
	S.D.	0.688	1.077	
Ythan	Mean	2.621	3.181	9.65%
	Max	4.141	4.47	3.83%
	S.D.	0.93	0.897	
St. Marks	Mean	2.478	2.479	0.1%
	Max	3.772	3.564	2.9%
	S.D.	0.751	0.828	
Adriatic	Mean	3.223	3.314	1.3%
	Max	4.249	4.661	4.7%
	S.D.	0.763	0.794	
Arctic	Mean	3.315	3.168	2.27%
	Max	4.5	5.41	9.19%
	S.D	0.79	0.877	
Antarctic	Mean	3.259	2.953	4.93%
	Max	4.742	4.985	2.49%
	S.D.	0.838	0.868	

Chapter 4 Arctic and Antarctic marine food webs

4.1. Abstract

Similar environmental and evolutionary constraints on food webs in extreme ecosystems such as the Arctic and Antarctic suggest that the food web structure of polar regions may be highly similar despite strong differences in geography, bathymetry, and oceanographic patterns. I compiled a dataset of 21 food webs for Arctic and Antarctic ecosystems to compare whole-web structural properties, node/taxa properties, properties of taxonomic groups, and key species such as krill and cod, to determine whether and how Arctic and Antarctic food webs differ. I also conducted a comprehensive comparability analysis to determine whether the energy-flow patterns and overall food web structure were broadly comparable across webs that differed in size, resolution, and method of assembly. The comparability analysis showed that the 21 food webs were broadly similar in structure despite major differences in species richness and resolution, with species richness being a dominant factor in resolving differences between the Arctic and Antarctic. Using a hierarchical analysis, exploring how food webs differ, starting with whole food webs properties, to node properties, to the properties of major taxonomic groups and key species, showed that at higher hierarchical levels Arctic and Antarctic webs were broadly similar except for differences in variability of feeding interactions and higher fractions of basal species in the Antarctic. Despite the lack of major differences from a whole-food web perspective, significant differences began to emerge as I focused on node properties, properties of taxonomic groups, and key species. I found that several of the node properties, such as generality and vulnerability, were significantly higher in the Antarctic than the Arctic. Furthermore, despite differences in resolution, key species, such as krill, were among the top five most connected species in 95% of the 21 webs. In conclusion, polar food webs seem to have

similar energetic dependence on key species, such as krill. Differences between the Arctic and Antarctic are primarily limited to the properties of nodes and major taxonomic groups, which may be due to local differences in geography, bathymetry, and oceanographic patterns as well as anthropogenic disturbances. Here, I have shown the utility of food webs in assessing the structure and function of ecosystems. When combined with environmental pressure, they can be used to predict how ecosystems will change under various scenarios of environmental change.

4.2. Introduction

Food webs, "who eats whom networks", or diagrammatic representations of energy flow in ecosystems, have become a popular way to describe the overall structure and function of ecological systems. In comparison to classical ecological approaches, which generally focus on quantifying individual species richness and abundance, food webs provide valuable information on community structure and species interactions (Williams & Martinez, 2000; Dunne, 2005; Thompson et al., 2012). Basic topological properties of food webs, such as size (S), connectance (C) and link density (L/S) can be used to identify key species which have a higher connectedness in comparison to other species in the food web, which may highlight the importance of certain primary producers or top predators in an ecosystem. Other structural properties such as the linkage distribution amongst nodes can be used to describe the level of generalists and specialists within an ecosystem, both of which strongly influence the paths of energy flow. On a larger scale, food webs allow us to understand the mechanisms behind changes in biodiversity, which can be caused by abiotic and biotic factors including habitat loss and degradation (Coll et al., 2008; Yule et al., 2010), species loss (Curtsdotter et al., 2011; Carscallen & Romanuk, 2012), and species invasions (Romanuk et al., 2009). Understanding the structure of an ecosystem and the importance of various energy pathways will allow us to manage our natural resources more efficiently and sustainably.

The polar regions are currently experiencing major shifts in community structure due to multiple anthropogenic disturbances such as climate change (Doney et al., 2011), pollution (Stark et al., 2014), fishing (McBride et al., 2014), shipping traffic (Corbett et al., 2010), and oil exploration (Agnew, 2002) among others. Many of the predicted biological changes threaten to seriously affect natural energy flow patterns in these ecosystems. Food webs thus represent an important way to simulate these potential environmental changes and can also be used to address specific questions such as the consequences of removing a highly connected commercially important species, such as krill. Despite the assumed similarity in structure between polar food webs (but see Carscallen & Romanuk 2012), we have only just begun to understand how they will respond to changing environmental conditions (Hop & Gjosaeter, 2013; Stark et al., 2014)

Food webs for Arctic and Antarctic ecosystems have been compiled since at least 1954, when one of the first polar food webs was described (Dunbar, 1954). These early food webs were typically weakly resolved with nodes representing large taxonomic groupings rather than particular species and had as few as 12 nodes. In contrast, as of 2015, many polar food webs are now highly resolved, showing a more even resolution across trophic levels. The largest and most complete polar food web constructed to date contains 492 nodes (Jacob et al., 2011). However, despite the increase in food web studies in the Arctic and Antarctic (Carscallen & Romanuk, 2012; de Santana et al., 2013), little is known about the drivers of similarities and differences across, and within, the polar regions.

One area of interest, is the question of comparability of food webs. With the improvement in data collection (Raymond et al., 2011) and development of food web validation techniques, including stable isotopes analysis (Stowasser et al., 2012; Carscallen et al., 2012) and model comparisons (Williams & Martinez, 2000; Williams & Martinez, 2008; Cattin et al., 2004) it is now possible to assess whether these comparisons between food webs are meaningful or whether they simply show differences in the methodology used to assemble the food webs. However, many questions still remain, including whether small and large webs are fundamentally comparable due to the very strong correlations between both species richness (*S*) and connectance (*C*) and other food web properties (Dunne et al., 2005). Thus, prior to formally comparing structural properties between Arctic and Antarctic ecosystems, it is first necessary to determine whether the food webs themselves can be compared. Although there is no widely accepted methodology for comparability, several techniques can be used including the sequential aggregation of similar nodes or the random removal of nodes (Carscallen & Romanuk, 2012; Dunne et al., 2008). Both of these techniques also shed light on the response of food webs to structural perturbations. Five models, including the random (Erdos & Renyi, 1959), cascade (Cohen et al., 1990), niche (Williams & Martinez, 2000), nested hierarchy (Cattin et al., 2004) and relaxed niche model (Williams & Martinez, 2008), have been used to determine whether the empirical webs are accurate representations of a natural ecosystem, as well as whether the webs were comparable. Lastly, the top five most connected nodes were compared across food webs to determine if, despite differences in assembly methodology and resolution, key species such as krill, which contribute largely to the energy pathways, show similar trends in link dominance across all food webs.

The question of whether there are fundamental differences in food web structure between polar regions has previously only been considered twice. Carscallen and Romanuk (2012) published a comparison of similarly constructed high resolution food webs for Arctic and Antarctic marine ecosystems focusing on ice-associated species. De Santana et al. (2013) conducted a comparison of food web structure between a large Arctic and Antarctic food web. These studies are informative and have provided evidence of some significant differences in energy flow patterns, particularly related to higher species richness and generality in the Antarctic. However, to date, no formal comparison between marine Arctic and Antarctic ecosystems have been conducted across published food webs. Due to similar extreme environmental conditions, it might be predicted that energy flow patterns in polar systems are fundamentally similar despite strong differences in community composition, such as nearly 50% more fish species in the Antarctic relative to the Arctic (Carscallen & Romanuk, 2012). Furthermore, large scale differences in geography, bathymetry, oceanographic patterns, and evolutionary history may result in markedly different structural properties and potentially very different responses to environmental change.

Understanding differences and similarities between polar food webs is increasingly important given the widespread changes that will occur in these ecosystems (IPCC, 2013), including range shifts towards higher latitudes (Muerter & Litzow, 2008; Spencer, 2008) and in some IPCC (2013) projections up to an 8ºC increase in temperature. Food web analysis has previously been extensively used to explore important questions related to the consequences of environmental change and the ability of ecosystems to adapt such as extinction patterns (Dunne & Williams, 2009), species invasions (Romanuk et al., 2009), and responses to disturbance such overfishing (Coll et al., 2008) among others. The Arctic and Antarctic biomes differ strongly geographically with large differences in many features such as the extent of marine-terrestrial habitat interactions that have a marked effect on species composition and food web ecology (McBride et al., 2014). To explore differences and similarities between, and within, Arctic and Antarctic ecosystems, I conducted a hierarchical analysis which creates a foundation of understanding for explicit studies exploring the impacts of anthropogenic disturbances. My analysis was focussed at four levels of resolution: 1) across structural properties associated with the whole web (such as richness and connectance), 2) across all node properties, 3) across node properties for various taxonomic groups such as fish, marine mammals, and invertebrates, and 4) node properties for key species in the webs such as highly connected species or species that are under considerable environmental pressure. Additionally, I explicitly address the question of whether it is possible to directly compare food webs constructed by different individuals at different resolutions, which has been a subject of considerable debate (Jordan, 2003; Sanchez-Carmona et al., 2012).

4.3. Methods:

4.3.1. Study Sites

The Arctic Ocean is almost completely bordered by marine-terrestrial biomes, whereas the Antarctic is, quite literally, its polar opposite, as it is a terrestrial biome completely surrounded by multiple oceans. In addition to being 30% larger (Arctic Ocean = 14.05 mil km^2, Antarctic ocean = 20.3 mil km^2), the Antarctic Ocean is on average four to five times deeper than the Arctic Ocean. The large difference in depth is primarily driven by differences in the shallow continental shelves, which, in the Arctic, can extend over 1000 km from shorelines, whereas in the Antarctic, extends 60 to 240 km. Another key difference between the two regions lies in the exchange of ocean waters. As the Arctic ocean is almost completely bordered by land, only two regions allow for water exchange in and out of the Arctic ocean, including; 1) the Bering Strait, and 2) the waters surrounding Greenland, Norway, and Icelandic seas. Alternatively, the Antarctic Ocean connects directly to the southern tip of the Atlantic, Pacific, and Indian Oceans. Although the polar regions have high latitudes, seasonal changes, and cold temperatures in commons, the vast differences in extent, geological structure, and oceanographic processes are likely to influence food web structure in each region.

Similar to Carscallen and Romanuk (2012), the spatial extent of the marine Arctic included the deep Eurasian and Canadian Basins, the surrounding continental shelf seas (Barents, White, Kara, Laptev, East Siberian, Chukchi, and Beaufort Seas), the Canadian Archipelago, and the transitional regions to the South through which exchanges between temperate and Arctic waters occurs. These transitional regions include the Bering Sea in the Pacific Ocean and large parts of the northern North Atlantic Ocean, including the Arctic sections of the Nordic, Iceland, Labrador Seas, and Baffin Bay.

The Antarctic marine region was defined as the Southern Ocean and its surrounding waters including the Weddell Sea, Amundsen Sea, Ross Sea, South Pacific Ocean, South Indian Ocean, and Scotia Sea. Additionally, the island chains of Bouvet Island, Scott Island, and the South Shetland Islands in the Southern Ocean were included.

4.3.2. Food web search

I conducted a thorough literature search for whole food webs that had been compiled for Arctic and Antarctic marine ecosystems and were published in either the primary literature or in data repositories such as the Global Web database (www.globalwebdb.com). I assembled a list of 21 previously published food webs for Arctic (n=12) and Antarctic (n=9) marine ecosystems that all shared the following features: 1) the web represented a complete set of taxa in an ecosystem including basal, intermediate, and top species (Table 4.1), 2) they were not source or sink webs, which are constructed with a focus on a specific taxa (i.e. whales, Greenland shark, krill) and the feeding chains that link that species to the rest of the web. These webs were not included as the taxa and link resolution tends to be biased towards the producer or consumer species of interest, thus only depicting a portion, or specific food chain, of the food web. 3) The webs were all focused on marine systems and did not include a substantial terrestrial component and 4) there were no biologically implausible energy pathways in the food webs. In total, these rules eliminated approximately 90% of the published food webs. Those webs which were included ranged from localised food webs compiled for specific habitats, such as the Barent Sea (Planque et al.,2014), Weddell Sea (Jacob et al., 2011), Ross Sea (Smith et al., 2007), Falkland Islands (Cheung & Putcher, 2005), and Antarctic Peninsula (Ballerini et al., 2014), to whole Arctic and Antarctic meta-webs that integrate information on species composition and links across time and space (Carscallen & Romanuk, 2012).

4.3.3. Comparability

Prior to formally comparing food web structure across webs, it is first necessary to determine whether the webs themselves can be compared, despite differences in resolution and assemble methodology. I used two methods to assess the comparability of the food webs. First, species loss simulations were conducted as in Dunne et al. (2002), and Carscallen and Romanuk (2012). The structural robustness (R_{50}) of food webs to species removal was calculated as the fraction of primary removals needed to collapse the webs to 50% of their original size. To relate the degree of food web robustness with extinction, I explored the potential effects of random species removals to trigger cascades of secondary extinctions. Secondary extinctions result when a consumer species loses all its prey items or when a cannibalistic species loses all of its prey items except itself. Second, I performed a sequential aggregation procedure in which nodes were aggregated according to the similarity in feeding links, which ranged from 0 to 100%. At each step of the aggregation procedure, the mean maximum similarity is calculated and nodes which have a similarity equal to, or higher, are aggregated into a single node. This procedure is repeated until no further node aggregations are possible. If the food webs are comparable, changes in food web properties, with increasing aggregation and random species extinctions, should be roughly equivalent across the webs (Carscallen & Romanuk, 2012). For both the aggregation and the extinction simulations I calculated the change in eight core food web properties which explain the majority of distinguishing structural features of a food web, including: node richness, connectance, links per species, fraction of top and intermediate species, standard deviation of generality and vulnerability, and mean clustering coefficient (see Figure 4.2 for definitions).

4.3.4. Web properties

To characterise the structure of the food web, I calculated 26 structural properties (Complete list:Figure 4.2). Two standard measures of food web trophic interaction richness are reported: links per species (*L/S*), which equals the mean number of species' predators plus prey, also referred to as link density; and connectance (*C*), where $C=L/S^2$, the proportion of all possible trophic links (S^2) that are actually realised (*L*), also referred to as 'directed connectance'. Seven properties give fractions of types of species in a food web: top (*%T*), fraction of taxa that lack any predators or parasites, intermediate (%*I*), fraction of taxa which have both predators and prey, fraction of basal taxa (%*B*), taxa that lack any prey items; fraction of cannibals (%*Can*); fraction of omnivores (%*Omn*), taxa with food chains of different lengths, where a food chain is a linked path from a non-basal to a basal species; fraction of herbivores plus detritivores (%*Herb*); and fraction of taxa involved in looping (%*Loop*) by appearing in a food chain twice. Short-weighted trophic position (*SWTP*) is the average of 'prey-averaged trophic position', one plus the mean trophic position of all the taxon's trophic resources, and 'shortest trophic position', one plus the shortest chain length from the consumer taxon to a basal taxon (William & Martinez, 2004). I report three related measures, the maximum trophic level (*TLMax*), the mean trophic level (*TLMean*) and the trophic level standard deviation (*TLSD*), all based on short-weighted trophic position. The standard deviation of mean generality (*GenSD*), describes how many prey items a species has, and vulnerability (*VulSD*), how many predators a species has. These two measures quantify the variabilities of species' normalized predator and prey counts (Schoener, 1989). I used diet discontinuity (*DietDis*) defined as the number of triplets of species with an "irreducible gap", i.e. a gap in a consumer's diet that cannot be made contiguous because of the constraints imposed by other consumers' diets, divided by the number of possible triplets (Stouffer et al., 2006) as a measure of intervality. Taxa similarity was calculated as the fraction of predator and prey links shared between nodes. Three measures were calculated for this including, mean similarity (*MeanSim*), the mean fraction of similar predator and prey links across all taxa, maximum similarity (*MaxSim*), which is the maximum fraction of similar predator and prey links for two taxa, and mean maximum similarity (*MeanMaxSim*), which is the mean maximum fraction of similar predator and prey links across all taxa. I also report one measure of 'small-world' network structure (Watts & Strogatz, 1998), the clustering coefficient (*CC*), which is the mean fraction of species pairs connected to the same species that are connected to each other (Dunne et al., 2002; Camacho & Guimera, 2002; Montoya & Sole, 2002; Williams et al., 2002).

4.3.5. Models

To determine the biological accuracy of the 21 empirical food webs included in this study, their food webs properties were compared against those predicted by five models, including, the random (Erdos & Renyi, 1959), cascade (Cohen et al. 1990), niche (Williams & Martinez, 2000), nested hierarchy (Cattin et al., 2004) and relaxed niche model (Williams & Martinez, 2008). If the empirical food web properties were within ±1 of the model means for each food web property, the empirical webs were considered biologically accurate.

The random model assigns feeding links, among species (S), with a probability equal to the connectance (C) of the empirical webs. This allows for food webs which are not bound by biological structuring, but still maintained the observed S and C of the empirical webs. The cascade model randomly assigns each species a niche value (n_i) along an interval [0, 1] and feeding links between species are assigned based on a probability $P = 2CS/(S\text{-}1)$ of consuming only species with a value on the interval less than its own. The niche model similarly assigns each species a niche value on an interval [0,1], but additionally assigns each species a feeding range (r_i) and feeding range center (c_i), with the condition that the center of the feeding range is less than its niche value. This allows up to half of a consumers' diet to include species with a niche value higher than its own. The nested hierarchy model builds on the niche model but does not rely on niches in a one-dimensional space (the niche axis), but focuses instead on groups of species and implicitly considers phylogenetic constrains and adaptation (Cattin et al., 2004). In this model, a consumers' i prey resources j are randomly chosen such that $n_j < n_i$ until either the consumer (i) obtains all its resource species, or obtains a resource species j, which is already consumed by another consumer. In this event, the consumer is grouped with the other consumers, sharing the same prey resource j, and the remaining prey resources are chosen at random from the pool of resources of this group until either all prey of consumer i are chosen or all the prey of the group have been chosen. The relaxed niche model is also an extension of the original niche model which has been giving an additional input called 'contiguity' (g) which ranges from 0 to 1 and modifies the width of the feeding ranges. When g=1, the model is identical to the niche model, whereas when g approaches 0 the width of the feeding ranges is increased allowing for consumers to potentially prey on more species, reducing the probability that a consumer will prey on any one particular species in its feeding range. This allows for non-interval webs to occur (Williams & Martinez, 2008).

4.3.6. Node Properties

To characterize taxa (nodes) in the food webs, eight node properties were calculated for all nodes across all food webs (n = 1911). Two measures of trophic position were calculated including prey-averaged trophic position (*PATP*), one plus the mean trophic position of all the taxon's trophic resources, and short-weighted trophic position (*SWTP*), the average of 'prey-averaged trophic position' and 'shortest trophic position', one plus the shortest chain length (*MinChLen*) from the consumer taxon to a basal taxon. The variance of prey-averaged trophic position (*PATPVar*) was also calculated. Four link properties were calculated including the number of predator links (*PredCount*) and prey links (*PreyCount*), the number of prey of prey links (*PreyofPrey*) and the maximum link similarity across all nodes (*MaxSim*).

Nodes were then categorized into eight taxonomic groups (TG), including; 1) mammals, 2) birds, 3) fish, 4) invertebrates, 5) bacteria, 6) basal, 7) detritus, and 8) other (eg. Salts), in order to explore i) differences in the distribution of species across taxonomic groups, ii) node properties within each group, and iii) which taxonomic group and taxa are the most connected. For the most connected species, the top five most connected species in each food web were selected to identify key taxa both across the Arctic and Antarctic as well as within each region.

4.3.7. Analyses

As many food web properties are highly correlated ($r > 0.7$), I ran a correlation analysis across all food web and node properties. Of the 26 original food web properties, 15 were excluded from statistical analyses, including, *S*, *%I*, *LinkSD*, *PATP*, *PATPSD*, *CC*, *ConsumerMeanTP*, *TPMax*, *ConsumerDirOmn*, *Cannibal*, *DD*, *VulSD*, *MeanSim*, *SimSD* and *SimMaxMean*. Of the eight node properties, two were excluded from statistical analyses, including, *PATP* and *SCL*. As the data was not normally distributed, as per the Kolmogorov-Smirnov & Lilliefors test, and showed a higher level heteroscedasticity, as per White's test, I ran a multivariate PERMANOVA, which uses a Bray-Curtis measure of similarity, to test for significant differences between Arctic and Antarctic webs across 1) all uncorrelated food web properties, 2) all uncorrelated node properties, 3) uncorrelated node properties for taxonomic groups and 4) uncorrelated node properties or key species. I used a SIMPER analysis, which uses a Bray-Curtis measure of similarity, to identify which food webs properties contributed to the majority > 50% of the similarities among food web properties between the Arctic and Antarctic webs. Lastly, significant results across all food web or node properties were further explored with a Kruskal-Wallis ANOVA (KW-ANOVA), which compares mean ranks as oppose to a traditional ANOVA which compares means, to determine significant differences between individual food web and node properties. As species richness is known to influence food web properties (Dunne et al., 2002) I used a multivariate PERMANOVA to test for significant differences between large and small webs. A SIMPER analysis was used to identify which food web properties contributed the most to differences between size based webs.

I used non-metric multidimensional scaling (nMDS) based on the Bray-Curtis dissimilarity index to visualize differences across 1) all food webs across both regions, 2) a subset (n = 6) of large highly resolved food webs across both regions, 3) all taxa (n = 1911), and 4) taxa categorized into 8 different groups including, i) mammals (n = 157), ii) birds (n = 86), iii) fish (n = 642), iv) invertebrates (n = 880), v) bacteria (n = 7), vi) basal (n = 108), vii) detritus (n = 29), and viii) other (n = 2) (e.g. salts). The nMDS used random starting configurations and 100 runs with real data. A two-dimensional representation was accepted as a good depiction of the data if the stress index was < 0.1 (Clark et al., 2014).

4.4. Results

The focus of this paper is a comparison of food web structure for Arctic and Antarctic marine ecosystems using a set of 21 complete ecosystem webs (Table 4.1) published over the last 60 years. The webs range from localized food webs complied for specific habitats, such as the Barents Sea (Planque et al., 2014), Weddell Sea (Jacob et al., 2011), Ross Sea (Smith et al., 2007), Falkland Islands (Cheung & Pitcher, 2005), and Antarctic Peninsula (Ballerini et al., 2014), to whole Arctic and Antarctic meta-webs that integrate information on species composition and links across time and space (Carscallen & Romanuk, 2012). In total there were 12 food webs from the Arctic ranging from 12 to 233 nodes with 20 to 2,218 feeding links, and 9 food webs in the Antarctic ranging from 14 to 492 nodes with 28 to 16,330 feeding links (Figure 4.1).

4.4.1. Comparability

Across all webs, the mean robustness to species loss was $R_{50} = 0.45$, when basal species were protected (i.e. not allowed to be removed in the simulation) for the deletion of random species (Figure 4.2). When the webs were grouped into region and size, there was little difference with the Antarctic being marginally more robust then the Arctic (mean $R_{50\text{Arctic}} = 0.44$, mean

$R_{50\text{Antarctic}} = 0.45$) and small webs being marginally more robust then large webs (mean $R_{50\text{Small}} = 0.45$, mean $R_{50\text{Large}} = 0.44$). One Arctic web had the lowest robustness ($R_{50} = 0.39$), which was a result of a low connectance and species richness. This was confirmed with a Kruskal-Wallis ANOVA which showed no significant difference in the average rate of species loss between Arctic and Antarctic ($H_{1,20} = 0.45$, $p = 0.5$), and small and large ($H_{1,20} = 1$, $p = 0.31$) webs during the species extinction scenario.

The random removal of nodes resulted in no consistent differences between the response of Arctic and Antarctic food webs across all food web properties (Figure 4.3). The only differences seen were primarily related to size and were seen in species richness (Figure 4.3 A), connectance (Figure 4.3 C), generality SD (Figure 4.3 E), and vulnerability SD (Figure 4.3 F). Furthermore, size seemed to create less variability in food web properties, specifically for connectance (Figure 4.3 C) and clustering coefficient (Figure 4.3 D). After approximately 80% of the nodes being removed, all food webs across six of the food web properties, not including species richness or links per species, exhibited strong changes in food web properties. Sequential node aggregation from 100% to 0% showed trends similar to the random species removals across the eight food web properties (Figure 4.4). Variability in food web properties can be seen as an effect of size, specifically in connectance (Figure 4.4 C), links per species (Figure 4.4 D), generality SD (Figure 4.4 E), and vulnerability SD (Figure 4.4 F). Food web properties also become more variable when approximately 80% of the nodes have been aggregated.

4.4.2. Food web Structure

The complete set of food web properties is listed in Table 4.1 for all Arctic and Antarctic food webs. Across all webs, mean taxa richness (S) was 48% higher in the Antarctic (mean $S_{\text{Antarctic}} = 114$) compared to the Arctic (mean $S_{\text{Arctic}} = 77$). Connectance (C) was 26% higher in the

Antarctic than the Arctic (mean $C_{\text{Arctic}} = 0.12$, mean $C_{\text{Antarctic}} = 0.15$). The mean number of links per species (L/S) was higher by approximately 3.8 in the Antarctic than the Arctic (mean $L/S_{\text{Arctic}} = 5.66$, mean $L/S_{\text{Antarctic}} = 9.45$). Mean short-weighted trophic position ($SWTP$) was slightly higher in the Arctic than the Antarctic (mean $SWTP_{\text{Arctic}} = 3.18$, mean $SWTP_{\text{Antarctic}} = 3.03$).

The fraction of top predators was slightly higher in the Arctic than the Antarctic (mean $\%T_{\text{Arctic}} = 17.15$, mean $\%T_{\text{Antarctic}} = 11.93$). The fraction of intermediate and basal species was higher in the Antarctic than the Arctic (mean $\%I_{\text{Arctic}} = 74.8$, mean $\%I_{\text{Antarctic}} = 76.6$; mean $\%B_{\text{Arctic}} = 8.05$, mean $\%B_{\text{Antarctic}} = 11.47$). Diet discontinuity was ~ 30% higher in the Arctic as in the Antarctic (mean $DietDis_{\text{Arctic}} = 0.22$, mean $DietDis_{\text{Antarctic}} = 0.17$). The clustering coefficient and looping were higher in the Antarctic than the Arctic (mean $CC_{\text{Arctic}} = 0.2$, Mean $CC_{\text{Antarctic}} = 0.24$; mean $\%Loop_{\text{Arctic}} = 0.16$, mean $\%Loop_{\text{Antarctic}} = 0.19$). Standard deviation of vulnerability (mean $\text{VulSD}_{\text{Arctic}} = 1.12$, mean $\text{VulSD}_{\text{Antarctic}} = 1$) and generality (mean $GenSD_{\text{Arctic}} = 0.87$, mean $GenSD_{\text{Antarctic}} = 0.85$) were slightly higher in the Arctic than the Antarctic. The fraction of cannibals was higher in the Antarctic that the Arctic (mean $\%Can_{\text{Arctic}} = 0.12$, mean $\%Can_{\text{Antarctic}} = 0.15$).

Multivariate PERMANOVA showed that across all food webs and uncorrelated food web properties there was no significant difference ($\text{Pseudo-F}_{1,\,20} = 0.6$, $p = 0.63$) between the Arctic and Antarctic. Non-metric multidimensional scaling (nMDS) was consistent in the lack of significant differences across Arctic and Antarctic food webs (stress = 0.13); however, a visual grouping was seen that indicated strong similarities within large ($S > 100$, $n = 6$) and small ($S < 100$, $n = 15$) webs (Figure 4.5). Multivariate PERMANOVA confirmed this and showed significant differences ($\text{Pseudo-F}_{1,20} = 31.27$, $p < 0.001$) in food web properties when webs were grouped by size. A SIMPER analysis showed that this pattern of differences being strongly related to the size of the web was primarily driven by variables related to gross trophic structure such as the proportion of herbivores, fraction top species, and fraction basal species. Fraction of herbivores explained 38% of the difference between large and small food webs ($p = 0.005$), followed by fraction of top species (25%), and basal species (17.5%).

To determine whether size of the web was driving any differences in Arctic and Antarctic webs I further explored differences in structure between webs that were either small ($S < 100$) or large ($S > 100$). Kruskal-Wallis ANOVA showed significant differences between five of the 11 uncorrelated food web properties. Two of these food web properties were higher in smaller webs, including, fraction of basal species (*%B*, $H_{1,21} = 7.01$, $p < 0.01$) and connectance (C, $H_{1,21} = 12.27$, $p < 0.001$), whereas the rest were higher in larger webs, including, fraction of herbivores (*%Herb*, $H_{1,21} = 6.41$, $p = 0.01$), generality SD (*GenSD*, $H_{1,21} = 9.22$, $p < 0.01$), and max similarity (*SimMaxMean*, $H_{1,21} = 4.57$, $p = 0.03$), showing that web size is a crucial determinant of differences in food web properties.

4.4.3. Models

I tested the 21 food webs against five models to determine if the empirical webs were accurate representations of natural ecosystems, and if they were comparable. Across all food webs, all models tended to underestimate food web properties (Mean ME = -1.31 to -0.23, ME SD = 1.02 to 4.74) (*Table 4.3*). Additionally, all models except the random model had a $|ME|$ which was < 1, indicating that the more biologically realistic models were a good fit. When the food webs were broken into Arctic (Mean ME = -1.9 to -0.31, ME SD = 0.41 to 2.92) and Antarctic webs (Mean ME = -0.56 to -0.13, ME SD = 0.43 to 0.75), all models slightly under predicted food web properties. No models had a Mean ME outside of ±1 in the Antarctic; however, in Arctic the

Niche and Random both had a Mean ME outside of ±1, indicating that the models did not accurately estimate the food web properties.

4.4.4. Node Properties

Node properties were calculated for each taxon/node for the Arctic (n = 986) and the Antarctic (n = 925). Across all nodes, both prey-averaged trophic position and short-weighted trophic position was slightly higher in the Arctic than the Antarctic (mean $PATP_{\text{Arctic}} = 3.5$, mean $PATP_{\text{Antarctic}} = 3.24$; mean $SWTP_{\text{Arctic}} = 3.03$, mean $SWTP_{\text{Antarctic}} = 2.83$) although variability in prey-averaged trophic position was similar in both (mean $PATP\text{Var}_{\text{Arctic}} = 0.47$, mean $PATPVar_{Antarctic} = 0.45$). The mean minimum chain length was slightly higher in the Arctic than Antarctic (mean $MinChLen_{\text{Arctic}} = 2.56$, mean $MinChLen_{\text{Antarctic}} = 2.41$). Three of the four link properties were higher in the Antarctic than the Arctic. The mean number of predator and prey links were 63% lower in the Arctic than the Antarctic (mean $PredCount_{\text{Arctic}} = 7.19$, mean $PredCount_{\text{Antarctic}} = 20.71$; mean $PreyCount_{\text{Arctic}} = 7.19$, mean $PreyCount_{\text{Antarctic}} = 20.71$). The mean maximum similarity was 32% lower in the Arctic then Antarctic (mean $MaxSim_{\text{Arctic}} = 0.51$, mean $MaxSim_{\text{Antarctic}} = 0.74$). There was no difference in the mean number of prey of prey between the Arctic and the Antarctic (mean $PreyofPrey_{\text{Arctic}} = 0.45$, mean $PreyofPrey_{\text{Antarctic}} = 0.45$).

Multivariate PERMANOVA across all food webs (n = 1911) showed a significant difference in uncorrelated node properties between the Arctic and Antarctic (Pseudo-$F_{1,1910} = 139$, $p < 0.001$). The Kruskal-Wallis ANOVAs showed that there were significant differences between five of the seven node properties. One of the node properties, short-weighted trophic position ($H_{1,\,1911} = 10.8$, $p < 0.001$), was higher in the Arctic, whereas number of prey links ($H_{1,\,1911} = 24$, $p < 0.001$), number of predator links ($H_{1,\,1911} = 147.9$, $p < 0.001$), and maximum similarity ($H_{1,\,1911} =$

390.9, $p < 0.001$), were higher in the Antarctic. Thus, despite the lack of strong significant differences across food web properties between Arctic and Antarctic webs from a whole-web structural perspective, strong differences were observed for node properties. This showed that while the structure of polar food webs may be similar, there are strong differences between the taxa in each region, and the distribution of feeding interactions among them.

4.4.5. Taxonomic groups

Across all taxonomic groups, four of the eight node properties were higher in the Antarctic than the Arctic: the number of prey and predator links were 1.97 and 2.82 times higher on average in the Antarctic than the Arctic, respectively and maximum similarity was 1.45 times higher on average in the Antarctic than the Arctic. For the other five node properties there were no clear distinctions between Antarctic and Artic food webs. An nMDS of the average node properties between all taxonomic groups revealed no strong differences between the Arctic and Antarctic except a strong segregation between higher (i.e. mammals, birds, fish, invertebrates) and lower (i.e. bacteria, basal species, detritus) trophic position taxa (Figure 4.6).

In the Antarctic, the number of predator links was inversely proportional to trophic position, increasing to a maximum of 68.24 (TG = basal), whereas in the Arctic, the number of predator links did not increase higher than 13.84 (TG = detritus) (Figure 4.7 E). A similar trend was seen in the number of prey links in the Antarctic, which increased significantly from birds to fish and invertebrates, reaching a maximum of 29.72 (TG = invertebrates) (Figure 4.7 F). Alternatively, the number of prey links in the Arctic decreased with trophic position, with a maximum of 11.39 (TG = mammals). The maximum similarity was consistently higher in the Antarctic than the Arctic (Figure 4.7 *G*). For example, for invertebrates and basal species, the maximum similarity was 53% and 234% higher in the Antarctic than the Arctic, respectively. All three of these node properties relate to feeding relationships such as generality and vulnerability indicating that there is a higher level of generality and vulnerability in the Antarctic than the Arctic, particularly for invertebrates and their prey.

4.4.6. Highly connected species

Across all food webs, the top five most connected species (n = 105) were either invertebrates (50%) or fish (36%). A few webs however showed that mammals (5%), basal species (4%), detritus (4%) or bacteria (1%) were the most highly connected species. Krill or amphipods were in the top five most connected species in 20 of the 21 food webs (Figure 4.1 E). Within the fish, cod or other Gadidae were in the top five most connected species in nine of the 21 food webs, seven of which were Arctic webs and two were Antarctic webs (Figure 4.1 F). Although Gadids do show a correlation between body and trophic position, eight out of the ten Gadids used in this analysis of highly connected species had a trophic position within 0.5 TL of the mean, excluding the two outliers.

4.5. Discussion

Food web studies, particularly across gradients of environmental disturbance (Coll et al., 2008; Yule et al., 2010), latitude (Baiser et al., 2012), and other gradients such as depth (Carscallen et al., 2016) are increasingly being used to track changes in energy flow patterns in ecosystems. The information that can be gleaned from the inclusion of species feeding interactions results in a highly detailed and comprehensive way of looking at the effects of disturbance affects ecosystems (Romanuk et al., 2006; Coll et al., 2011).

Despite considerable interest in assembling food webs for polar regions, few studies have attempted a comparison of food web structure across or within the Arctic and Antarctic. My results show only weak differences in whole-web structure between Arctic and Antarctic food webs, primarily related to higher fractions of basal species, higher similarity between species, and higher standard deviation of similarity in the Antarctic. Taken together these differences suggest that in the Arctic there is a higher consumer diversity relative to the Antarctic and that there may be more isolated energy pathways in the Arctic that are derived from fewer resources than in the Antarctic. Additionally, despite obvious differences in species richness and connectance across the 21 webs, their topology was largely comparable, retaining their structure throughout aggregation and species extinction simulations, showing broadly similar fits to food web models, and similar patterns in the dominance of species links.

In 20 of the 21 Arctic and Antarctic food webs, krill or amphipods were among the top five most connected species, followed closely by cod, which were in the top five most connected species for nine of the 21 food webs. While food webs are typically biased towards highly connected or key species such as krill or cod, the conservation of node properties for key species suggests that regardless of the resolution of the rest of the food web, the similarities and differences in the energy pathways that connect these focal species to the rest of the food web are conserved across food webs constructed at various levels of aggregation. Although this supports the comparability of the polar food webs used in this study, it does raise concern given the extensive fishing of species like krill and cod, and the dependence of many predatory species. Smith et al. (2011) conducted a study across a range of marine ecosystem models to explore the effects of fishing on low-trophic position species. They found that even when fishing within the sustainable yield guidelines, there were large impacts on various aspects of community structure including significant shifts in species abundances. Other less direct effects of overfishing have been found in regions such as the North Sea, where the fishing of piscivorous cod has increased the abundance of certain fish, such as the herring. This increase in herring was then found to supress cod recruitment, further reducing the cod population in the region (Hjermann, et al., 2013).

Given the similarity in environmental conditions it was no surprise that the Arctic and Antarctic food webs were generally structurally similar. Although, a previous study by Carscallen and Romanuk (2012), found broad similarities in the topological structure of Arctic and Antarctic marine sea-ice meta-food webs, my analysis differed completely from de Santana et al. (2013). A key difference between the studies was comparability. In Carscallen and Romanuk (2012) the Arctic and Arctic food webs were constructed using strict guidelines and methodology, which yielded two food webs of similar resolution and levels of error. Alternatively, de Santana et al. (2013) utilized two previously published food webs which differed significantly in resolution and assembly methodology, yielding overall results suggesting strong differences between the Arctic and Antarctic ecosystems. The inconsistency across these findings highlights the importance of comparability when analysing differences in the structure of food webs.

Across all 21 food webs and eight food web properties, approximately 80% of the nodes needed to be removed or aggregated to significantly change food web properties (Figure 4.3 and Figure 4.4). This result suggests that despite significant differences in methodology and resolution, food webs behave similarly during node removal and aggregation, maintaining fundamental structural differences. A similar method to assess comparability was conducted by Dunne et al. (2008) in a study where they compared Cambrian food webs. A challenge they faced was the lack of certainty in the feeding links of the Cambrian food webs, which were mainly speculative due to incomplete information about feeding interactions. To determine whether or not the inclusion of these low-certainty links (i.e. assembly error) would influence food web properties, they simulated both the sequential removal of low-certainty and random links. Their analysis revealed two key findings: 1) the removal of random links produced similar changes in food web properties as the removal of low-certainty links, and 2) that both random and low-certainly link removal did not significantly change (± 20%) the structural properties of the food webs until approximately 66% of the links were removed. This suggests that even if a large portion of a food web is assembled using incorrect data, errors have a minimal impact of the overall structure of the food web.

When model predictions were compared across all webs as well as between the Arctic and Antarctic (Table 4.3) the models results were a good fit, despite slightly underestimating food web properties. Williams and Martinez (2000; 2008) tested the accuracy of these models in predicting the structure of both terrestrial and marine food webs. They highlight that across all food web properties, the models predictive capacity increases from the random to cascade, niche, nested hierarchy, and finally the relaxed-niche model. These results were consistent with our mean model error (Mean ME) results which ranged from -1.31 to -0.23 (Table 4.3) suggesting that the 21 Arctic and Antarctic models are accurate representations of biologically realistic ecosystems, despite differences in methodology and resolution. The use of model food webs can further be used to compare webs with different species richness and connectance (Dunne et al., 2005). As both species richness and connectance are correlated with many food web properties (Dunne et al., 2002), in many cases it is necessary to standardize the data for these differences prior to conducting comparative analyses.

One of the largest drivers behind the increase in Polar food web research, revolves around the question of whether Arctic and Antarctic webs will respond similarly to climate change and other anthropogenic disturbances (Carscallen & Romanuk, 2012). A key component to addressing this question may be in the difference between the energetic pathways and distribution of feeding interactions. Coll et al. (2008) hypothesized that food webs that exhibited features of degradation would have a reduction in the mean and maximum trophic levels, reduction in fraction of top predators, and increases in the fraction of basal species. Additionally, degraded food webs would show a simplification in energy flow pathways, as evidenced from decreases in connectance and shorter food-chain length. It is possible that due to extreme environmental conditions that the Arctic and the Antarctic historically had a similar food web structure prior to human disturbances, in which case these hypothesized predictors of degradation can be applied between them, showing signs of degradation in both regions. The Antarctic shows a lower mean and maximum trophic level, lower fraction of top predators, and a higher fraction of basal species potentially suggesting an overexploitation of high trophic position species (Table 4.5). In contrast, the Arctic shows a lower connectance and number of links per species, suggesting a simplification of its energy pathways.

These results suggest that variations in climate change and other anthropogenic disturbances such as overfishing, may be pushing both the Arctic and Antarctic into a further state of degradation. Supporting evidence of both patterns of degradation can be seen when looking at historical fisheries data. Over the last 1.5 decades fishing has increased by over 25% across the Arctic and Antarctic regions from approximately 142,000 to 178,000 tons per year, ranking them as the regions with the second highest increase in fishing pressure (FAO, 2014). Fishing pressure in the Arctic has been primarily on species such as pollock, haddock, and cod, all three of which are key intermediate generalist species (FAO, 2014), which contribute strongly to the complexity of the energy pathways. Alternatively, in the Antarctic, whaling and sealing over the last centuries has dramatically reduced populations of top predators (Aronson et al., 2011). The overfishing of krill, which are the primary food source for many of the higher trophic position species, is putting additional strain on high trophic level species (Surma et al., 2014).

Despite strong environmental similarities in polar marine ecosystems I identified a number of key differences between Arctic and Antarctic webs and the properties of species and taxonomic groups. As anthropogenic disturbances will only increase in polar regions, analyses of food web structure such as the comparison for 21 polar food webs presented here will be increasingly important in tracking the consequences of environmental change and predicting the robustness and resilience of Arctic and Antarctic marine ecosystems to increasing human disturbance.

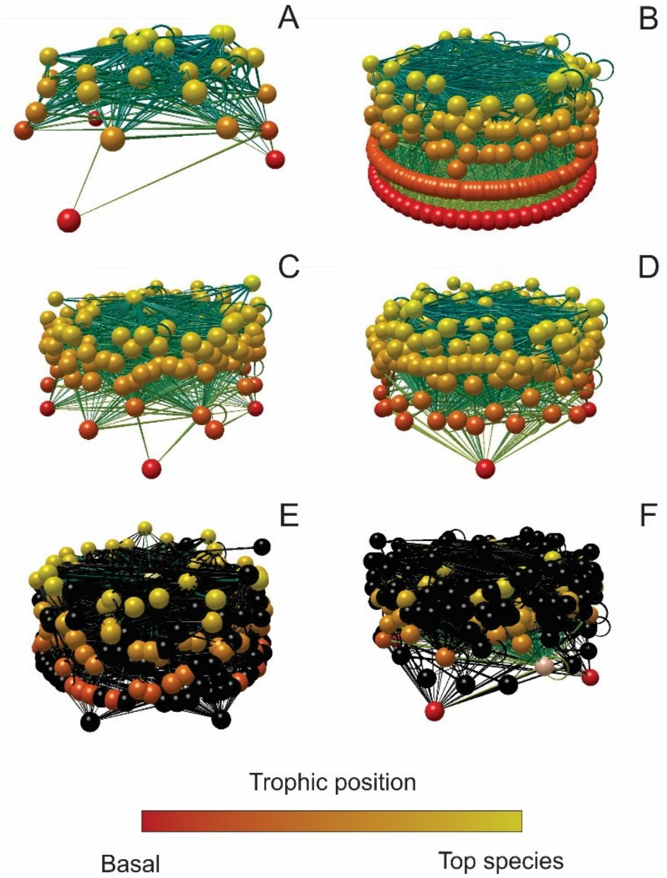


Figure 4.1: 3-D representation of food webs. A) Small polar food web, B) Large polar food web, C) Arctic food web, D) Antarctic food web, E) Top species: Cod in the Arctic- Highlighted nodes within one degree of separation, F) Top species: Krill in the Antarctic – Highlighted nodes within one degree of separation.

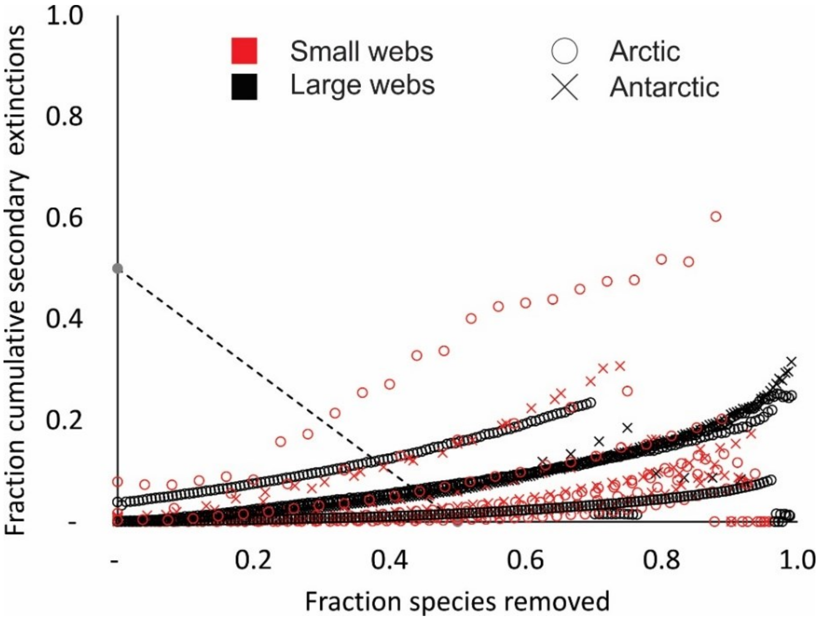


Figure 4.2: Fraction of cumulative secondary extinctions during the sequential removals of random species for each of the 21 food webs. Dotted diagonal line represent the R_{50} value, which equates to the point at which the food web has been reduced to 50% of its original size. Size of the food webs are represented in colour and the region is represented by the shape of the points.

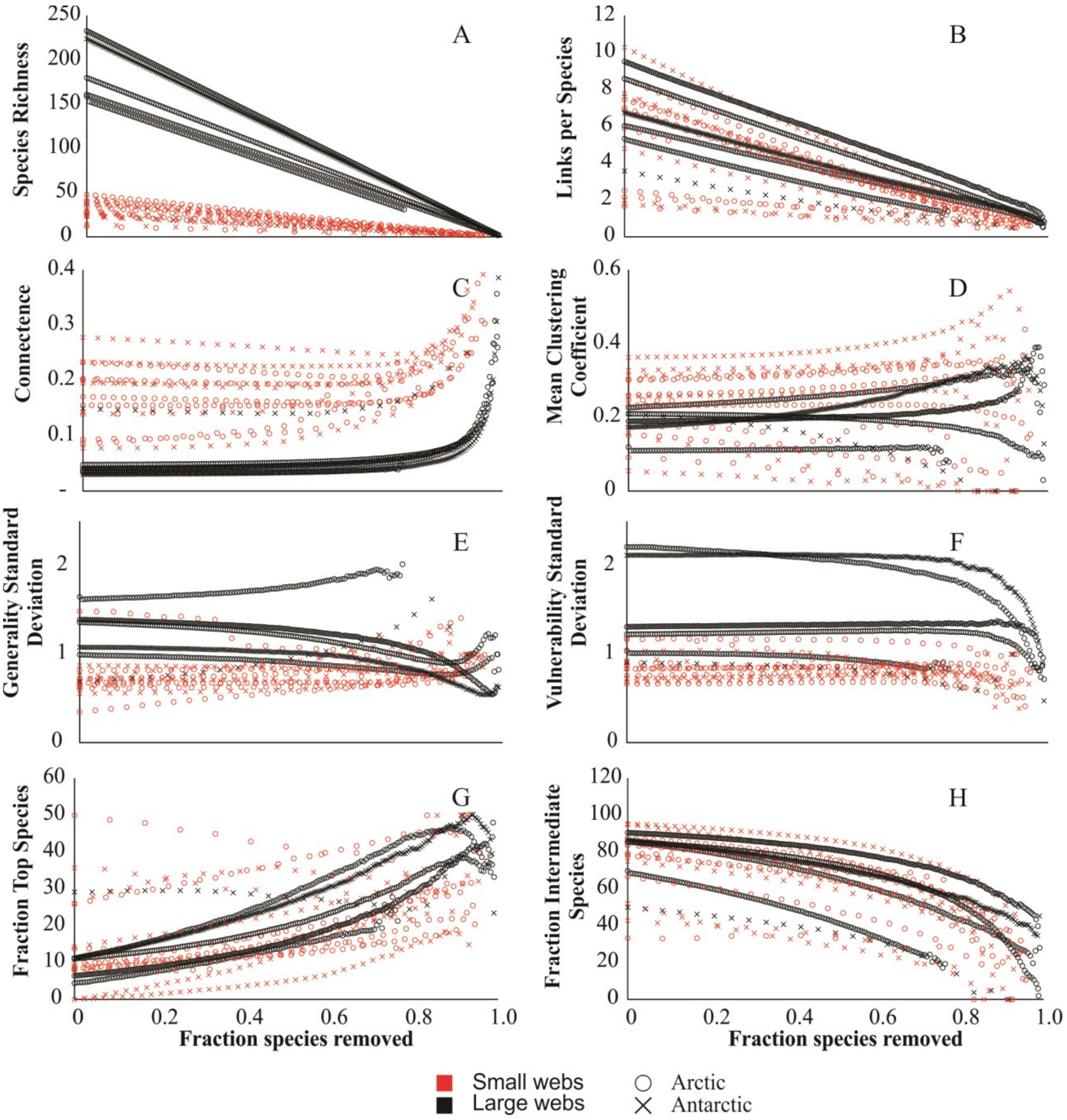


Figure 4.3: Sequential random extinctions on nodes and its effect on eight food web properties. A) species richness (S), B) links per species (L/S), C) connectance (C), D) mean clustering coefficient (MeanCC), E) generality standard deviation (GenSD), F) vulnerability standard deviation (VulSD), G) fraction top species (%T), H) fraction intermediate species (%I). Size of the food webs are represented in colour and the region is represented by the shape of the points.

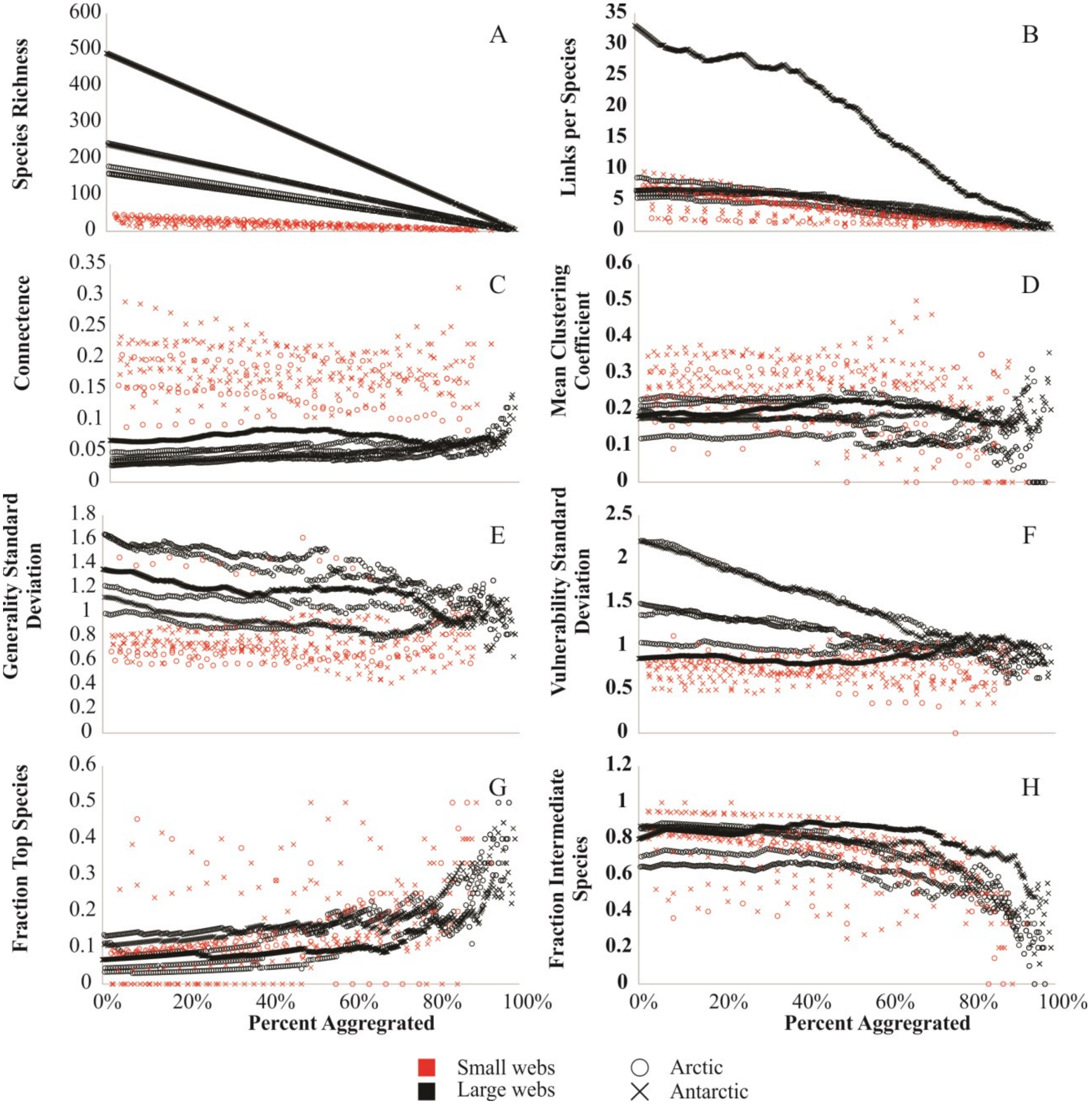


Figure 4.4: Sequential aggregation of similar nodes and its effect on eight food web properties. A) species richness (S), B) links per species (L/S), C) connectance (C), D) mean clustering coefficient (MeanCC), E) generality standard deviation (GenSD), F) vulnerability standard deviation (VulSD), G) fraction top species (%T), H) fraction intermediate species (%I). Size of the food webs are represented in colour and the region is represented by the shape of the points.

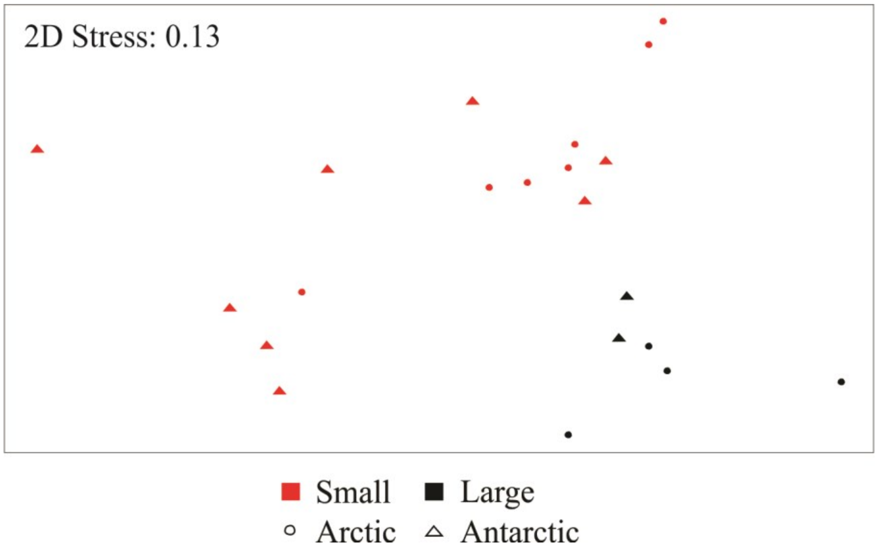


Figure 4.5: Non-metric multidimensional scaling (nMDS) of food web properties across all food webs categorized into large (S > 100, black) and small (S < 100, red) webs.

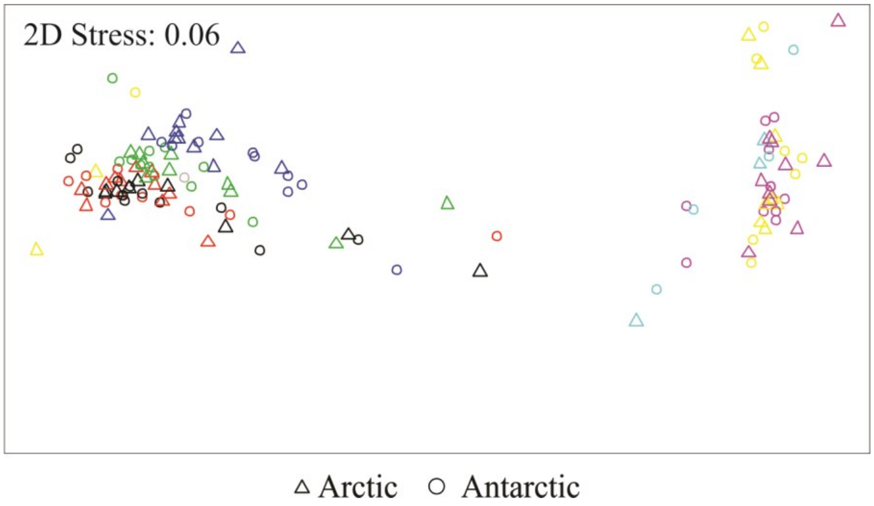


Figure 4.6: Non-metric multidimensional scaling (nMDS) of average node properties for each taxonomic group across all food webs. 1) Mammals (light blue), 2) birds (purple), 3) fish (red), 4) invertebrates (yellow), 5) bacteria (green), 6) basal (dark blue), 7) detritus (black).

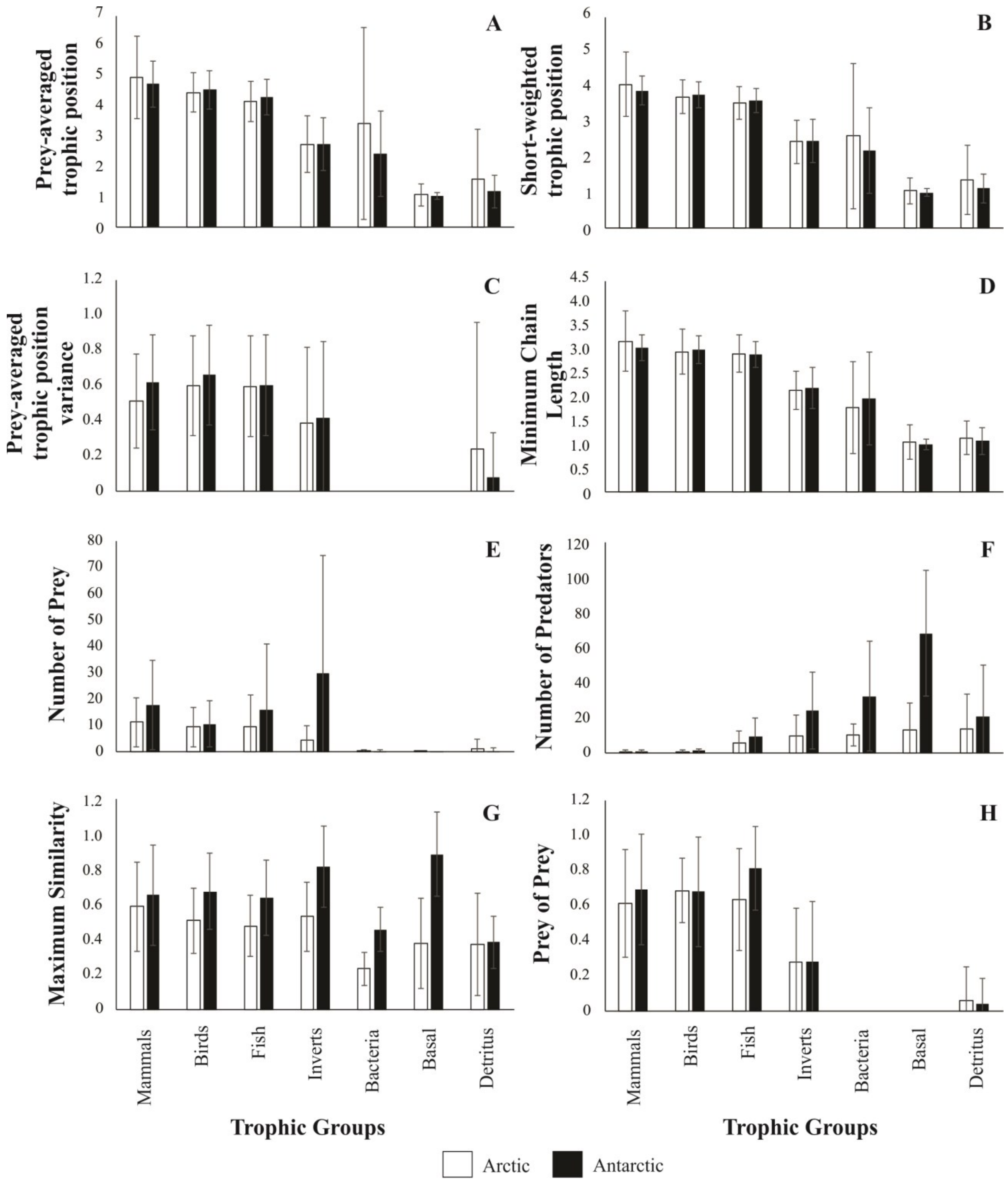


Figure 4.7: Average node properties for each taxonomic group for the Arctic and Antarctic food webs. A) Prey-averaged trophic position (PATP), B) Short-weighted trophic position (SWTP), C) Prey-averaged trophic position variability (PATPVar), D) Minimum chain length (MinChLen), E) Number of Prey (Prey), F) Number of predators (Pred), G) Maximum similarity (MaxSim), H) Prey of prey (PreyofPrey). Error bars represent standard deviation.

Table 4.1: Food web properties for all 21 webs used.

Region	Label	Size	Reference	Date	Location	S	%T	%I	%B	%H	C	L/S	GenSD	VulSD
Ant	Ant-2	Large	Carscallen & Romanuk, 2012	2012	Sea-ice	239	10.88	87.03	2.09	5.44	0.03	6.59	1.13	2.21
Ant	Ant-8	Large	Jacobs et al., 2005	2005	Weddell Sea	492	6.71	79.67	13.62	32.11	0.07	33.19	1.36	0.86
Arc	Arc-10	Large	Kortsch et al., 2015	2015	Boreal	180	11.11	85.56	3.33	27.78	0.05	8.59	1.36	1.23
Arc	Arc-12	Large	Planque et al., 2014	2014	Barent Sea	233	6.44	90.56	3.00	26.18	0.04	9.52	1.39	1.31
Arc	Arc-6	Large	Carscallen & Romanuk, 2012	2012	Sea-ice	161	11.18	85.71	3.11	4.35	0.04	6.03	0.99	2.21
Arc	Arc-9	Large	Kortsch et al., 2015	2015	Marine	159	25.79	69.81	4.40	33.33	0.03	5.33	1.04	1.65
Ant	Ant-1	Small	Ballerini et al., 2014	2014	Wester Peninsula	24	29.17	50.00	20.83	8.33	0.15	3.58	0.69	0.91
Ant	Ant-3	Small	Cheung & Pitcher, 2005	2005	Falkland Islands	44	0.00	95.45	4.55	2.27	0.23	10.30	0.87	0.73
Ant	Ant-4	Small	Cornejo-Donoso & Antezana, 2008	2008	Peninsula	28	14.29	78.57	7.14	0.00	0.28	7.79	0.55	0.84
Ant	Ant-5	Small	Erfan & Pitcher, 2005	2005	Peninsula	39	0.00	94.87	5.13	10.26	0.20	7.62	0.73	0.69
Ant	Ant-9	Small	Hop & Gjosaeter, 2013	2013	Arctic and Barents Sea	14	35.71	42.86	21.43	14.29	0.14	2.00	0.63	0.93
Ant	Ant-6	Small	Palomares et al 2005	2005	Kerguelen Islands	24	8.33	75.00	16.67	4.17	0.20	4.79	0.68	0.72
Ant	Ant-7	Small	Smith et al., 2007	2007	Ross Sea	23	26.09	52.17	21.74	4.35	0.08	1.78	0.76	1.03
Arc	Arc-1	Small	Bradstreet & Cross, 1982	1982	High Arctic Ice Edge	12	50.00	33.33	16.67	16.67	0.14	1.67	0.62	1.18
Arc	Arc-11	Small	Nilsen et al., 2008	2008	North Norway	27	25.93	66.67	7.41	0.00	0.09	2.52	0.35	1.17
Arc	Arc-2	Small	Aydin et al., 2002	2002	East	37	8.11	83.78	8.11	8.11	0.23	8.59	0.81	0.76
Arc	Arc-3	Small	Aydin et al., 2002	2002	West	34	8.82	85.29	5.88	2.94	0.20	6.85	0.61	0.84
Arc	Arc-4	Small	Aydin et al., 2002	2002	West & Basin	48	8.33	87.50	4.17	10.42	0.16	7.46	0.68	0.84
Arc	Arc-5	Small	Blanchard et al., 2002	2002	Barent Sea	41	9.76	78.05	12.20	2.44	0.17	7.00	0.72	0.67
Arc	Arc-7	Small	Dommasnes et al., 2001	2001	Barent Sea	29	13.79	79.31	6.90	3.45	0.20	5.90	0.65	0.90
Arc	Arc-8	Small	Dunbar, 1954	1954	Arctic & sub-Arctic	25	8.00	84.00	8.00	4.00	0.09	2.16	1.49	0.89

Region	Label	Size	Reference	Date	Location	LinkSD	SimMean	SimStdDev	SimMax	SimMaxMean	PATP	TLSD	TLMax	Loop
Ant	Ant-2	Large	Carscallen & Romanuk, 2012	2012	Sea-ice	1.20	0.08	0.11	1.00	0.54	3.98	0.90	5.48	0.08
Ant	Ant-8	Large	Jacobs et al., 2005	2005	Weddell Sea	0.77	0.09	0.18	1.00	0.89	2.67	1.11	5.17	0.26
Arc	Arc-10	Large	Kortsch et al., 2015	2015	Boreal	0.96	0.07	0.09	1.00	0.47	3.13	1.05	5.20	0.15
Arc	Arc-12	Large	Planque et al., 2014	2014	Barent Sea	0.99	0.06	0.09	1.00	0.46	3.17	1.04	5.43	0.13
Arc	Arc-6	Large	Carscallen & Romanuk, 2012	2012	Sea-ice	1.18	0.10	0.12	1.00	0.51	4.07	0.91	5.89	0.17
Arc	Arc-9	Large	Kortsch et al., 2015	2015	Marine	0.96	0.06	0.10	1.00	0.52	2.93	1.01	5.34	0.00
Ant	Ant-1	Small	Ballerini et al., 2014	2014	Wester Peninsula	0.56	0.13	0.19	1.00	0.61	2.78	1.18	4.68	0.00
Ant	Ant-3	Small	Cheung & Pitcher, 2005	2005	Falkland Islands	0.44	0.23	0.16	0.95	0.63	4.87	1.33	6.38	0.52
Ant	Ant-4	Small	Cornejo-Donoso & Antezana, 2008	2008	Peninsula	0.31	0.27	0.23	0.95	0.75	4.14	1.15	5.65	0.00
Ant	Ant-5	Small	Erfan & Pitcher, 2005	2005	Peninsula	0.41	0.17	0.20	0.93	0.62	3.96	1.36	5.89	0.33
Ant	Ant-9	Small	Hop & Gjosaeter, 2013	2013	Arctic and Barents Sea	0.56	0.11	0.18	1.00	0.55	2.75	1.12	4.17	0.00
Ant	Ant-6	Small	Palomares et al 2005	2005	Kerguelen Islands	0.45	0.16	0.19	0.94	0.60	3.42	1.41	5.45	0.17
Ant	Ant-7	Small	Smith et al., 2007	2007	Ross Sea	0.60	0.08	0.19	1.00	0.53	2.79	1.08	4.49	0.17
Arc	Arc-1	Small	Bradstreet & Cross, 1982	1982	High Arctic Ice Edge	0.57	0.14	0.21	1.00	0.54	2.79	1.03	4.25	0.00
Arc	Arc-11	Small	Nilsen et al., 2008	2008	North Norway	0.53	0.08	0.12	0.80	0.42	4.62	1.31	6.60	0.19
Arc	Arc-2	Small	Aydin et al., 2002	2002	East	0.40	0.22	0.19	1.00	0.64	3.66	1.13	5.03	0.24
Arc	Arc-3	Small	Aydin et al., 2002	2002	West	0.39	0.17	0.16	0.83	0.55	4.79	1.41	6.68	0.26
Arc	Arc-4	Small	Aydin et al., 2002	2002	West & Basin	0.43	0.14	0.15	0.88	0.58	3.64	1.09	5.53	0.19
Arc	Arc-5	Small	Blanchard et al., 2002	2002	Barent Sea	0.41	0.14	0.15	0.91	0.57	3.50	1.26	5.10	0.24
Arc	Arc-7	Small	Dommasnes et al., 2001	2001	Barent Sea	0.40	0.20	0.19	1.00	0.64	3.35	0.92	4.50	0.07
Arc	Arc-8	Small	Dunbar, 1954	1954	Arctic & sub-Arctic	0.86	0.13	0.18	1.00	0.55	6.34	2.77	10.34	0.40

Region	Label	Size	Reference	Date	Location	Cannibal	DirectOmniv	CC	ConDirOmni	ConMeanTL	SWTP	DD	TopGen
Ant	Ant-2	Large	Carscallen & Romanuk, 2012	2012	Sea-ice	0.10	0.84	0.17	0.86	3.43	3.38	0.19	1.89
Ant	Ant-8	Large	Jacobs et al., 2005	2005	Weddell Sea	0.10	0.51	0.18	0.59	2.65	2.43	0.10	0.95
Arc	Arc-10	Large	Kortsch et al., 2015	2015	Boreal	0.13	0.67	0.21	0.70	2.85	2.79	0.12	1.01
Arc	Arc-12	Large	Planque et al., 2014	2014	Barent Sea	0.11	0.69	0.19	0.71	2.89	2.83	0.11	1.17
Arc	Arc-6	Large	Carscallen & Romanuk, 2012	2012	Sea-ice	0.11	0.84	0.23	0.87	3.51	3.43	0.35	1.33
Arc	Arc-9	Large	Kortsch et al., 2015	2015	Marine	0.06	0.59	0.12	0.62	2.74	2.66	0.09	0.93
Ant	Ant-1	Small	Ballerini et al., 2014	2014	Wester Peninsula	0.00	0.71	0.21	0.89	2.94	2.53	0.11	1.28
Ant	Ant-3	Small	Cheung & Pitcher, 2005	2005	Falkland Islands	0.32	0.93	0.36	0.98	3.96	3.82	0.25	0.00
Ant	Ant-4	Small	Cornejo-Donoso & Antezana, 2008	2008	Peninsula	0.18	0.93	0.33	1.00	3.54	3.36	0.32	1.54
Ant	Ant-5	Small	Erfan & Pitcher, 2005	2005	Peninsula	0.28	0.85	0.26	0.89	3.35	3.23	0.21	0.00
Ant	Ant-9	Small	Hop & Gjosaeter, 2013	2013	Arctic and Barents Sea	0.00	0.57	0.16	0.73	3.03	2.59	0.05	1.20
Ant	Ant-6	Small	Palomares et al 2005	2005	Kerguelen Islands	0.21	0.79	0.31	0.95	3.28	2.90	0.19	1.57
Ant	Ant-7	Small	Smith et al., 2007	2007	Ross Sea	0.00	0.57	0.06	0.72	3.01	2.57	0.01	1.50
Arc	Arc-1	Small	Bradstreet & Cross, 1982	1982	High Arctic Ice Edge	0.00	0.58	0.09	0.70	2.93	2.60	0.17	1.40
Arc	Arc-11	Small	Nilsen et al., 2008	2008	North Norway	0.04	0.89	0.15	0.96	3.75	3.55	0.09	1.13
Arc	Arc-2	Small	Aydin et al., 2002	2002	East	0.27	0.84	0.30	0.91	3.33	3.14	0.39	1.24
Arc	Arc-3	Small	Aydin et al., 2002	2002	West	0.26	0.91	0.30	0.97	3.86	3.69	0.54	1.46
Arc	Arc-4	Small	Aydin et al., 2002	2002	West & Basin	0.17	0.85	0.23	0.89	3.17	3.08	0.38	1.54
Arc	Arc-5	Small	Blanchard et al., 2002	2002	Barent Sea	0.29	0.85	0.26	0.97	3.19	2.92	0.27	1.43
Arc	Arc-7	Small	Dommasnes et al., 2001	2001	Barent Sea	0.14	0.90	0.25	0.96	3.15	3.00	0.36	1.91
Arc	Arc-8	Small	Dunbar, 1954	1954	Arctic & sub-Arctic	0.00	0.40	0.17	0.43	5.47	5.11	0.00	0.46

Table 4.2: Description of food web properties

Food- Web Properties		**Description**
Species	*TS*	Number of species in the food web after being converted into a trophic web
Links/Species	*L/S*	Number of pred/prey links per species
Link Standard deviation	*LinkSD*	Standard deviation of the links per species
Clustering Coefficient	*CC*	Probability that two taxa linked to the same taxa are also linked
Connectance	*C*	Proportion of actual trophic links to all possible links (L/S^2)
Percentage of Top predator	*%T*	Species with prey and not predators
Percentage of Intermediate species	*%I*	Species with both predators and prey
Percentage of Basal species	*%B*	Species with predators and no prey
Percentage of Herbivores	*%H*	Species who prey on primary producers
Percentage of Cannibals	*%Can*	Species which prey on their own species
Percentage of Omnivores	*%Omni*	Species which prey on primary producers and consumers
Consumer direct omnivory	*ConDirOmni*	Fraction of intermediate species that feed on more than one trophic level
Mean consumer trophic position	*ConMeanTL*	mean PATP of all intermediate species in the food web
Trophic level max	*TLMax*	Maximum trophic level in the food web using prey-averaged algorithm
Trophic level mean	*TLMean*	Average trophic level for PATP
Trophic level standard deviation	*TLSD*	Standard deviation of trophic level among the entire web for PATP
Short-weighted trophic position	*SWTP*	the average of 'prey-averaged trophic position'
Diet Discontinuity	*DietDis*	Number of triplets of species with an "irreducible gap" (measure of intervality)
Generality standard deviation	*GenSD*	The number of prey of a taxa standardized by L/S
Vulnerability standard deviation	*VulSd*	The number of predators of a taxa standardized by L/S
Loop	*Loop*	Percent of taxa in a loop (food chain where the taxa appears twice)
Mean Similarity	*SimMean*	Mean link similarity across all nodes
Similarity standard deviation	*SimStdDev*	Similarity standardized by L/S
Mean maximum similarity	*SimMaxMean*	Mean of the maximum similarity for every node
Clustering coefficient	*CC*	Average % of pairs of nodes connected to another node and connected to eachother
Top generality	*TopGen*	Species with the highest number of prey

Table 4.3: Overall model performance for all 21 food webs across all food web properties. Mean ME is the model error average across all food web properties; ME SD is the standard deviation; Mean ME is a good estimate if it falls within ±1.

Region	Model	Mean ME	ME SD
All	Random	-1.31	4.74
All	Cascade	-0.52	1.02
All	Niche	-0.56	2.51
All	Nested Hierarchy	-0.31	1.12
All	Relaxed Niche	-0.23	1.09
Antarctic	Random	-0.52	1.30
Antarctic	Cascade	-0.56	1.45
Antarctic	Niche	-0.39	1.90
Antarctic	Nested Hierarchy	-0.18	0.81
Antarctic	Relaxed Niche	-0.13	0.82
Arctic	Random	-1.90	7.39
Arctic	Cascade	-0.49	1.03
Arctic	Niche	-0.69	3.09
Arctic	Nested Hierarchy	-0.41	1.38
Arctic	Relaxed Niche	-0.31	1.31

Table 4.4: Ecoregions of the Arctic and Antarctic (Spalding et al., 2007)

Arctic Ecoregions	Southern Ocean Ecoregions
North Greenland	Macquarie Island
North and East Iceland	Heard and Macdonald Islands
East Greenland Shelf	Kerguelen Islands
West Greenland Shelf	Crozet Islands
Northern Grand Banks-Southern Labrador	Prince Edward Islands
Norther Labrador	Bouvet Island
Baffin Bay-Davis Strait	Peter the First Island
Hudson Complex	South Sandwich Island
Lancaster Sounds	South Georgia
High Arctic Archipelago	South Orkney Islands
Beaufort-Amundsen-Viscount Melville-Queen Maud	South Shetland Islands
Beaufort Sea – Continental coast and shelf	Antarctic Peninsula
Chukchi Sea	East Antarctic Wikes Land
Eastern Bering Sea	East Antarctic Enderby Land
East Siberian Sea	East Antarctic Dronning Maud Land
Laptev Sea	Weddell Sea
Kara Sea	Amundsen/Bellingshausen Sea
North and East Barents Sea	Ross Sea
White Sea	Bounty and Antripodes Islands
	Campbell Islands
	Auckland Island

Table 4.5: Mean, min, max and SD for all 26 food web properties across the Arctic and Antarctic.

	Arctic				Antarctic			
	Mean	**Min**	**Max**	**SD**	**Mean**	**Min**	**Max**	**SD**
Species	76.92	12	233	76.38	114.13	23	492	169.42
%Top	17.15	6.44	50	13.36	11.93	0	29.17	10.88
%Intermed	74.8	33.33	90.56	17.75	76.60	50	95.45	17.4
%Basal	8.05	3	21.43	5.61	11.47	2.09	21.74	7.74
%Herbivore	11.84	0	33.33	11.04	8.37	0	32.11	10.12
Connectance	0.12	0.03	0.23	0.07	0.15	0.03	0.28	0.09
Links/Species	5.66	1.67	9.52	2.74	9.45	1.78	33.19	9.95
GenStdDev	0.87	0.35	1.49	0.35	0.85	0.55	1.36	0.27
VulStdDev	1.12	0.67	2.21	0.43	1	0.69	2.21	0.5
LinkStdev	0.66	0.39	1.18	0.28	0.59	0.31	1.2	0.28
SimMean	0.12	0.06	0.22	0.05	0.15	0.08	0.27	0.07
SimStdDev	0.15	0.09	0.21	0.04	0.18	0.11	0.23	0.04
SimMax	0.96	0.8	1	0.07	0.97	0.93	1	0.03
SimMaxMean	0.54	0.42	0.64	0.07	0.65	0.53	0.89	0.12
TroLev	3.75	2.75	6.34	1.01	3.57	2.67	4.87	0.79
TroLevStdDev	1.23	0.91	2.77	0.48	1.19	0.9	1.41	0.17
TLMax	5.7	4.17	10.34	1.59	5.4	4.49	6.38	0.62
Loop	0.16	0	0.4	0.12	0.19	0	0.52	0.18
Cannibal	0.12	0	0.29	0.1	0.15	0	0.32	0.12
DirectOmniv	0.74	0.4	0.91	0.16	0.77	0.51	0.93	0.16
ClusterCoeff	0.2	0.09	0.3	0.07	0.24	0.06	0.36	0.1
ConsumerDirectOmniv	0.8	0.43	0.97	0.17	0.86	0.59	1	0.14
ConsumerMeanTL	3.37	2.74	5.47	0.72	3.27	2.65	3.96	0.4
SWTL	3.18	2.59	5.11	0.68	3.03	2.43	3.82	0.5
DietDiscontinuity	0.22	0	0.54	0.17	0.17	0.01	0.32	0.1
TopGen	1.25	0.46	1.91	0.34	1.09	0	1.89	0.72

Chapter 5 Changes in the structure of an Antarctic food web across depth

5.1. Abstract

Changes in food web structure across gradients represent an avenue for exploring the effects of abiotic and biotic factors on the structure of food webs. Depth gradients are unique in that taxa shift from utilizing phytoplankton to detritus, as depth increases. Here I create and compare two depth dependent food webs, starting from a previously assembled Antarctic marine meta-web, by removing one of two basal resources to create a phytoplankton and detrital food web. While the structure of these sub-webs remains similar, difference in species interactions were found. Low trophic position species, particularly herbivore-detritivores, were found to have a higher abundance in the detrital food web. Additionally, differences in vulnerability and generality suggest that the detrital food web may contain more energy pathways which connect low trophic position to higher trophic position taxa. My results suggest that food webs remain highly coupled across a depth gradient; however, species interaction strength varies, altering the energy flow pathways.

5.2. Introduction

Studies of food web topology or structure are often used to represent the structure of an ecological community or ecosystem at one point in time or are integrated spatially and temporally. These "snapshot" webs and "meta-webs" have provided a wealth of data on how energy flows in ecological systems. Hundreds of food webs are now available in the literature and in databases, and comparative studies across systems have shown strong patterns in food web properties related to biogeography (Holt, 1996; Gravel et al., 2011; Cirtwill et al., 2016) and habitat type (Dunne et al., 2002; Cirtwill et al., 2016). More recently, ecologists have begun to explore gradient food webs: separate food webs for a defined ecosystem or community arrayed along environmental gradients such as elevation (Ramos-Jiliberto et al., 2010), or along river systems (Romanuk et al. 2006). Gradient food webs hold considerable promise for exploring how food web structure changes as a result of ecological drivers such as biogeography, seasonality, range shifts, and species invasions. For example, Baiser et al. (2012) found that linkage density and species richness of pitcher plants increases with latitude; Cirtwill et al. (2015) found that in freshwater ecosystems niche-breadth scaled with latitude; Ramos-Jiliberto et al. (2010) found that nestedness of plant-pollinator food webs decreased as elevation increased; and Piechnik et al. (2008) found that on six experimental islands, the fraction of specialists increased while the fraction of generalists decreased as food webs assembled.

In both aquatic and terrestrial systems many ecological interactions change along altitudinal or depth gradients. In terrestrial systems, topological changes along elevation gradients have recently been explored (Ramos-Jiliberto et al., 2010); however, studies of how food web topology changes along depth gradients are mostly unexplored. Across a depth gradient, many abiotic and biotic factors, which affect the structure and function of food webs, vary. For instance, environmental variability tends to decline in both magnitude and frequency with depth, creating differences in benthic community structure and dynamics along a depth gradient (Garrabou et al., 2002; Brandt et al., 2007); changes in salinity can alter trophic dynamics of benthic energy pathways (Bremner et al., 2006; Prado et al., 2014); and nutrient availability changes as a result of upwelling which supplies primary producers with essential nutrients in the photosynthetically active region of the water column (Hoppema et al., 2015).

In most freshwater and marine systems there is a major shift in resource use from surface or upper pelagic zones to deep or benthic webs from utilizing phytoplankton as their primary basal resource to detritus (Polis et al., 1997; Galloway et al., 2013). With this change in the dominant basal resource, many aspects of the ecology of the system may change, from species composition and interaction strengths, to foraging techniques and growth rates. While a meta-web will include all species and potential links between species in a system regardless of whether they interact only weakly or even not at all (such as is the case of temporally integrated webs in a highly seasonal system), in ecosystems that show strong differences between pelagic and benthic communities, species have either specialized within a particular niche in the water column, or move freely throughout it. This results in differences in species composition and interactions strengths across a depth gradient changing the flow of energy (Frainer et al., 2016).

Here I explore how changes in the basal resource, across depth, affect the structure of an Antarctic marine food web. I assembled two depth-dependent webs, each having a unique basal resource which reflects its location along the depth gradient. Starting with a previously published meta-web of the Weddell Sea, a surface web was assembled for all species that depend on phytoplankton, while a deep water web was assembled for all species that depend on detritus. I focused on comparing overall structural food webs properties, as well as the more specific node properties, between the phytoplankton and detrital food webs.

5.3. Methods

In this study, I use a Weddell Sea food web, as described in Jacob et al. (2011), as a baseline food web from which phytoplankton and detritus driven source webs were assembled to explore changes in food web structure and community composition related to the primary nutrient resource across the depth gradient (Figure 5.1). The Weddell Sea food web was assembled through an extensive literature search, including data from over 500 peer reviewed publications, field observation and stomach content analysis. The data was used to infer directional feeding interactions between species based on field and lab observation, body size, behaviors and stable isotopes (Brose et al. 2005; Jacob et al. 2005). In the event where interactions were between species at different life stages (e.g. larvae, juvenile, adults), both "species" were treated as adults. In comparison to other Antarctic marine food webs, the Weddell Sea web is one of the most highly resolved (Species (S) = 492; feeding links (L) = 16,330), specifically for lower trophic position species such as phytoplankton and zooplankton (Chapter 4). The high resolution of lower trophic position species in particular is unique amongst polar marine food webs, which typically are only highly resolved (to species level) for fish and other higher trophic level species (Chapter 4). For example, in the Weddell Sea web, invertebrates and basal taxa account for 71% (n = 349) and 13% (n = 62) of the nodes in the food web (Jacob et al., 2005). In comparison, in a previously published Antarctic meta-web (Carscallen & Romanuk, 2012) invertebrates and basal taxa only account for 18% (n = 44) and 1.6% (n = 4) of the 239 nodes of the Antarctic food web. Additionally, the Antarctic meta-web (Carscallen & Romanuk, 2012) only had 1574 feeding links, 10% of the amount found in the Weddell Sea web.

I collected depth ranges from primary literature and databases, such as FishBase (Froese & Pauly, 2016) and SeaLifeBase (Palomares & Pauly, 2016), for 71% (n = 352) of the taxa in the Weddell Sea meta-web, including 62 basal taxa, 217 species of invertebrates, 47 fish species, 12 bird species, and 14 species of mammals (Figure 5.2). Of the 140 taxa that I was unable to find depth ranges for, 132 were invertebrates, one was a fish, three were birds, and four were basal species (i.e. POM, sediment). Given the large depth ranges for many of the higher trophic position taxa, I was unable to segregate the meta-web into depth specific webs (e.g. 0-20 m, 21-50 m, 51-100 m). Instead, the Weddell Sea meta-web was segregated based on the dominant basal resource input such that two sub-webs were compiled at the two boundaries (i.e. surface and bottom) of the depth gradient: a phytoplankton web and a detrital web. To compile the sub-webs, I manually removed either phytoplankton or detritus nodes from the Weddell Sea meta-web and, subsequently, all taxa which solely depend on these nutrient resources. To even the resolution between the detrital and phytoplankton webs, basal species in the phytoplankton web were aggregated into a single node, reducing the number of primary producer basal species from 62 to one.

5.3.1. Study Site

The Antarctic is one of the most unique habitats on the planet with an average depth of 400-800 m, a maximum depth of 7000 m, and extreme environmental conditions. On an annual basis the Antarctic experiences 24 h of light during polar summers and 24 h of dark during polar winters, in addition to coastal temperatures varying from -60 to +10° C and winds reaching over 200 km/h. Many taxa migrate during the winter months to avoid the extreme cold and harsh weather, such as the Arctic tern which migrates from the Arctic to Antarctic (Fijn et al., 2013), while others have adapted to withstand the cold, such as nematodes and fish which have evolved specialized cold-tolerance mechanisms (Wharton & Ferns, 1995; Wharton et al., 2002) and antifreeze proteins (DeVries & Cheng, 2005). This combination of a harsh surface environment and a vast and deep environment creates a significant gradient in the environmental conditions across depth.

The Weddell Sea (Figure 5.3) is roughly 3.4 million km^2 and is bordered by the Antarctic Peninsula to the west and the Antarctic continent to the south. Relative to the rest of the Antarctic, the Weddell Sea has a relatively large continental shelf which extends roughly 240 km from the Antarctic Peninsula and 480 km from the southern edge of the Weddell Sea. The continental shelf is relatively shallow, only reaching depths up to 500 m, while the abyssal plains can reach depths greater than 6000 m.

5.3.2. Food web properties

For each food web, I calculated 26 structural properties (Table 5.1). Two standard measures of food web trophic interaction richness are reported: links per species (*L/S*), which equals the mean number of species predators, plus prey, divided by the number of species in the web, also referred to as link density; and connectance (C), where $C=L/S^2$, the proportion of all possible trophic links (S^2) that are actually realized (L), also referred to as 'directed connectance'. Six properties give fractions of types of species in the food web: top (*%T*), fraction of taxa which lack any predators; intermediate (%I), fraction of taxa which have both predators and prey; basal (*%B*), fraction of species which have no prey; fraction of taxa which are cannibals *(%Can*); fraction of taxa which are both herbivores and detritivores (*%Herb*); and fraction of taxa involved in looping (*%Loop*) by appearing in a food chain twice. Short-weighted trophic position (*SWTP*) is the average of 'prey-averaged trophic position', one plus the shortest chain length from the consumer taxon to a basal taxon; (William &Martinez, 2004). I report three related measures, the maximum trophic position (*TPMax*), the mean trophic position (*TPMean*), and the trophic position standard deviation (*TPSD*), all based on short-weighted trophic position. The standard deviation of mean generality (*GenSD*) and vulnerability (*VulSD*), describes how many prey and predators a taxon has. These two measures quantify the variabilities of species normalized predator and prey counts (Schoener, 1989). I used diet discontinuity (*DietDis*) defined as the number of triplets of species with an "irreducible gap", i.e. a gap in a consumer's diet that cannot be made contiguous because of constraints imposed by other consumers' diets, divided by the number of possible triplets (Stouffer et al., 2006) as a measure of intervality.

Taxa similarity was calculated as the fraction of predator and prey links shared between nodes. Three measure were calculated for this including, mean similarity (*MeanSim*), the mean fraction of similar predator and prey links across all taxa, maximum similarity (*MaxSim*), which is the maximum fraction of similar predator and prey links for two taxa, and mean maximum similarity (*MeanMaxSim*), which is the mean maximum fraction of similar predator and prey links across all taxa. I also report one measure of ‘small-world’ network structure (Watts & Strogatz, 1998), the clustering coefficient (*CC*), which is the mean fraction of species pairs connected to the same species that are connected to each other (Dunne et al., 2002; Camacho & Guimera, 2002; Montoya & Sole, 2002; Williams et al., 2002).

Cumulative degree distributions (Dunne et al., 2002; Williams, 2009) were used for the trophic links, in addition to the predator and prey links in order to more rigorously explore differences in generality and vulnerability (Figure 5.4). Cumulative degree distributions show the fraction of trophic species P (k) which have k or more trophic links (for both predator and prey; Dunne et al., 2002). When comparing between the phytoplankton and detrital webs, the degree distributions were compared based on the maximum degree (i.e. maximum number of predators and prey species) and the degree of the exponential decay.

5.3.3. Node properties

To characterize taxa (nodes) in the food webs, eight node properties were calculated for all nodes across the phytoplankton and detrital sub-webs (n = 764). Two measures of trophic position were calculated including ‘prey-averaged trophic position’ (*PATP*), one plus the mean trophic position of all of a taxa’s trophic resources, and ‘short-weighted trophic position’ (*SWTP*), the average of ‘prey-averaged trophic position’ and ‘shortest chain length’, one plus the shortest chain length (*SCL*) from the consumer taxa to a basal taxon. The variance of prey-averaged trophic position (*PATPVar*) was also calculated. Four link properties were calculated including the number of predator links (*PredCount*) and prey links (*PreyCount*), the number of prey of prey links (*PreyofPrey*) and the maximum link similarity across all nodes (*MaxSim*).

5.3.4. Functional groups

Taxa were grouped into five categories based on their *SWTP*, and *SCL*. The five trophic categories of taxa were: basal species (*SCL* = 0, *SWTP* = 1), herbivore-detritivores (*SCL* = 1, *SWTP* = 2), omnivores (*SCL* = 1, *SWTP* > 2), primary carnivores (*SCL* > 2) and secondary carnivores (*SCL* >3).

5.3.5. Statistical analyses

I compared the mean and standard error of seven of the eight node properties including: prey-averaged trophic position variance (*PATPVar*), short-weighted trophic position (*SWTP*), shortest chain length (*SCL*), number of prey links (*PreyCount*), number of predator links (*PredCount*), maximum similarity (*MaxSim*), and the number of prey of prey (*PreyofPrey*). Node properties which had a correlation above 0.7 were excluded from further analyses, which excluded *PATP, SCL,* and *PreyofPrey* (Table 5.2). As the data was not normally distributed, as per the Kolmogorov-Smirnov test and showed signs of heteroscedasticity, as per White's test, I ran a multivariate PERMANOVA, which uses a Bray-Curtis measure of similarity, to test for differences between in uncorrelated node properties across sub-webs (i.e. *PATPVar*, *SWTP*, *PreyCount*, *PredCount*, *MaxSim*). I used a SIMPER analysis, which uses a Bray-Curtis measure of similarity, to test for the contribution of each node property to the differences between overall sub-webs (factor depth: surface and bottom) as well as for individual functional groups between subwebs. Lastly, I ran a Kruskal-Wallis (KW-ANOVA) test, which compares mean ranks as oppose to a traditional ANOVA which compares means, to determine which node properties had significant differences between overall sub-webs (factor depth: 2 levels) and for individual functional groups between sub-webs.

Non-metric multidimensional scaling (nMDS) based on the Bray-Curtis dissimilarity index was used to visualize differences across: 1) all taxa across both food webs and 2) taxa categorized into the five functional groups including; i) basal (n = 8), ii) herbivore-detritivores (n = 230), iii) omnivores (n = 168), iv) primary carnivores (n = 346), and v) secondary carnivores (n = 12). The nMDS used random starting configurations and 100 runs with real data. A two-dimensional representation was accepted as a good depiction of the data if the stress index was <0.1 (Clark, et al., 2014). All statistical analyses were done using R (version 3.2.1) and Statistica 8.0.

5.4. Results

5.4.1. Food web properties

5.4.1.1. Meta-web

The meta-web had a taxa richness of 492 (*S*), with an average of 33.2 links per species (*L/S*) and a connectance (*C*) of 0.07. The mean short-weighted (*SWTP*) and prey-averaged trophic position (*PATP*) was 2.43 and 2.67. The fraction of top (*%T*), intermediate (*%I*) and basal (*%B*) species was 6.7, 79.7, and 13.6%. Diet discontinuity (*DietDis*) was 0.1. Clustering coefficient and looping were 0.18 and 0.26, respectively. Standard deviation of vulnerability and generality were 1.36 and 0.86, respectively. The fraction of cannibals was 0.1. (Table 5.3)

5.4.1.2. Phytoplankton and detrital webs

A complete set of food web properties is shown in Table 5.3 for the phytoplankton web, detrital web, and the meta-web. Taxa richness was 27% higher in the detrital web than the phytoplankton web (S_{Phyto} = 336, S_{Det} = 428). Connectance was 37% higher in the phytoplankton web (C_{Phtyo} = 0.08, C_{Det} = 0.06). The number of links per species was lower on average in the detrital web by 7% or approximately two links (L/S_{Phyto} = 28.32, L/S_{Det} = 26.4). Mean short-weighted and prey-averaged trophic position were 12% and 15% higher in the phytoplankton web ($SWTP_{Phyto}$ = 3.56, $SWTP_{Det}$ = 3.17; $PATP_{Phyto}$ = 4.54, $PATP_{Det}$ = 3.9). Additionally, the phytoplankton web had a slightly higher number of higher trophic position species compared to both the detrital and meta-food webs (Figure 5.5). The fraction of top predators was 20% higher in the phytoplankton web whereas the fraction of intermediate species was similar in both webs ($\%T_{Phyto}$ = 9.63, $\%T_{Det}$ = 7.71; $\%I_{Phyto}$ = 90.5, $\%I_{Det}$ = 91.1). The fraction of basal species was also similar in both webs ($\%B_{Phyto}$ = 0.9, $\%B_{Det}$ = 1.2). Diet discontinuity was 56% higher in the phytoplankton web ($DietDis_{Phyto}$ = 0.15, $DietDis_{Det}$ = 0.09). The clustering coefficient was slightly higher in the detrital web whereas looping was 27% higher in the phytoplankton web (CC_{Phyto} = 0.19, CC_{Det} = 0.2; $Loop_{Phyto}$ = 0.38, $Loop_{Det}$ = 0.3). Standard deviation of vulnerability and generality were 16% and 23% higher in the detrital web than the phytoplankton web ($GenStdDev_{Phyto}$ = 1.16, $GenStdDev_{Det}$ = 1.43; $VulStdDev_{Phyto}$ = 0.76, $VulStdDev_{Det}$ = 0.88). There was a 27% difference between the fraction of cannibals (Can_{Phyto} = 0.15, Can_{Det} = 0.12).

5.4.2. Node properties

Node properties were calculated for each taxon in the phytoplankton (n = 336), detrital (n = 428), and meta-food webs (n = 492). In the meta-web, the mean prey-averaged trophic position (*PATP*) and short-weighted trophic position (*SWTP*) were 2.67 and 2.42, respectively. The variability in prey-averaged trophic position (*PATPVar*) was 0.35 and the mean shortest chain length (*SCL*) was 1.18. The mean number of predators and prey was 33.2 ($PredCount_{Meta}$) and 33.2 ($PreyCount_{Meta}$), respectively. The mean maximum similarity (*MaxSim*) and number of prey of prey (*PreyofPrey*) were 0.89 and 0.28, respectively.

In the phytoplankton and detrital webs, the mean prey-averaged trophic position and short-weighted trophic position were higher in the detrital web (mean $PATP_{Phyto}$ = 2.9, mean $PATP_{Det}$ = 3.94; mean $SWTP_{Phyto}$ = 2.62, mean $SWTP_{Det}$ = 3.17). Additionally, mean variability in prey-averaged trophic position was also higher in the detrital web (mean $PATPVar_{Phyto}$ = 0.46. mean $PATPVar_{Det}$ = 0.7). The mean shortest chain length was slightly higher in the detrital web than in the phytoplankton web (mean SCL_{Phyto} = 1.34, mean SCL_{Det} = 1.39). Three of the four link properties were higher in the phytoplankton web than in the detrital web. The mean number of predator and prey links were 37% higher in the phytoplankton web (mean $PreyCount_{Phyto}$ = 33.3, mean $PreyCount_{Det}$ = 26.4; mean $PredCount_{Phyto}$ = 33.3, mean $PredCount_{Det}$ = 26.4). There was no difference in the mean maximum similarity between the phytoplankton and detrital webs (mean $MaxSim_{Phyto}$ = 0.88, mean $MaxSim_{Det}$ = 0.88). The mean number of prey of prey was 28% higher in the detrital web than the phytoplankton web (mean $PreyofPrey_{Phyto}$ = 0.31, mean $PreyofPrey_{Det}$ = 0.39) (Figure 5.6). Multivariate PERMANOVA showed significant differences between phytoplankton and detrital webs across five node properties which were uncorrelated, including *PATPVar*, *SWTP*, *PreyCount*, *PredCount*, and *MaxSim* (Pseudo-$F_{1,763}$ = 7.18, $p <$ 0.001). Furthermore, the SIMPER analysis showed that generality (*PreyCount*) and vulnerability (*PredCount*) contributed 95% of this difference.

5.4.2.1. Functional groups between both webs

When taxa were categorized by functional groups (basal, herbivore-detritivores, omnivore, primary carnivore, secondary carnivore) and compared between sub-webs, multivariate PERMANOVA showed that across sub-webs, two of the functional groups showed significant differences, including: herbivore-detritivores (Pseudo-$F_{1,\,229} = 11.97$, $p < 0.001$) and Omnivores (Pseudo-$F_{1,167} = 2.9$, $p = 0.04$). SIMPER analysis highlighted that generality (*PreyCount*) and vulnerability (*PredCount*) contribution at least 95% to differences between sub-webs within these two functional groups. KW-ANOVA showed significant differences between uncorrelated node properties within three functional groups including, herbivore-detritivores, omnivores, and secondary carnivores. Two node properties showed significant differences between webs within herbivore-detritivores, including the number of predators (*PreyCount*; $H = 92$, $p < 0.001$) and number of prey (*PredCount*; $H = 12.2$, $p < 0.001$). One node property showed significant differences between webs within omnivores and secondary carnivores, including the number of prey (*PreyCount*; $H = 4.11$, $p = 0.04$) and short-weighted trophic position (*SWTP*; $H = 6.4$, $p = 0.011$), respectively.

This was consistent with nMDS which did not reveal any strong differences in the centroids of each functional group, but did show a weak difference in variance, in the node properties within each functional group between webs (stress = 0.065; Figure 5.7).

5.4.2.2. Degree Distributions

The phytoplankton and detrital sub-webs differed in their cumulative degree distribution for the number of predators and prey. The phytoplankton web had 58% fewer maximum predator links and 12% more maximum prey links in comparison to the detrital web (Max $PredCount_{Phyto} = 96$, Max $PredCount_{Det}$ = 228; Max $PreyCount_{Phyto}$ = 190, Max $PreyCount_{Det}$ = 221). In comparison, the meta-web had an equal number of maximum predator links as the detrital web (Max $PredCount_{Meta}$ = 228) and a higher maximum number of prey links than the detrital web (Max $PreyCount_{Meta}$ = 280) (Figure 5.4).

5.5. Discussion

Analysis of food web structure across environmental and geographical gradients is a powerful method to determine functional differences in energy flow patterns (Piechnik et al., 2008; Baiser et al., 2011). Depth gradients, such as the one I focus on here for the Weddell Sea, are particularly interesting as many of the biotic and abiotic factors that influence energy flow change across the depth gradient. For example, phytoplankton are the primary source of nutrients in many ecosystems but typically only live within the photosynthetically active region of water, however, as depth increases, consumer taxa shift from feeding on phytoplankton to detritus (Sierszen et al., 2006). Additionally, environmental conditions, which can influence species diversity and feeding interactions (Tylianakis et al., 2008; Harmon et al., 2009; Harley, 2011), also vary across the depth gradient (Sierszen et al., 2006; 2014).

Here, I show how food web structure differs between the two boundaries of a depth gradient in an Antarctic marine ecosystem. My study revealed three results of interest. First, similarities in food web properties between the sub-webs suggest that despite changes in the biotic and abiotic factors across the depth gradient, the food webs are broadly structurally similar. Second, despite broad similarities in topology, there were differences in generality (*PredCount*) and vulnerability (*PreyCount*) between sub-webs, suggesting differences in species interaction strength across the depth gradient. Third, herbivore-detritivores showed significant differences in both generality (*PredCount*) and vulnerability (*PreyCount*), suggesting differences in the number of energy pathways which connect low to high trophic positon species. Here I discuss the drivers behind the similarities in the two sub-webs and explore how the differences in node specific properties alter energy flow. Additionally, I discuss the methodological challenges associated with segregating a meta-web into individual depth dependent food webs.

Despite differences in biotic and abiotic factors across depth gradients, our results showed very few structural differences between the phytoplankton and detrital food webs, with less than 1% difference in the percent top predators, intermediate, and basal taxa between sub-webs. Furthermore, the distribution of trophic positions was relatively similar, with a slightly higher fraction of higher trophic position species in the phytoplankton web, likely due to the lower fraction of herbivore-detritivores (i.e. *SWTP* = 2). Another explanation for the similar structure between sub-webs may be that the broad depth ranges (Figure 5.2) of higher trophic position taxa allow them to forage and occupy niches throughout the water column, creating a bridge between the detrital and phytoplankton food webs (Berrara-oro, 2002; Kortsch et al., 2015). For example, Black rockcod (*Notothenia coriiceps*), has a depth range of 0-550m, and although it is typically a benthic feeder, preying on polychaetes, gastropods, clams and isopods, during the summer months it preys on krill and salps which typically reside in the upper region of the water column (Barrera-Oro, 2002: Froese & Pauly, 2016). Strong interactions between higher trophic position taxa and both phytoplankton and detrital food webs has also been found in Arctic food webs. Aydin et al. (2002) assembled flow-based food webs for the Eastern (EBS) and Western (WBS) Bering Sea and compared the percent of energy for each taxon which originated from either detritus or phytoplankton food webs. Although their food webs had a significantly lower resolution, (EBS *S* = 38, WBS *S* = 36), they also found that among higher trophic position taxa, energy was obtained from both food webs. This highlights the fact that large portions of food webs across a depth gradient may in fact share a similar species composition and structure.

Nutrient cycles are also an important component of food webs to consider when assessing the appropriateness/applicability of depth gradient food webs. When taxa residing in the phototrophic portion of the water column excrete waste or die (i.e. create detritus), the organic material sinks and is utilized by the benthic (i.e. detrital) communities as a nutrient source. In return, the microbial communities in the detrital food webs break down the organic material, releasing micronutrients back into the water column which are utilized by the primary producers (Krumins et al., 2013; Zou et al. 2016). The rate at which detritus is recycled through the nutrient loop governs the amount of primary production and has a direct effect on the food web structure and function (Moore et al., 2004). The fact that depth gradient food webs are coupled both between higher trophic position taxa and their prey, in addition to the nutrient cycle of basal taxa, raises the question as to whether there are actually depth dependent food webs, or merely the preferences for taxa to reside in a distinct niche within the water column based on physiological requirements and nutrient/prey availability and abundance.

Although the overall structure was similar, differences between the phytoplankton and detrital webs were seen within functional groups and node specific properties. The largest difference seen was in low trophic position species, particularly herbivore-detritivores. When assembling both sub-webs, either phytoplankton or detritus taxa were removed from the meta-web to create bottom and surface webs, respectively. This yielded a significant difference in the number of secondary extinctions which occurred. Although there were only two secondary extinctions when phytoplankton taxa were removed to assemble the detrital web, the removal of detritus from the phytoplankton web yielded 90 secondary extinctions. These secondary extinctions occurred as a result of primary consumers loosing there only prey (i.e. detritus or phytoplankton) during the sub-web assembly process. Surprisingly, when detritus was removed there was no diversity in the functional group of taxa that went extinct, with 100% of them being herbivorous invertebrates. This result suggests discrepancies in the ability of taxa to shift their prey between detritus and phytoplankton which may arise as a result of the depth distribution of each nutrient resource. Phytoplankton typically reside close to the surface of the water column where there is the optimal level of nutrients, ocean mixing, temperature, and light (Trimborn et al., 2013; Kavanaugh et al., 2015). Alternatively, detritus can be found almost everywhere within a water column, despite being primarily utilized by benthic communities, where phytoplankton are not available. Despite detritus being present in the phototrophic region of the water column, I chose to remove it from the food webs as it did not represent the primary source of nutrients for taxa inhabiting the upper water column.

The lack of great differences between the sub-webs may also be due to the fact that binary food webs do not capture interaction strengths. Many species, such as seals, birds and fish, feed on a variety of prey throughout the year; however, they will alter their feeding habits depending on prey abundance and availability (Barrera-oro, 2002; Harcourt et al., 2002). Our results reflected this behavior to some extent with a relatively high level of generality (Mean $L/S_{\mathrm{Phyto}} = 28.3$, Mean $L/S_{\mathrm{Det}} = 26.3$) in both webs. There were, however, large differences in the maximum number of predator (Max $Pred_{\mathrm{Det}} = 228$, MAx $Pred_{\mathrm{Phyto}} = 96$) and prey (Max $Prey_{\mathrm{Det}} = 221$, Max $Prey_{\mathrm{Phyto}} = 190$) links. This is likely due to the difference in number of herbivorous invertebrates which was higher in the detrital sub-web and serve as an abundant food resource for higher trophic position taxa. The inclusion of such a large number of herbivore-detritivores is also likely to distribute predation pressure, reducing the amount of energy flowing from any one particular low trophic position taxa to high trophic position taxa.

Currently, assembling food webs relies on a variety of previously published resources, typically experimental and observational data. However, the methodology for data collection is not consistent from author to author, creating a large amount of variability in both the quality and quantity of data. When assembling a food web, this variability can create unknown or uncertain feeding interactions and taxa composition, resulting in taxa being lumped into trophic or functional groups (Brown & Gillooly, 2003), changing the structure of the food web. Brown & Gillooly (2003) highlighted the fact that although there have been large advancements in the ability of researchers to collect data of a higher quality and quantity, in addition to advancing their understanding of species interactions, there is still much progress to be done. Although the Antarctic meta-web used in this study (Jacob et al., 2011) was much more highly resolved then other Antarctic webs (e.g. Carscallen & Romanuk, 2012), particularly in lower trophic position taxa, there was still significant differences in resolution between basal resources. The original meta-web was comprised of 66 basal resources, 62 of which were phytoplankton, and only three were detritus. When the depth gradient webs were assembled, the difference in basal taxa resolution yielded differences in the node properties of higher trophic position taxa between the phytoplankton and detrital web. However, this created challenges from a comparability standpoint. Many food web properties, such as the number of trophic levels, links per species and the shortest chain length have been known to be constrained by the resolution of the web (Martinez, 1991). To mitigate this difference in resolution between the two sub-webs, in addition to avoiding artifacts in the food web properties, I chose to aggregate the basal taxa in the phytoplankton web to match the resolution in the detrital web. As a result, I was unable to detect differences in whole-web structural properties.

Balancing the resolution between food webs while retaining their unique topological differences poses an interesting challenge, particularly in binary food webs which do not capture species abundance or interaction strength, making biological differences difficult to explore. However, if I negate the fact that the basal taxa in both webs were highly aggregated, it is not uncommon for higher trophic position species to be present in both shallow and deep-water food webs, as seen in our webs. Sierszen et al (2014) found that changes in the distribution of invertebrates, forage fish and piscivorous fish, across a depth gradient, affected the strength of the trophic linkages to higher trophic position taxa, but did not significantly alter the species composition. Lower trophic position species tend to be affected by the changes in primary productivity and microbial community composition, both of which are heavily influenced by environmental conditions (Ghiglione et al., 2012). However, as depth increases, differences in the frequency and magnitude of environmental conditions is reduced, varying its effect on community dynamics (Garrabou et al., 2002). Higher trophic position taxa are most likely not affected by environmental conditions to the same extent as low trophic position species due to their large feeding ranges and physiology (e.g. body size), depth range (Mean = 466m, SD = ±422) and relatively high generality (Mean $PreyCount_{Phyto}$ = 37.2, Mean $PreyCount_{Det}$ = 35.6) which allow them travel to more hospitable regions where prey is more abundant and environmental conditions are more optimal.

Our comparison of Antarctic marine phytoplankton and detrital food webs revealed that despite shifting basal resources, the structure of the food webs remains relatively similar. Furthermore, many of the higher trophic position species were present in both webs, suggesting that across depth gradients, food webs remain coupled, with many taxa acquiring energy from multiple food chains. Despite the similarities, differences in species interactions, specifically generality (*Preycount*) and vulnerability (*PredCount*) were found both across all uncorrelated node properties between the sub-webs, including within three functional groups. Specifically, the species composition of herbivore-detritivores differs significantly, highlighting key differences in vulnerability and generality within each food web. These results suggest that there are different energy flow pathways which connect low trophic position taxa to high trophic position taxa.

Figures:

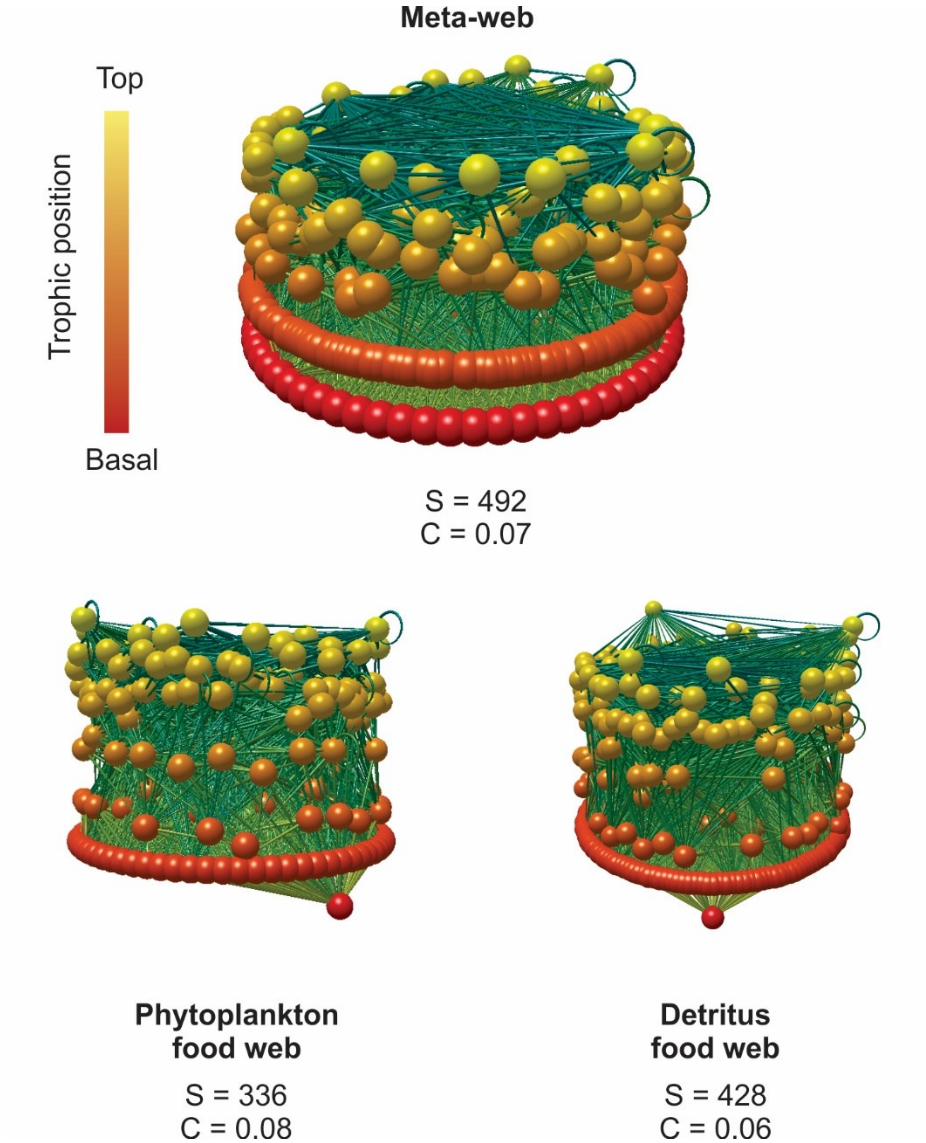


Figure 5.1: 3-D representation of food webs, including the meta-web (top), phytoplankton web (bottom left) and detrital food web (bottom right). Colour gradient and vertical distribution of nodes represent trophic position, transitioning from red (basal species) to yellow (top species).

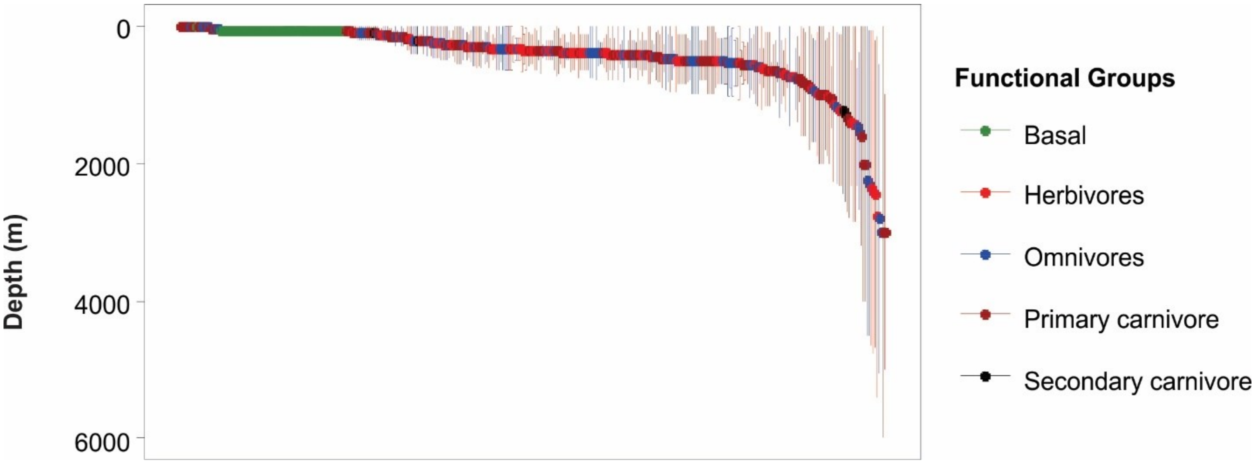


Figure 5.2: Weddell sea meta-web mean depth ranges for basal (green), herbivore-detritivores (red), omnivores (blue), primary carnivores (brown) and secondary carnivores (black) taxa. Error bars represent minimum and maximum recorded ranges.

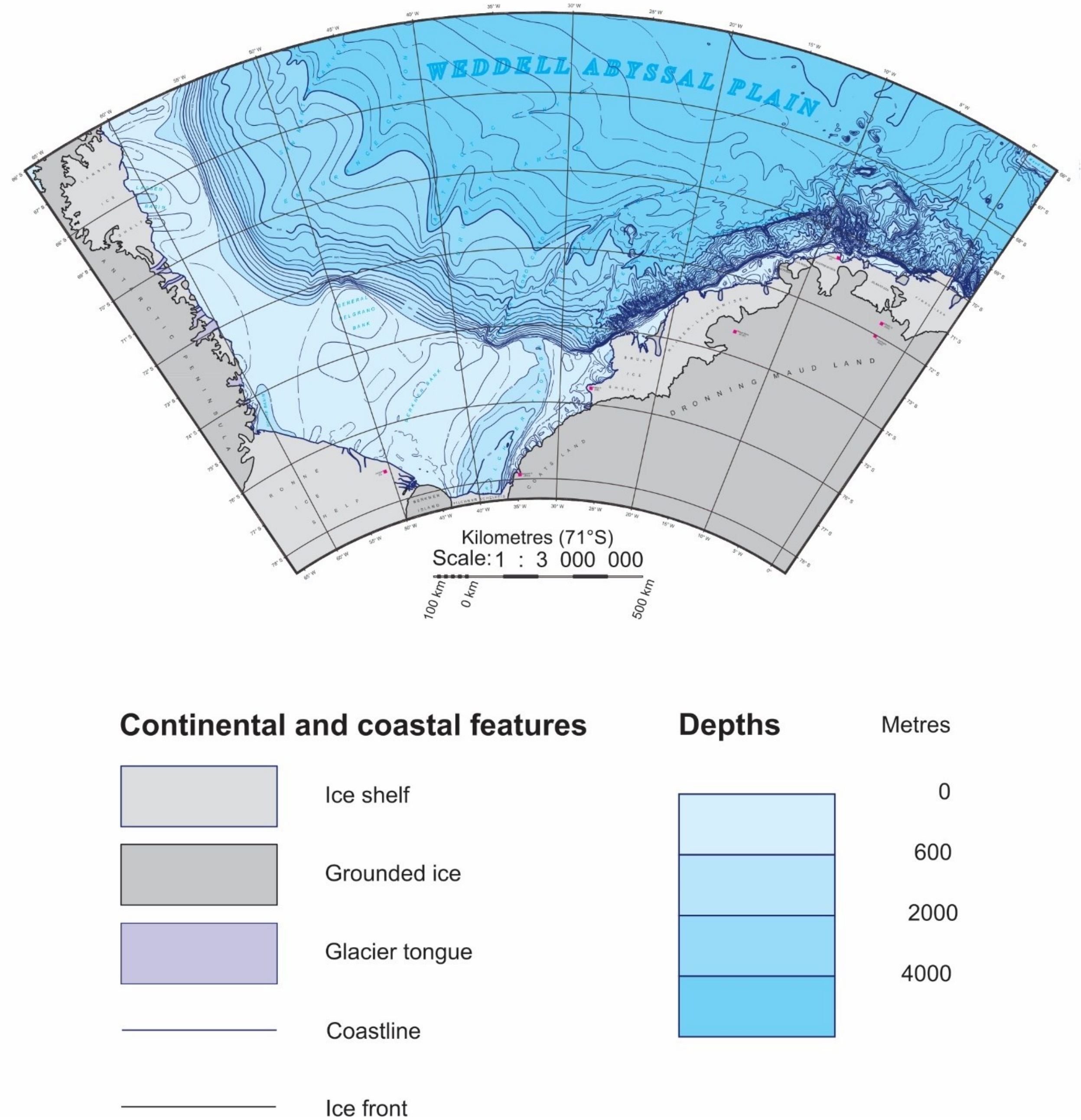


Figure 5.3: Bathymetric chart of the Weddell Sea, Antarctica (Schenke et al., 1997)

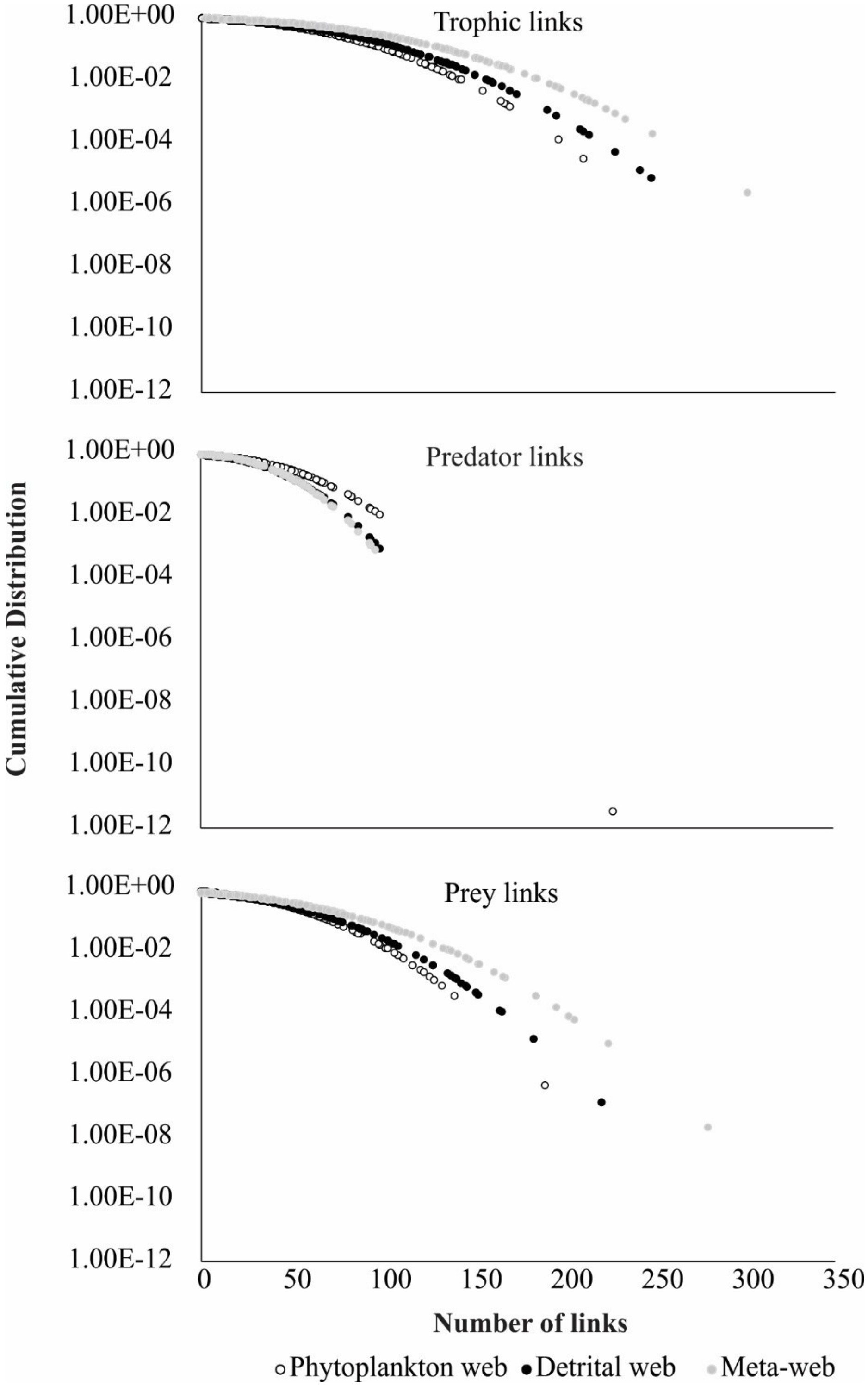


Figure 5.4: Log plots of the cumulative distribution of predator and prey links in the phytoplankton (white), detrital (black) and meta- (grey) webs. All three food webs show an exponential decay behavior. The distribution of the number of predator and prey links is a representation of the vulnerability and generality of the species.

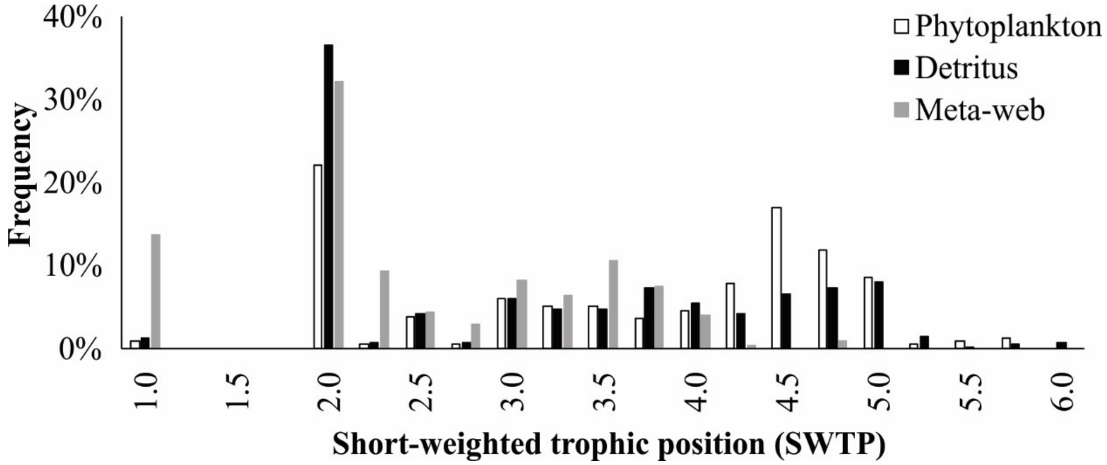


Figure 5.5: Distribution of short-weighted trophic position for the phytoplankton (white), detrital (black) and meta- (grey) food-webs.

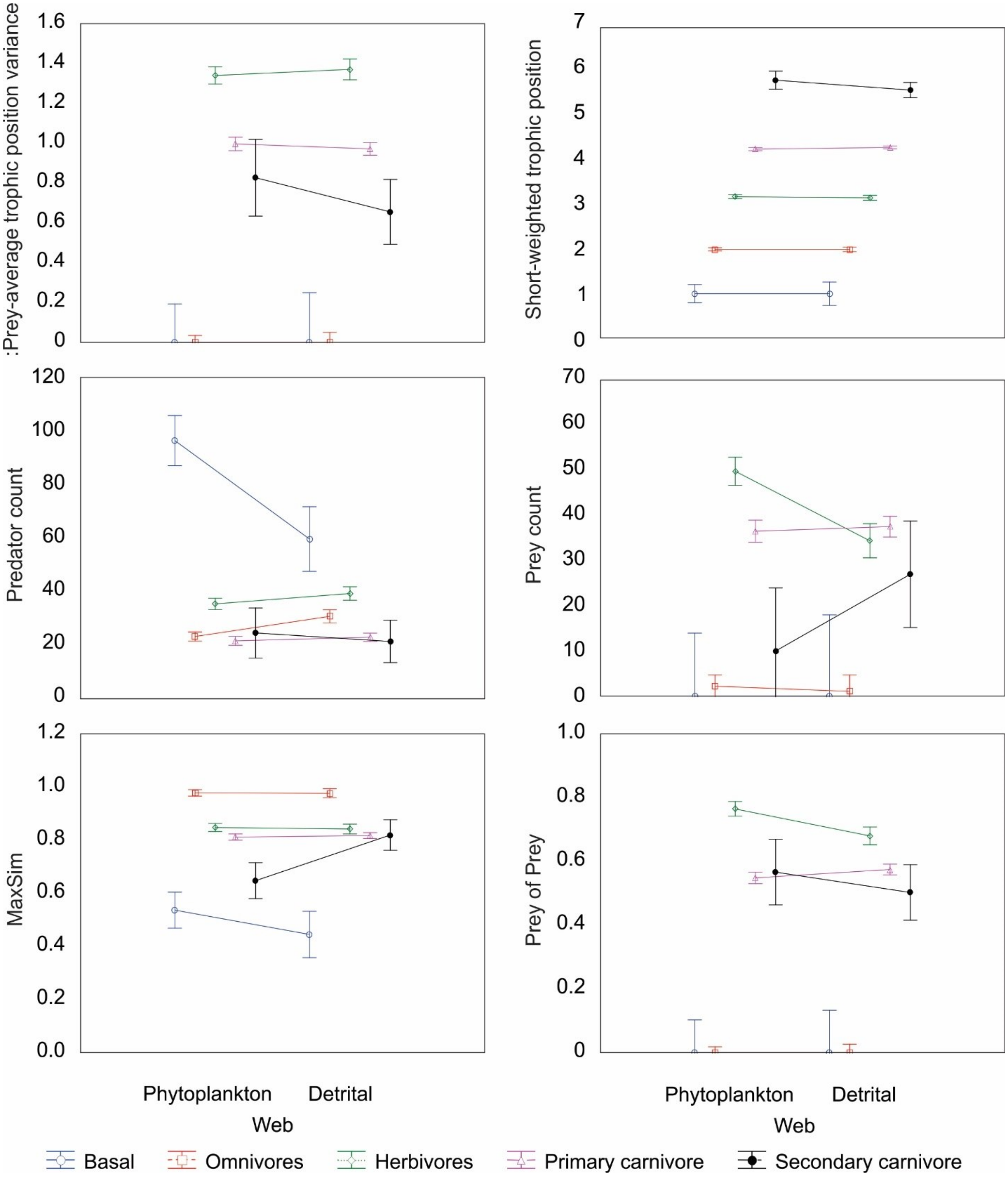


Figure 5.6: Mean independent node properties for each functional group in the detrital and phytoplankton webs. Basal (blue), omnivore (red), herbivore-detritivores (green), primary carnivore (purple), secondary carnivore (black). Error bars represent standard error.

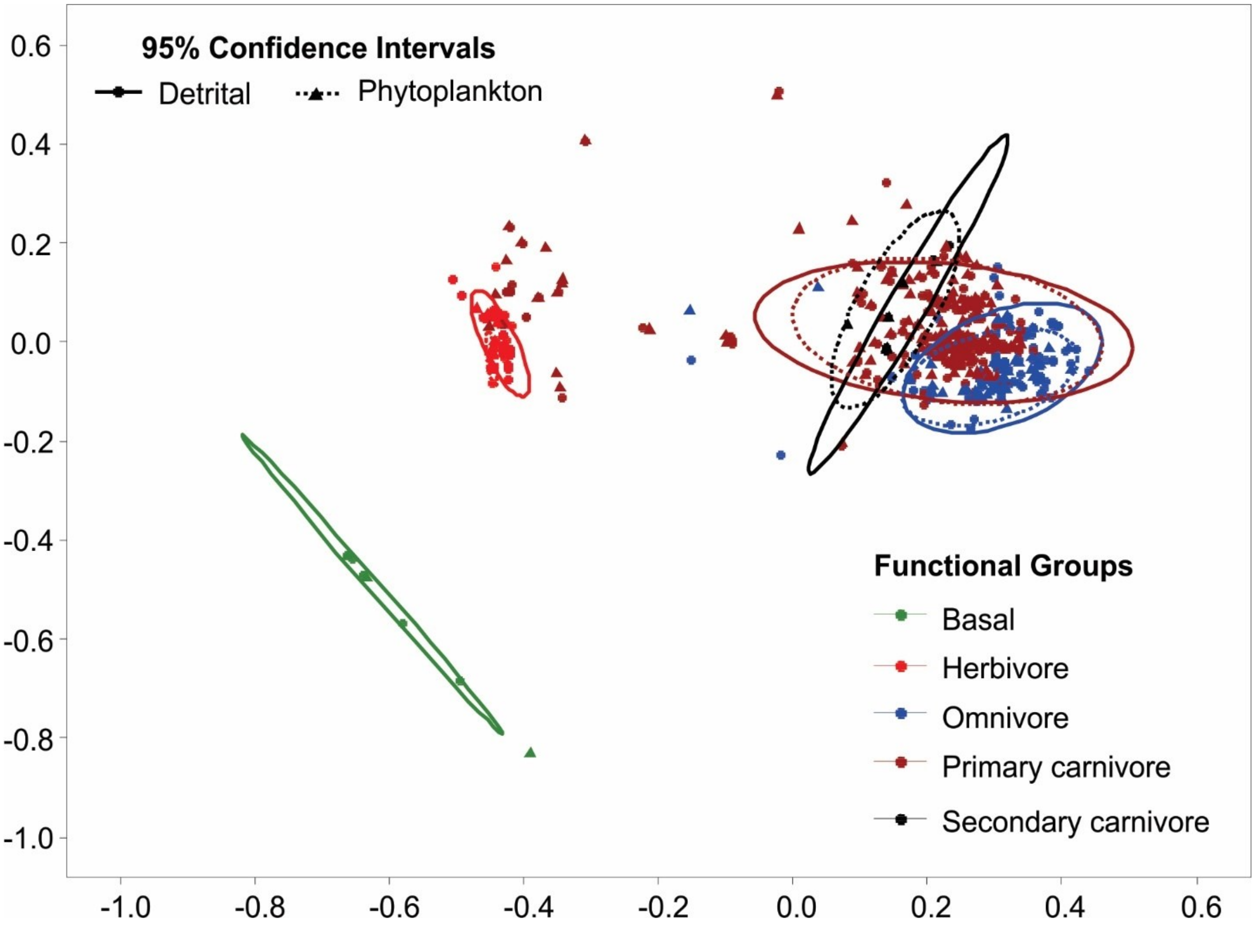


Figure 5.7: Non-metric multidimensional scaling (nMDS) overlaid with 95% confidence intervals for each function group in each food web.

Table 5.1: Description of food web properties

Food- Web Properties		**Description**
Species	*TS*	Number of species in the food web after being converted into a trophic web
Links/Species	*L/S*	Number of pred/prey links per species
Clustering Coefficient	*CC*	Probability that two taxa linked to the same taxa are also linked
Connectance	*C*	Proportion of actual trophic links to all possible links (L/S^2)
Percentage of Top predator	*%T*	Species with prey and not predators
Percentage of Intermediate species	*%I*	Species with both predators and prey
Percentage of Basal species	*%B*	Species with predators and no prey
Percentage of Herbivores	*%H*	Species who prey on primary producers
Percentage of Cannibals	*%Can*	Species which prey on their own species
Percentage of Omnivores	*%Omni*	Species which prey on primary producers and consumers
Consumer direct omnivory	*ConDirOmni*	Fraction of intermediate species that feed on more than one trophic level
Mean consumer trophic position	*ConMeanTL*	mean PATP of all intermediate species in the food web
Trophic level max	*TLMax*	Maximum trophic level in the food web using prey-averaged algorithm
Trophic level mean	*TLMean*	Average trophic level for PATP
Trophic level standard deviation	*TLSD*	Standard deviation of trophic level among the entire web for PATP
Short-weighted trophic position	*SWTP*	the average of 'prey-averaged trophic position'
Diet Discontinuity	*DietDis*	Number of triplets of species with an "irreducible gap" (measure of intervality)
Generality standard deviation	*GenSD*	The number of prey of a taxa standardized by L/S
Vulnerability standard deviation	*VulSd*	The number of predators of a taxa standardized by L/S
Loop	*Loop*	Percent of taxa in a loop (food chain where the taxa appears twice)
Mean Similarity	*SimMean*	Mean link similarity across all nodes
Similarity standard deviation	*SimStdDev*	Similarity standardized by L/S
Mean maximum similarity	*SimMaxMean*	Mean of the maximum similarity for every node
Clustering coefficient	*CC*	Average % of pairs of nodes connected to another node and connected to each other
Top generality	*TopGen*	Species with the highest number of prey

Table 5.2: Node property correlation matrix for phytoplankton and detrital food webs. Node properties with a correlation above 0.7 were excluded from statistical analyses.

	PATP	**PATPVar**	**SCL**	**SWTP**	**PreyCount**	**PredCount**	**MaxSim**	**PreyofPrey**
PATP	1	0.66	0.74	0.99	0.36	-0.08	-0.35	0.78
PATPVar	0.66	1	0.3	0.6	0.59	0.13	-0.25	0.7
SCL	0.74	0.3	1	0.84	0.23	-0.24	-0.25	0.35
SWTP	0.99	0.6	0.84	1	0.35	-0.12	-0.34	0.71
PreyCount	0.36	0.59	0.23	0.35	1	-0.01	-0.16	0.41
PredCount	-0.08	0.13	-0.24	-0.12	-0.01	1	0.06	0.05
MaxSim	-0.35	-0.25	-0.25	-0.34	-0.16	0.06	1	-0.27
PreyofPrey	0.78	0.7	0.35	0.71	0.41	0.05	-0.27	1

Table 5.3: Food web properties for phytoplankton, detrital and meta-web.

Web	Phytoplankton	Detrital	Meta-web
S	336	428	492
%T	8.63	7.71	6.71
%I	90.48	91.12	79.67
%B	0.89	1.17	13.62
%Herb	22.02	36.45	32.11
C	0.08	0.06	0.07
L/S	28.32	26.39	33.19
GenStdDev	1.16	1.43	1.36
VulStdDev	0.76	0.88	0.86
LinkStdev	0.67	0.85	0.77
SimMean	0.09	0.09	0.09
SimStdDev	0.16	0.15	0.18
SimMax	1	1	1
SimMaxMean	0.85	0.88	0.89
PATP	4.54	3.94	2.67
PATPStdDev	1.77	1.85	1.11
Max PATP	7.43	7.88	5.17
Loop	0.38	0.3	0.26
%Can	0.15	0.12	0.1
%Omn	0.72	0.58	0.51
CC	0.19	0.2	0.18
ConDirOmni	0.73	0.59	0.59
ConMeanTP	3.58	3.19	2.65
SWTP	3.56	3.17	2.43
DD	0.15	0.09	0.1
TopGen	1.13	1.19	0.95

Chapter 6 Variation in microalgae fatty acid proportions across a latitudinal gradient and the implications of a warming climate

6.1. Abstract

Microalgae are among some of the oldest organisms on the planet and provide key nutrients to the vast majority of ecosystems. One particular class of nutrients, fatty acids, is particularity important, as many higher trophic position species are unable to synthesis specific fatty acids, which they use for a variety of physiological processes. However, as climate change continues to alter the environmental conditions and distribution of species, microalgae will likely shift in community composition and nutritional content. Here, I analyse fatty acid profiles of 1348 strains of microalgae, from around the globe, to assess whether consistent changes in fatty acid proportions are seen across climate regions. I found that despite environmental and phenotypic variability, both of which affect fatty acid production, there are consistent changes in fatty acids proportions across climate regions. Furthermore, proportions of specific essential fatty acids such as EPA and ARA show an inverse relationship with temperature, which may lead to deficiencies in higher trophic position taxa that depend on them.

6.2. Introduction

Microalgae are the base of the majority of aquatic ecosystems, providing a source of essential nutrients. Fatty acids produced by microalgae are of particular importance as they are utilized by all consumers in the ecosystem (Arts, et al., 2015). As global temperatures continue to rise, shifts in species' phenology, range, and physiology (Bellard et al., 2014; Doney et al., 2012) threaten to alter the structure and function of ecosystems (Van der Putten, 2012). The polar regions, which experience some of the most pronounced warming (Christensen et al., 2007;

Turner et al., 2005), are particularly at risk as the majority of species, both terrestrial and marine, tend to migrate towards higher latitudes as temperatures rise (Root et al., 2003; Perry et al., 2005; Sorte et al., 2010). Across taxonomy, species which have a smaller body size, and thus typically a shorter generation time, have the greatest range shifts (Perry et al., 2005). These effects of warming are particularly true for microscopic organism, which not only experience range shifts but also changes in their productivity and community composition (Hinder et al., 2012; Suikkanen et al., 2013; Thomas et al., 2012). Empirical studies have shown that variation in oceanic and atmospheric conditions caused by climate change have already begun to affect the productivity (Paerl & Paul, 2011), abundance (Hinder et al., 2012) and structure and function (Sarmento et al., 2010) of microbial ecosystems in various regions.

Fatty acids (FA) have been shown to be crucial for many animals as they are directly linked to key physiological functioning and biochemical processes (Arts et al., 2000; Pernet et al., 2007). Essential fatty acids (EFA) are a particularly important class of compound as species at higher trophic positions are unable to synthesize them or are only able to synthesize them in quantities well below their physiological requirements (Fuiman et al. 2015). Instead, EFA are transported through the food chain, originating in the basal trophic level and accumulating within each higher trophic level, eventually reaching top predators, including humans. Two EFA in particular, arachidonic acid (ARA) and eicosapentaenoic acid (EPA) are critical for survival (Arendt et al., 2005), growth (Copeman & Laurel. 2010), and development (Bell et al., 2003) in marine species, particularly in larvae and embryos (Fuiman et al., 2015).

The predicted changes in community composition in response to warming temperature is likely to be exasperated in regions where that warming is most pronounced. A recent study by Hixon et al. (2016) found that across a latitudinal temperature gradient, EPA content was likely to drop by

8.2% of total FA content after only a 2.5°C increase in water temperature. Given that the global mean sea-surface temperature has risen by approximately 0.8°C per decade since the 1950's (Armour et al., 2016), an extensive decline in the amount of EFA threatens to restructure aquatic ecosystems. In this study I explore the FA profiles, including two EFA (EPA and ARA), of 1348 strains of microalgae across a latitudinal gradient to assess the potential changes which may occur as a result of a temperature changes.

6.3. Methods

6.3.1. Data collection

In this study, I used a dataset of microalgae FA profiles which were characterized using gas chromatography (GC) mass spectrometry by Lang et al. (2011). The initial dataset was comprised of 76 FA from 2076 strains of microalgae from 18 different habitats (i.e., fresh water, marine, brackish) around the globe and spanning from 82.46 °S to 75.39 °N. The dataset was culled to remove strains without latitudinal and longitudinal coordinates of their origin, and FA that, on average, represented less the 1% of the total FA mass, and/or could not be separated by GC (i.e. 17:0/16:3), leaving 14 FA. Algae were then categorized into three broad climate regions including, polar (90°S – 60°S, 60°N-90°N, n = 32), temperate (60°S – 30°S, 30°N – 60°N, n = 1180), and tropical (30°S – 30°N, n = 136). To reduce the dataset further, only FA that showed a consistent pattern of increase or decrease in proportion across climate regions were retained. The final dataset included 1348 strains of algae from 11 phyla, 25 classes, 481 genera and 721 species, and seven FA, including: 1) 16:0; 2) 16:1n-7; 3) 16:3n-3; 4) 18:0; 5) 18:1n-9; 6) 18:2n-6; and 7) 18:3n-3. After removing FA, the data was not re-normalized and was represented as the proportion of the total FA content, as reported by Lang et al. (2011).

6.3.2. FA and latitudinal gradients

Strains of microalgae were categorized based on three criteria. Three independent case studies were done to explore whether trends found across the entire final data set were seen when the microalgae strains were categorised based on habitat and taxonomy (Figure 6.1). First, microalgae strains were grouped into fresh water (n = 772) and marine (n = 113) species. Second, strains were grouped by phylum (n = 11). Phyla which did not contain FA profiles for each of the climate regions were excluded, leaving four phyla: Chlorophyta (n = 799), Cyanobacteria (n = 162), Streptophyta (n = 90), and Heterokontophyta (n = 101). Thirdly, although ARA (20:4n-6) and EPA (20:5n-3) did not represent more then 1% on average across all strains of microalgae, they were compared across a latitudinal gradient due to their nutritional importance. A subset of 379 strains containing ARA and/or EPA were categorised by habitat (Marine = 64, freshwater = 205), and phyla (Chlorophyta = 128, Streptophya = 24, Heterokontophyta = 73) (Figure 6.2).

6.3.3. Statistical analyses

I compared means and standard deviations of the seven FA, and ARA and EPA, across three climate regions, based on three groupings including; 1) all strains (n = 1348), 2) habitat type (freshwater (n = 772), marine (n = 113)) and 3) phylum (Chlorophyta (n = 799), Cyanobacteria (n = 162), Heterokontophyta (n = 101), and Streptophyta (n = 90). I was unable to normalize the FA using the centred log ratio (Filzmoser et al., 2009). Instead, Kruskal-Wallis analysis of variance (KS-ANOVA) was used to test for differences in mean proportion of each FA between climate regions. Mann-Whitney-Wilcoxon test was used as a post-hoc analysis to identify pairwise differences when KS-ANOVA indicated a significant effect among groups.

6.4. Results

6.4.1. Across all strains

Of the 14 FA which represented, on average, more then 1% of the total FA composition across all algae strains, consistent patterns of change across a latitudinal gradient were observed in seven FA (Table 6.1). As latitude increased, proportions of saturated (SFA; 16:0, 18:0) and monounsaturated (MUFA; 16:1n-7, 18:1n-9) FA decreased, whereas polyunsaturated FA (PUFA; 16:3n-3, 18:2n-6, 18:3n-3) increased. KS-ANOVA found significant differences between proportions of two SFA (16:0, $H = 17.64$, $p = 0.001$; 18:0, $H = 17.26$, $p < 0.001$) and a PUFA (18:2n-6, $H = 11.66$, $p < 0.01$) (Figure 6.3; Figure 6.4). Further post-hoc analysis revealed that the differences in proportions of 16:0 and 18:2n-6 were driven by significant differences between the polar and temperate (16:0, $W = 12939$, $p < 0.001$; 18:2n-6, $W = 25002$, $p < 0.01$), and polar and tropical regions (16:0, $W = 1184.5$, $p < 0.001$; 18:2n-6, $W = 2994.5$, $p < 0.001$) where 16:0 and 18:2n-6 were both lower in the polar region. Alternatively, the pattern in 18:0 was driven by differences between temperate and tropical regions (18:0, $W = 67249$, $p < 0.001$), with 18:0 content being higher in the tropical region.

6.4.2. Within freshwater and marine

Of the 1348 strains of microalgae, 885 strains had FA profiles for each climate region, for both freshwater ($n = 772$) and marine ($n = 113$) (Table 6.2). In freshwater strains, mean proportion of SFA (16:0, 18:0) and MUFA's (16:1n-7, 18:1n-9) decreased with latitude, while PUFA (16:3n-3, 18:2n-6, 18:3n-3) increased (Table 6.2). Three FA showed significant variation in proportion between climate regions including, 16:0 ($H = 11.25$, $p < 0.01$) and 18:0 ($H = 18.29$, $p < 0.001$), which were both highest in the tropics, and 18:3n-3 ($H = 5.96$, $p = 0.05$), which was highest in the polar region (Figure 6.5; Figure 6.6). For SFA, 16:0 showed significant differences between polar and tropical (W = 243, $p < 0.01$) and temperate and tropical (W = 14830, $p < 0.01$); however, 18:0 only showed significant differences between temperate and tropical regions (W = 14880, $p < 0.001$). PUFA 18:3n-3 was highest in the polar regions and showed a significant difference only between polar and tropical climate regions (W = 621.5, $p = 0.02$). In marine strains, SFA 18:0, MUFA 18:1n-9, and PUFA 18:3n-3 tended to decreased with latitude, whereas PUFA 18:2n-6 increased (Table 6.2). No significant differences were found between climate regions for marine strains.

6.4.3. Within each phylum

When broken into phyla across all habitats, data for each climate region was available for four of the 11 phyla, including Chlorophyta, Heterokontophyta, Streptophyta, and Cyanobacteria. Although each of the four phyla showed patterns of changing FA proportions across a latitudinal gradient, there were no consistent trends with SFA, MUFA, and PUFA, either within each phyla or across them (Figure 6.7). Within Chlorophyta, 16:3n-3, 18:0, and 18:1n-9 tended to decrease as latitude increased, whereas 18:2n-6, and 18:3n-3 both increased as latitude increased. However, no significant differences across climate regions were found. Within Heterokontophya, significant differences between climate regions were only found for PUFA 16:3n-3 (H = 38.88, $p < 0.001$) which was highest in the polar regions and showed significant differences between polar and temperate, and temperate (W = 183, $p < 0.001$) and tropical (W = 12, $p = 0.02$) regions. Within Streptophyta, significant differences were found for SFA 18:0 (H = 7.07, $p = 0.03$), which was highest the tropical regions and showed significant differences between temperate and tropical regions (W = 91, $p < 0.01$). Within Cyanobacteria, significant differences were found between climate regions for 16:3n-3 (H = 6.8, $p = 0.03$) and 18:0 (H =

15.9, $p < 0.001$). Differences in the proportions of PUFA 16:3n-3 were driven by differences between the polar and tropical regions (W = 102.5, $p < 0.01$), whereas differences in proportions of the SFA 18:0 were driven by differences between temperate and tropical regions (W = 1705.5, $p < 0.001$).

6.4.4. ARA and EPA

A data subset comprised of 379 strains of microalgae containing arachidonic acid (ARA) and eicosapentaenoic acid (EPA) was also analysed. On average, strains contained 6% ARA and 8.2% EPA across all climate regions. Although there were no consistent patterns in proportions both of FA across a latitudinal gradient (Figure 6.10), there were significant differences between climate regions (ARA, H = 37.53, $p < 0.001$; EPA, H = 19.53, $p < 0.001$). When the strains were categorized according to environment, marine strains showed a significantly ($F_{1,1} = 14.14$, $p < 0.001$) higher mean fraction of ARA and EPA than freshwater (freshwater (n=205): Mean ARA = 5.14, Mean EPA = 7.66; marine (n=64): Mean ARA = 12.24, Mean EPA = 11.21). Although marine strains showed a consistent pattern of increasing EPA with latitude (Table 6.3), the differences between climate regions were not significant. When strains were grouped into phyla, fractions of ARA and EPA tended to change across latitude within three and one phyla, respectively. The fraction of ARA tended to increase with latitude in Chlorophyta and Heterokontophyta, and decreased in Streptophyta. Fractions of EPA tended to decrease with latitude within Streptophyta. The only changes which were significant were for ARA within Chlorophyta (H = 25.96, $p < 0.001$) and Heterokontophyta (H = 6.3, $p = 0.04$). However, the only significant difference in the fraction of ARA was between temperate and tropical climate region (W = 893, $p = 0.01$).

6.5. Discussion

FA of microalgae play a crucial role in the survival of many higher trophic position species (Pethybridge et al., 2015). Previous studies, which explore the effects of temperature and climate change on FA content, typically focus on EFAs, and have shown that they generally decrease as temperature increases (Renaud et al., 2002; Renaud et al., 2005; Hixon et al., 2016). In this study, I compile the largest scale analyses of the effects of latitudinal gradients on microalgae FA and the resulting implications towards temperature increase, ocean stratification, and microbial community shifts. Here I focus on four results of particular interest. First, despite large amounts of phenotypic and environmental variability, which alter FA profiles, certain FA do show consistent changes in proportions across a latitudinal gradient. Second, of the four FA, in fresh water and marine strains, which showed consistent changes across climate regions, only one PUFA, 18:3n-3, differed in its pattern of change across climate regions. This suggests that despite differences in samples sizes between fresh water and marine strains, patterns in changes in freshwater and marine FA proportions are relatively consistent. Third, in marine strains of algae, ARA and EPA represented a higher proportion of total FA than in freshwater strains. Lastly, the proportion of total FA that was EPA in marine strains increased as latitude increased.

One particular challenge in identifying consistent patterns in microalgae FA profiles is species level variability. Although broad taxonomic groupings (i.e., phyla, class) have been shown to have FA profiles that can be used as a “finger print” by which microalgae can be identified, the level of variability that exists at more specific taxonomic groupings (i.e., species) hinders the ability to identify distinguishing aspects of their FA profiles (Lang et al., 2011). Despite this, there were strong patterns of change across climate region in the proportions of the seven fatty acids focused on in this study. Given the strong differences in average temperatures which decrease as latitude increases, this is not surprising. Previous studies highlight the importance of environmental factors on the proportions of FA within various microalgae strains. For instance, Renaud et al. (1995) found that the levels of PUFA decreased as temperatures increased with a strong inverse correlation between temperature and PUFA production in *Nitzchia paleacea*. Additionally, Sato et al. (1979) found that the proportion of SFA, 16:0 and 18:0 increased as temperature increased in *Anabaena variabilis*. Our results were consistent with previous findings showing an overall decrease in SFA and increase in PUFA as latitude increased (i.e. temperature decreased).

Pronounced temperature increases in the polar regions not only have a direct effect on microalgae, such as altering growth rates and their biochemical composition, but also indirect effects as well. Hydrological conditions are significantly influenced by the rate at which the sea-ice melts, and in the polar regions, such melting has caused higher volumes of freshwater to enter into the polar oceans (Bintanja et al., 2013; Van As et al., 2014). Although many freshwater and marine strains of microalgae are able to withstand a range of salinity, many of them exhibit shifts in the growth rates and FA content and composition. Freshwater polar strains, for example, are able to grow in brine pockets; however, when salinity reaches about 60% they are unable to grow (Grant & Horner, 1976). Similarly, many marine strains modifying their FA composition to cope with changes in salinity, and have been shown to have a higher total lipid content (i.e. % dry weight) as salinity increases (Renaud & Parry, 1994). This ability to adapt to varying salinity may explain why marine strains and freshwater strains show similar patterns in three of the FA explored in this study.

A large influx of fresh water may allow non-native strains, potentially freshwater strains, of algae to establish themselves. In this event, the microbial species composition within the polar regions could significantly shift, altering the nutritional composition of the base of the food web. Our results highlight that FA such as ARA and EPA represent a higher proportion of total FA content in marine strains in comparison to freshwater strains (Freshwater: Mean ARA = 5.14, Mean EPA = 7.66; Marine: Mean ARA = 12.24, Mean EPA = 11.21; Figure 6.10). Although these are proportions and do not take into consideration the possibility that freshwater strains have a higher total FA content, shifts in the overall nutritional content of the algae are still likely to occur. Other PUFA, such as 18:2n-6 and 18:3n-3, show the same pattern where they represent a greater proportion of total FA at higher latitudes, whereas SFA and MUFA are less. Furthermore, temperature has also been shown to have a strong effect on EPA levels. Renaud et al., (1995, 2002) found that in several marine strains of microalgae, including diatoms, crytomonads, Rhodomonas sp. and others, EPA levels dropped as temperature was increased. This could create severe physiological challenges for higher trophic position species that are unable to synthesize PUFA (Brett et al., 1997; Hixon et al., 2016).

Our analysis suggests that across a latitudinal gradient there exists strong patterns of variation in specific FA’s, including EFA. Given the projected temperature increases, specifically in the polar regions, FA profiles will likely shift, having implications for nutrition of all higher trophic position taxa that rely on these both for EFA and as an energy source. However, our results also highlight the need for additional synthesis of data, particularly relating to the effects of biotic interactions on species composition, which may play a strong role in determining the microbial community structure and function.

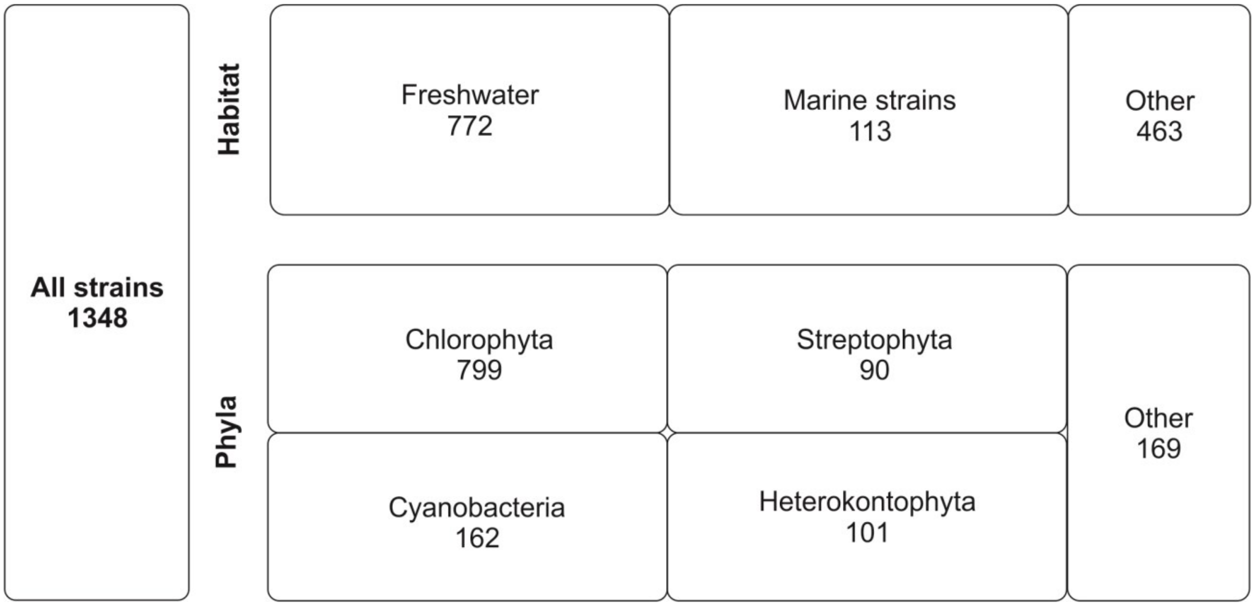


Figure 6.1: Number of strains within each category used in these analyses

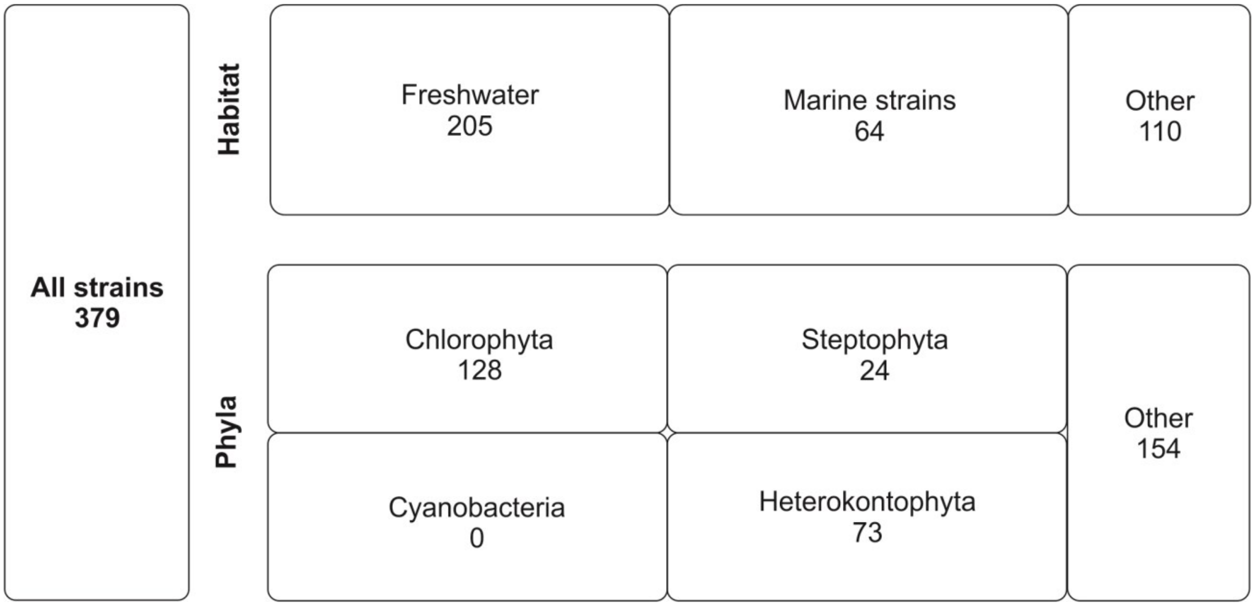


Figure 6.2: Number of strains containing either EPA or ARA, broken down by category

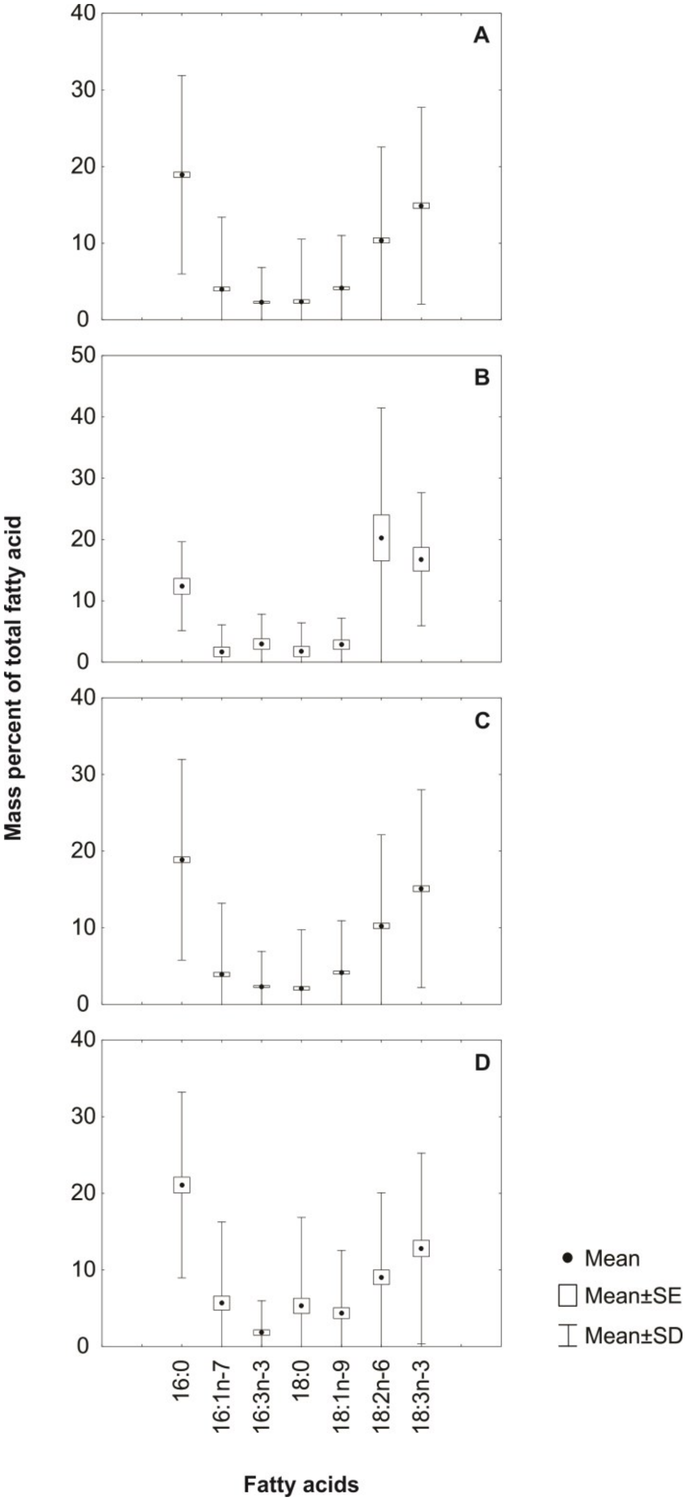


Figure 6.3: Mean, standard error, and standard deviation of the proportion of total fatty acid of fatty acids showing significant differences across climate regions. Top: 16:0, Middle: 18:0, Bottom: 18:2n-6.

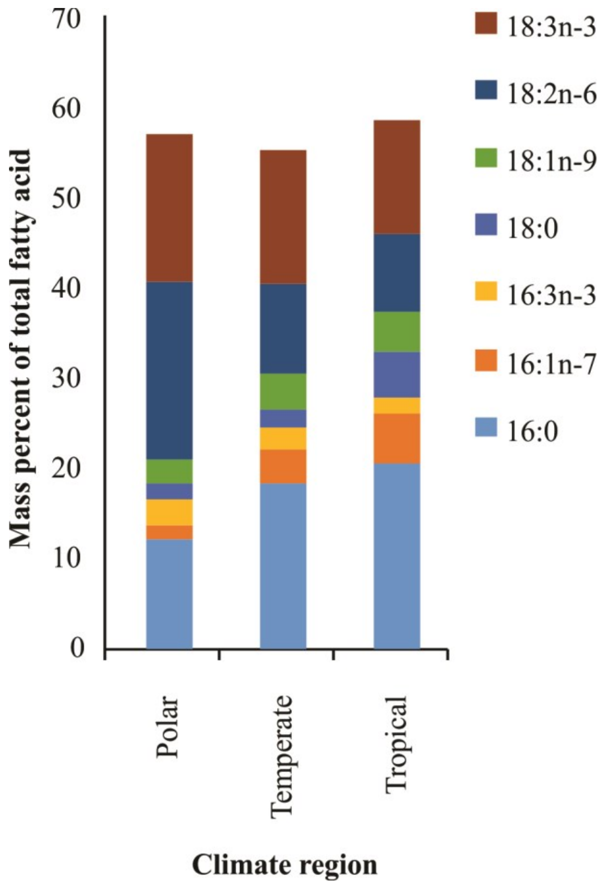


Figure 6.4: Mean proportions of total fatty acid across all strain of algae grouped by climate region.

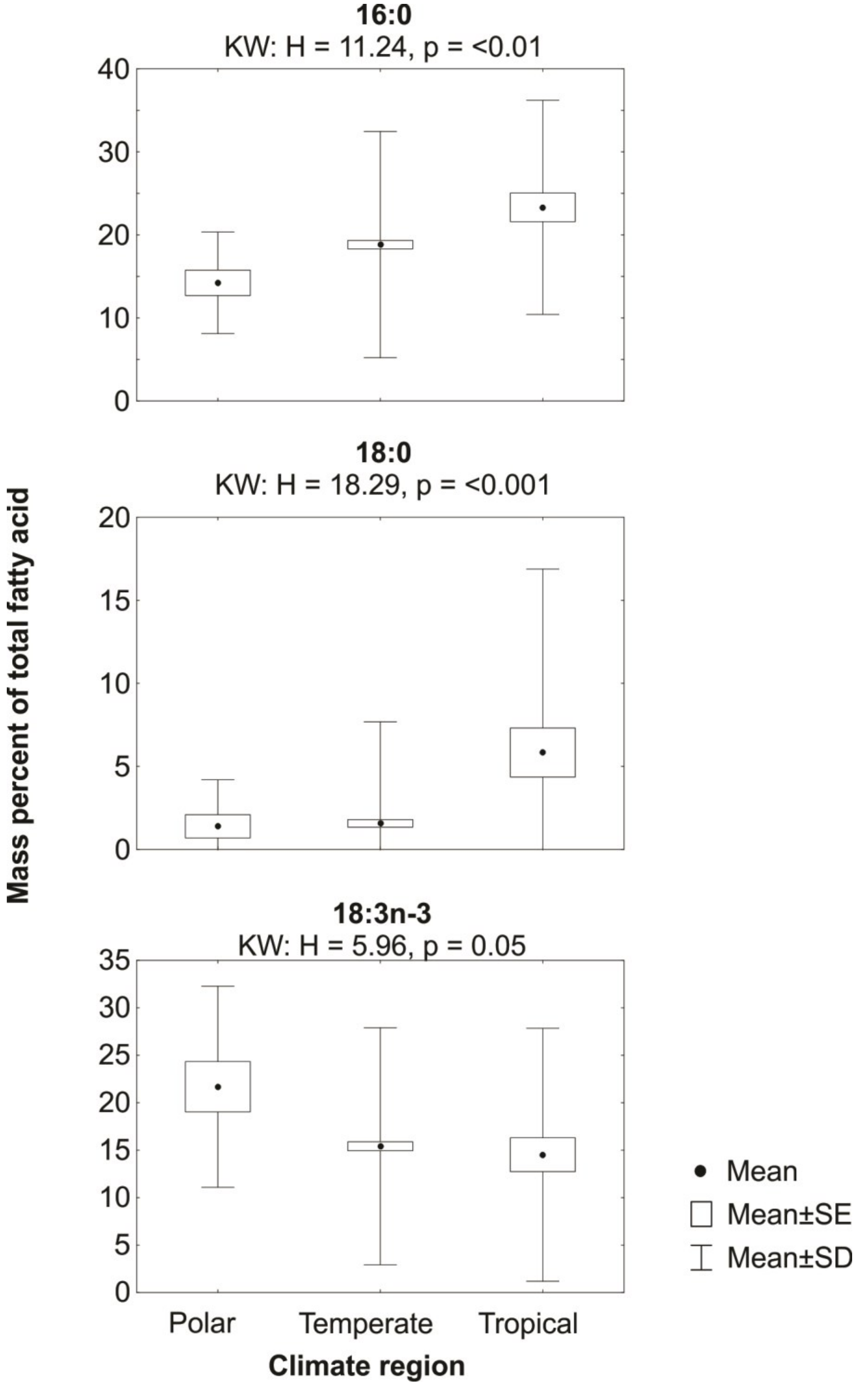


Figure 6.5: Mean, standard error, and standard deviation of the proportions of total fatty acids in freshwater strains which showed significant differences across climate regions. Top: 16:0, Middle: 18:0, Bottom: 18:3n-3.

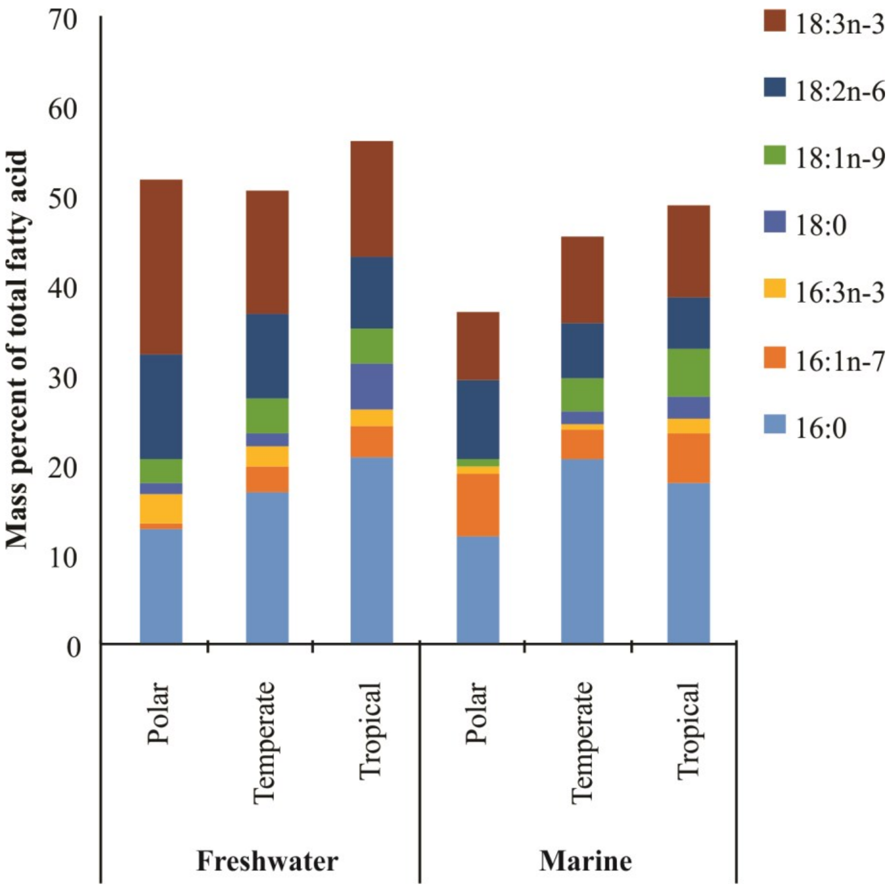


Figure 6.6: Mean fraction of total fatty acid content across all strains of algae grouped by climate region within freshwater and marine strains.

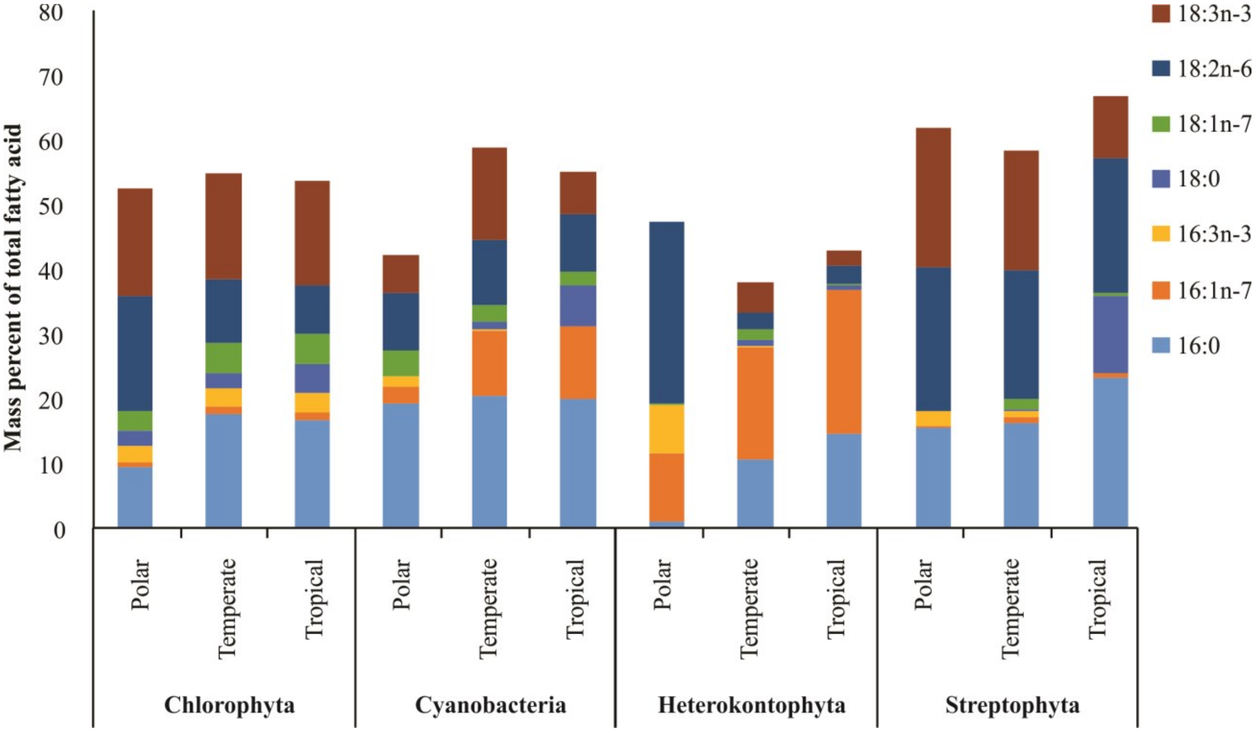


Figure 6.7: Mean fraction of total fatty acid content across all strain of algae grouped by climate region within phylum (Chlorophyta, Cyanobacteria, Heterokontophyta, Streptophyta).

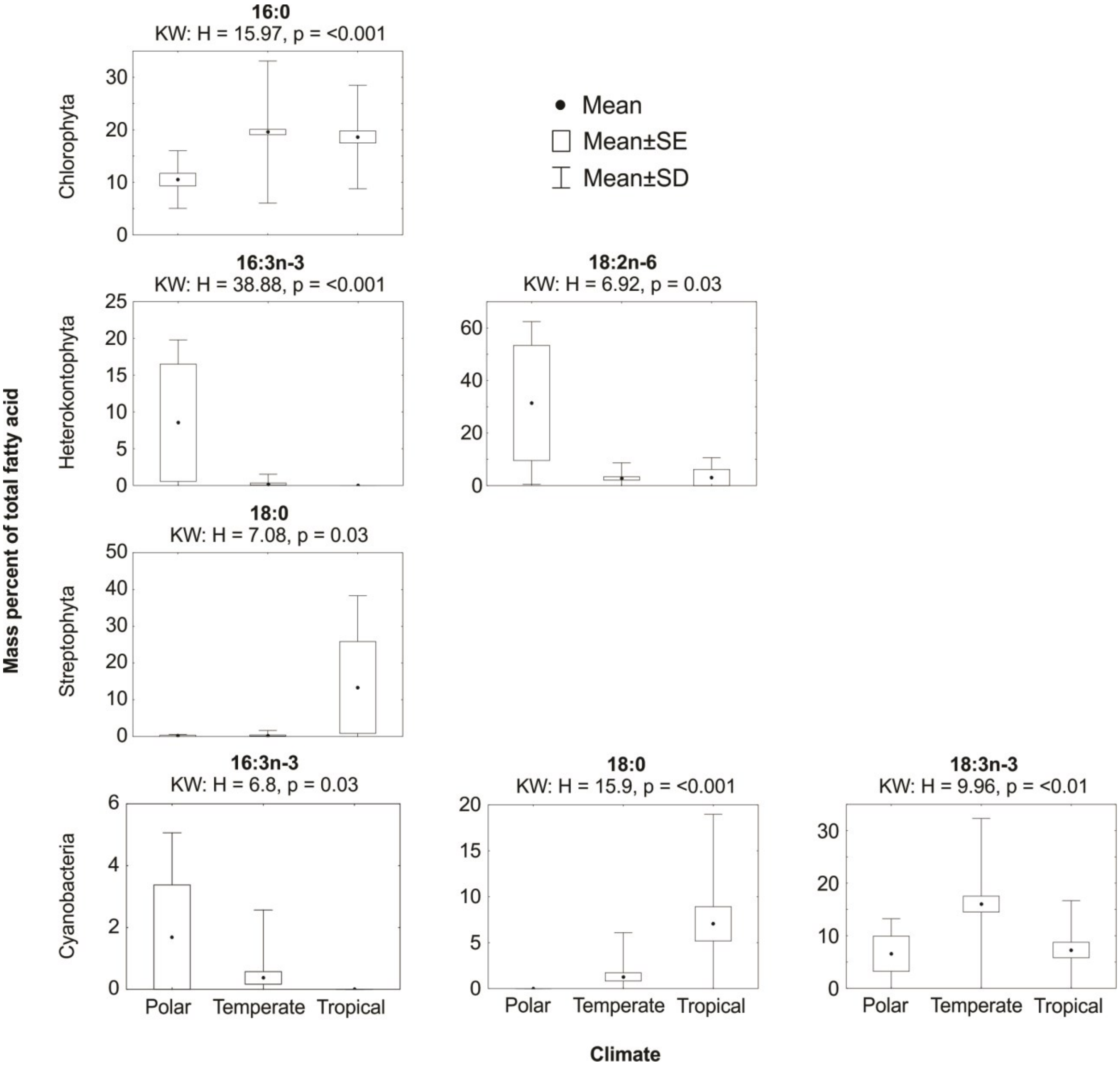


Figure 6.8: Mean, standard error, and standard deviation of the proportion of total fatty acids which showed significant differences within phyla (Chlorophyta, Heterokontophyta, Streptophyta, Cyanobacteria) across climate regions. Top: 16:0, Middle: 18:0, Bottom: 18:3n-3.

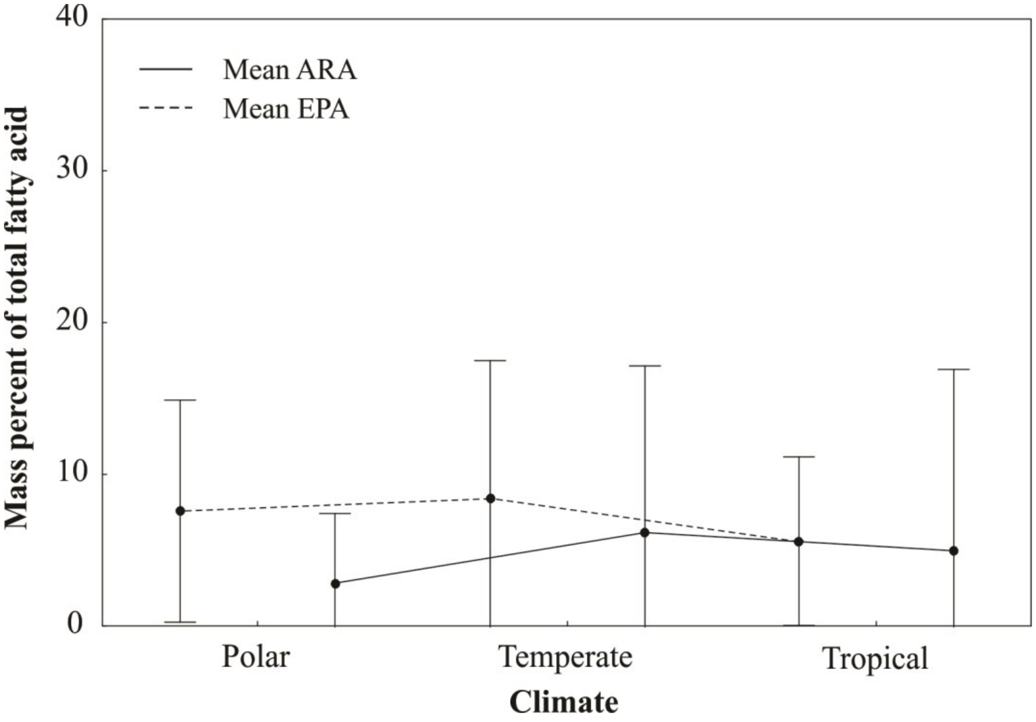


Figure 6.9: Mean proportion of total fatty acid represented by ARA and EPA across all strains in each climate region. Error bars represent standard deviation.

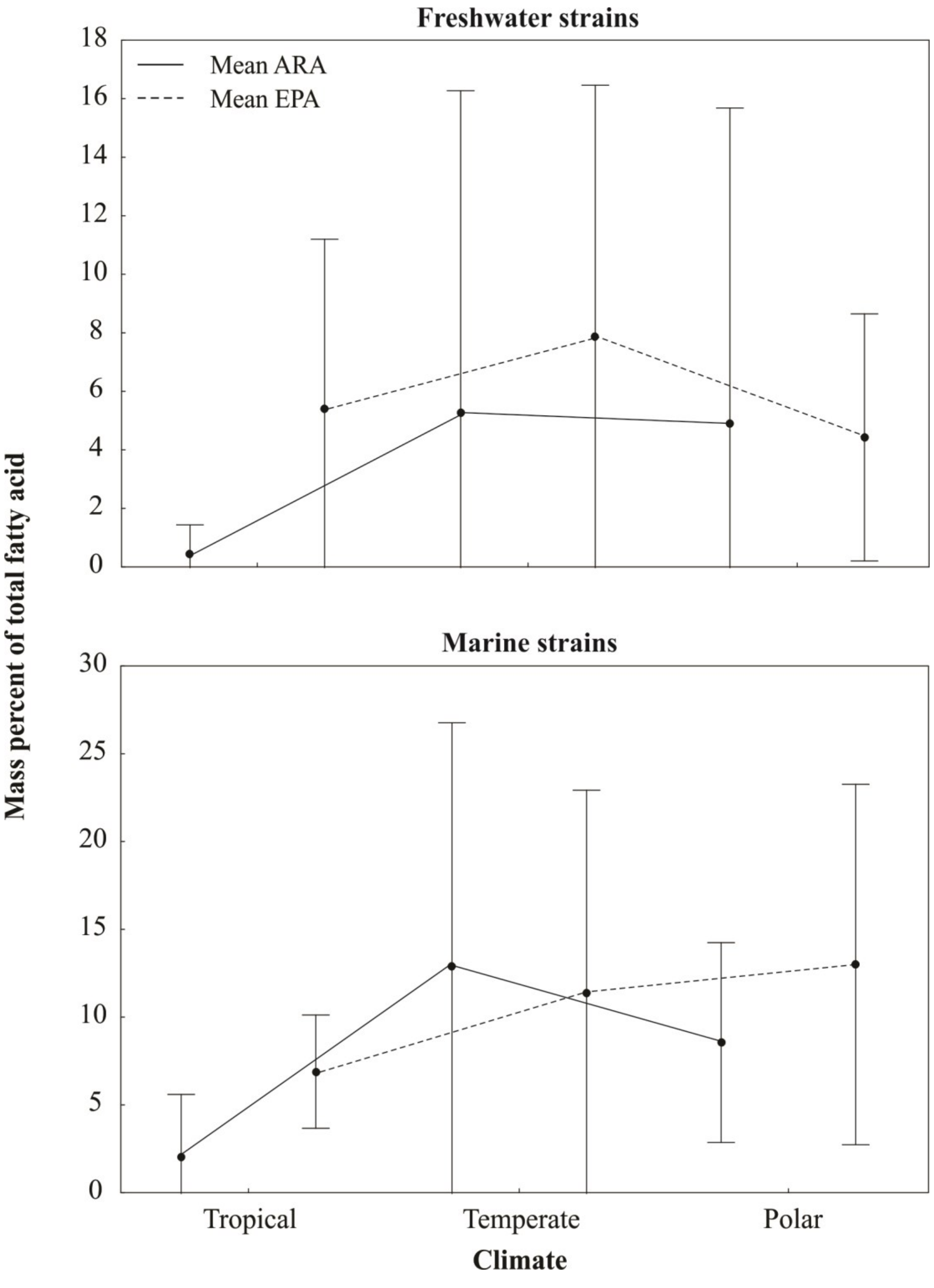


Figure 6.10: Mean fraction of total fatty acid content of ARA and EPA across all strain of algae grouped by climate region and habitat (i.e. freshwater and marine). Error bars represent standard deviation.

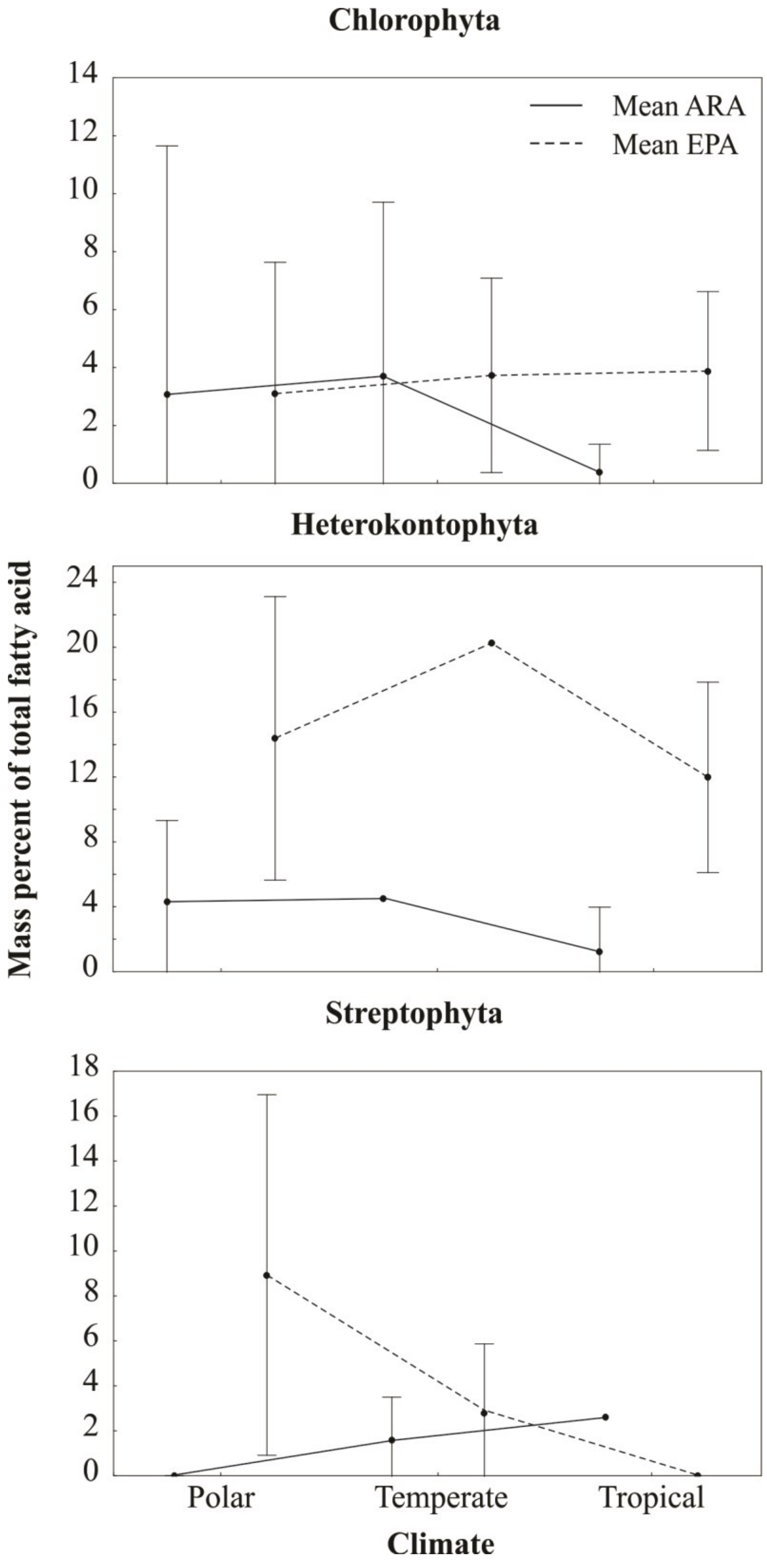


Figure 6.11: Mean fraction of total fatty acid content of ARA and EPA across all strain of algae grouped by climate region and phylum. Error bars represent standard deviation

Table 6.1: Fatty acid proportions (mass percent) and relative differences between polar and tropical regions for eight fatty acids showing general patterns of change across a latitudinal gradient.

Fatty Acid	Tropical (SD)	Temperate (SD)	Polar (SD)	Difference
SFA				
16:0	21.1 (12.1)	18.9 (13.1)	12.4 (7.2)	-8.7%
18:0	5.3 (11.5)	2.1 (7.7)	1.7 (4.7)	-3.6%
MUFA				
16:1n-7	5.7 (10.6)	3.9 (9.3)	1.7 (4.4)	-4.0%
18:1n-9	4.4 (8.2)	4.1 (6.8)	2.9 (4.3)	-1.5%
PUFA				
16:3n-3	1.8 (4.1)	2.3 (4.6)	2.8 (4.9)	+1.1%
18:2n-6	9.0 (11)	10.2 (11.9)	20.3 (21.2)	+11.2%
18:3n-3	12.8 (12.4)	15.1 (12.9)	16.8 (10.9)	+4.0%

Table 6.2: Difference in fraction of total fatty acid content for eight fatty acids showing general patterns of increase or decreasing across a latitudinal gradient within freshwater and marine strains of algae.

	Freshwater				**Marine**			
Fatty Acid	Tropical (SD)	Temp (SD)	Polar (SD)	Diff.	Tropical (SD)	Temp (SD)	Polar (SD)	Diff.
SFA								
16:0	23.3 (12.9)	18.8 (13.6)	14.2 (6.1)	-9.1	20.1 (10.9)	23 (12.7)	13.5 (12.7)	-6.6
18:0	5.8 (11)	1.6 (6.1)	1.4 (2.8)	-4.4	2.8 (4.9)	1.7 (5.5)	0.0 (0)	-2.8
MUFA								
16:1n-7	3.8 (10.6)	3.4 (8.9)	0.9 (1.6)	-3.8	6 (12.5)	3.7 (8.6)	7.7 (10.9)	+1.7
18:1n-9	4.3 (9.5)	4.3 (7.2)	2.9 (3.7)	-1.4	5.9 (12.4)	4.2 (6.2)	1 (1.5)	-4.9
PUFA								
16:3n-3	1.9 (4.6)	2.5 (4.8)	3.6 (5.3)	+1.6	2 (5)	0.6 (1.7)	0.85 (1.3)	-1.2
18:2n-6	9.1 (12.9)	10.6 (12.3)	13.2 (11.3)	+9.1	6.4 (7.1)	6.8 (9.8)	9.8 (6.5)	+3.5
18:3n-3	14.5 (13.3)	15.4 (12.5)	21.7 (10.6)	+7.2	11.7 (12.7)	10.6 (14.4)	8.5 (9.4)	-3.2

Table 6.3: Mean arachidonic acid (ARA) and eicosapentaenoic acid (EPA) proportions (mass percent) of total FA in strains of algae from freshwater and marine environments in each climate region.

	Mean ARA (SD)	**Mean EPA (SD)**
Freshwater		
Polar	0.5 (1)	5.4 (5.8)
Temperate	5.3 (11)	7.9 (8.6)
Tropical	4.9 (10.7)	4.4 (4.2)
Marine		
Polar	8.6 (5.7)	13.0 (10.2)
Temperate	12.9 (11.6)	11.4 (11.6)
Tropical	2.1 (10.3)	6.9 (3.2)

Chapter 7 Conclusion

My thesis focused on understanding the structure and function of polar marine food webs. Through assembling and comparing food webs in the polar regions, from whole-web to species levels, I showed that despite differences in species composition and species richness, the topology of polar food webs is broadly similar. Here, I summarise my findings and highlight critical future work which is needed.

7.1. Thesis Synthesis

Environmental conditions play an extremely important role in natural selection, species life history, and the overall development of ecosystems over time. Chapter 2 represents one of the first attempts to assemble and compare Arctic and Antarctic marine food webs. Given the similarities in the harsh environmental conditions that exist in both regions, it was not surprising that Arctic and Antarctic marine sea-ice associated food webs shared many similar structural properties. More interesting was that despite the food webs having a low resolution, particularly for low-trophic position species, differences in node specific properties indicated that the energy pathways in each ecosystem were unique (Chapter 2 & 4). One noticeable difference between the Arctic and Antarctic was the difference in the diversity of fish taxa, which, in the Antarctic, was much higher. This reduction in the number of intermediate trophic position fish taxa reduced the mean number of feeding interactions, constraining the energy flow from the bottom to the top of the web. As a result, the Arctic web was less robust to the loss of low trophic position species. This is particularly concerning given the potential impacts of climate change on the polar regions, which includes sea-ice loss, temperature increases, and species range shifts, all of which will have strong impacts on low trophic position species (Doney et al., 2011).

One indirect effect of climate change which we are only beginning to understand is the connection between surface and benthic food webs. The results of Chapter 5, in addition to other work by Zou et al. (2015) and Krumins et al. (2013), show the interdependence of phytoplankton (i.e. surface) and detrital (i.e. benthic) communities. Higher trophic position species in large bodies of water tend to have large ranges, specifically across depths, that allows them to directly interact with both phytoplankton and detrital communities (Chapter 5). However, the energy that flows from the phytoplankton community to the detrital community in the form of dead organic material and feces is rarely taken into account. This suggests that although taxa which solely inhabit deep waters may not be directly impacted by the effects of climate change, such as sea-ice loss, they will likely be affected due to changes in the composition and abundance of energy that flows from the surface communities. However, surface communities were found to have a lower level of generality and vulnerability, which is likely to reduce their robustness. For ecosystems that already depend on a few key prey species, this further increases the constraints on feeding interactions and increases the vulnerability of the ecosystem to disturbance, particularly in the Arctic.

Utilizing static (i.e., binary) food webs to explore the structure and function of food webs poses several challenges, particularly when trying to compare them. The low resolution of low trophic position taxa in the Arctic and Antarctic food webs used in Chapter 2 and the variability observed in the published food webs in Chapter 4, highlighted the need to address two methodological questions in food web theory: 1) do food webs based on presence-absence feeding interactions accurately predict the trophic position of species? and 2) given the high level of variability in the quality of data and assembly methodology, how can we determine if webs are comparable? In Chapter 3 I compared binary estimates of trophic position with estimates based on stable isotope values of nitrogen ($\delta^{15}N$) and showed that binary estimates based solely on feeding links were highly correlated to stable isotope values. Furthermore, when both were compared to more quantitative flow-based estimates (gut-content), binary estimates performed as well, or better than flow-based estimates of trophic position. This highlights the fact that although there are more precise techniques to determine the trophic position, no additional precision is gained by detailed analysis of biomass flows between species. To address the problem of methodological variability, I designed a comprehensive comparative hierarchical analysis (Chapter 4) and showed that despite differences in resolution and assembly methodology, that the polar food webs used were generally comparable.

Abiotic and biotic factors that lead to changes in individual species abundances and life history variables may have large effects on the structure and function of entire food webs. For example, global warming is likely to have a strong negative impact on key prey species, such as krill, through direct and indirect mechanisms. The declines in sea-ice cover and increase in melting rates not only threaten to affect multiple aspects of the krill lifecycle, but also impact its primary prey, microalgae. Microalgae provide many higher trophic position taxa with nutrients along the food chain including essential fatty acids, such as ARA and EPA. My results from Chapter 6 suggests that given the projected temperature changes in the polar regions, fatty acids profiles will likely change, with potentially important nutritional implications for higher trophic position taxa.

Through direct and indirect factors, the polar ecosystems described here are likely to experience strong changes in their structure and function due to climate change. Despite consistent structural similarities between the two polar regions there are key differences in species composition and feeding interactions which lead to differences in the energy flow pathways between each region. My research suggests that the Arctic and Antarctic are likely to manifest the impacts of the effects of climate change differently. Because the Arctic has been shown to have a lower species richness and fewer energy pathways (Chapter 2), it may experience larger changes in its structure and function as climate change continues to alter abiotic and biotic factors than the Antarctic.

7.2. Future Directions

In this thesis I have shown that over the last 60 years the basic topological structure of published Arctic and Antarctic food webs has not changed significantly outside of increases in species level resolution. However, while smaller, less resolved, polar food webs have similar topology to many larger, more resolved, webs, they do not allow an understanding of species level change, which is critical for the polar regions. One area in particular that needs to be accounted for in future work is the temporal (i.e., seasonal) changes in the structure and function of food webs, particularly Arctic and Antarctic food webs. Over the course of the year, species composition, population abundances, and even species interactions (i.e., prey switching) completely restructures the food webs. To fully understand how climate changes will impact polar food webs, high resolution webs along a temporal gradient will be an important future direction.

Appendices A Supplementary Figures

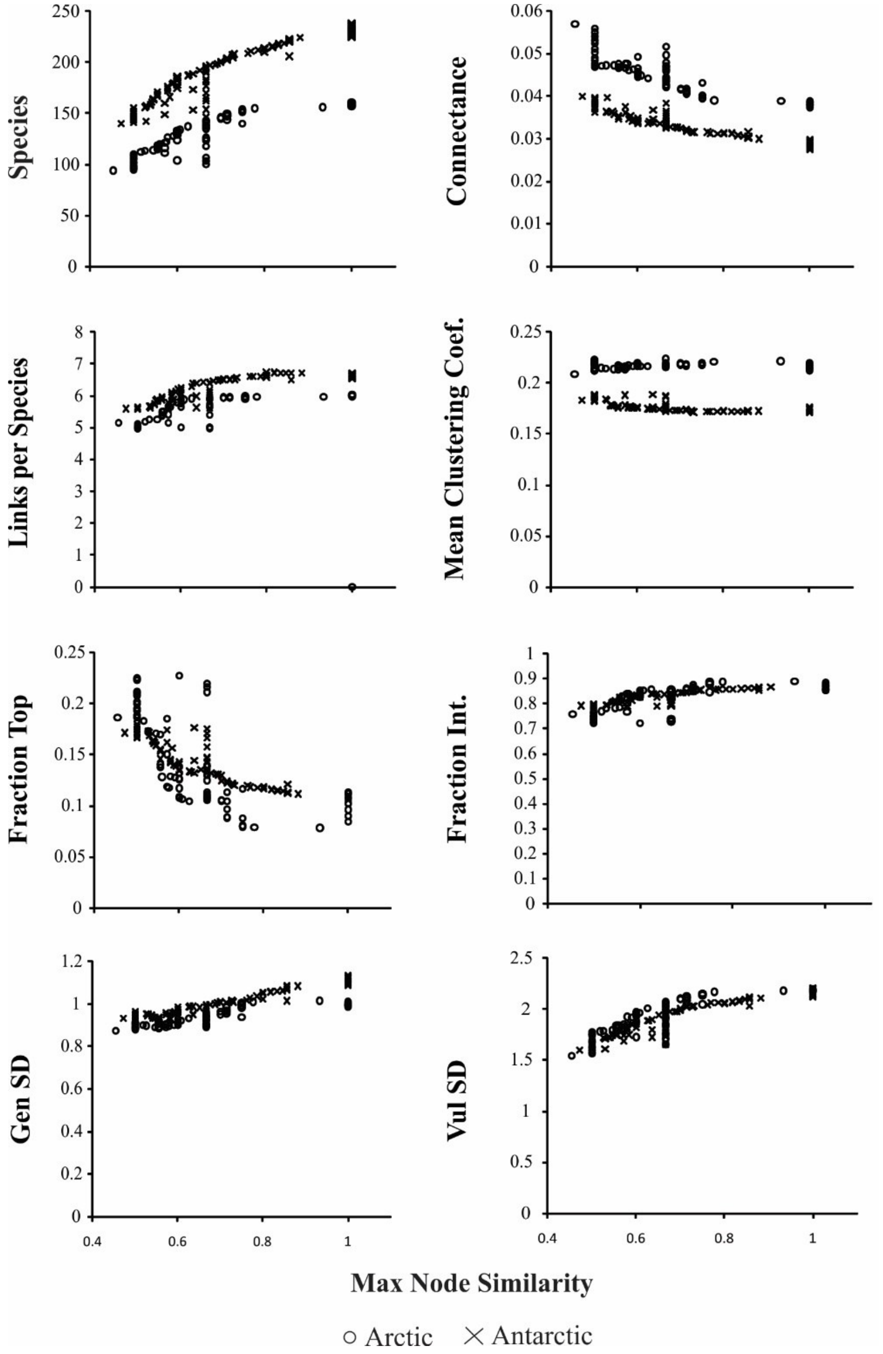
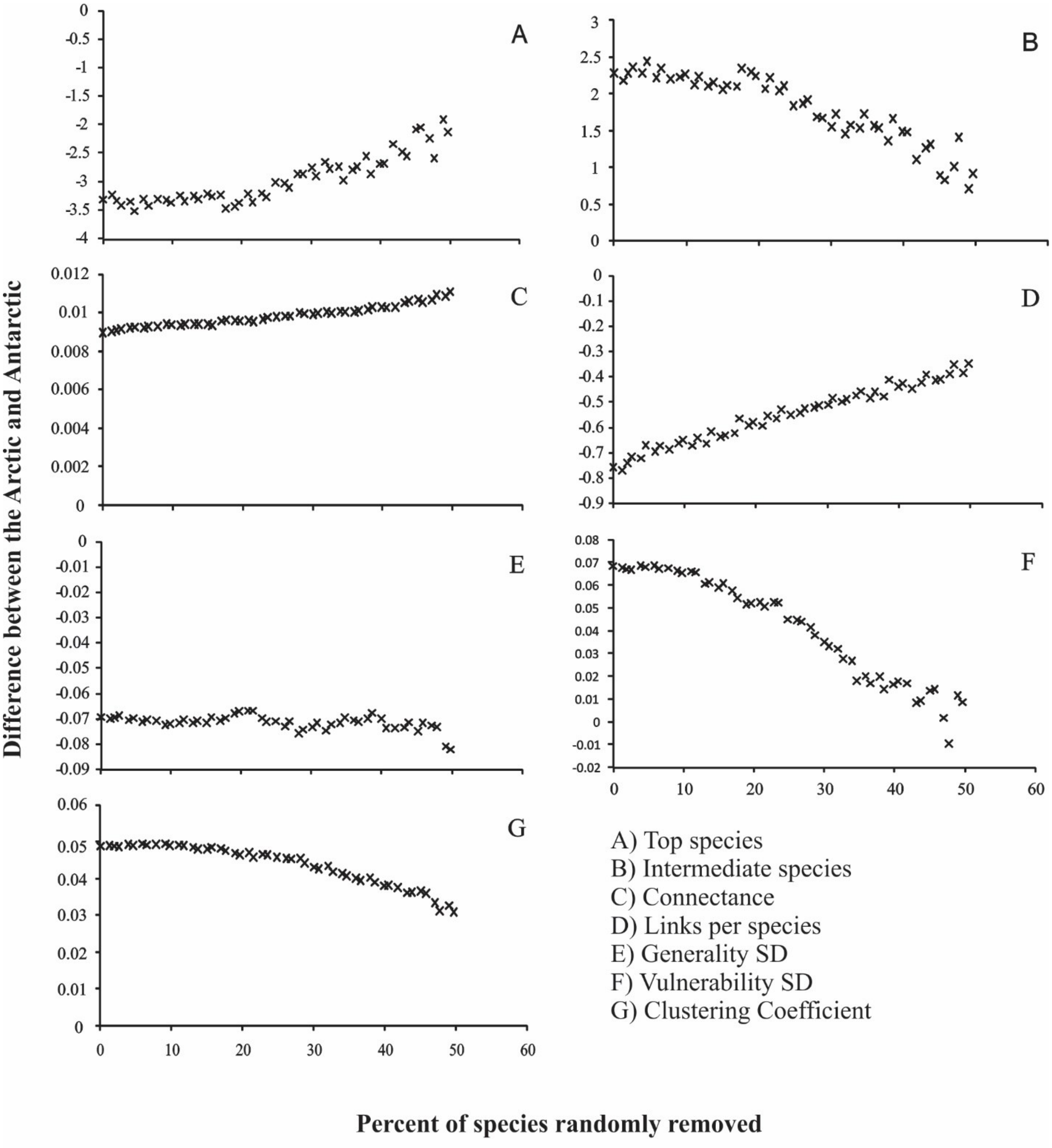


Figure A.1: Changes in the food web properties as a result of aggregating the Arctic and Antarctic with a minimum similarity ranging from 100% to 50%. A) Number of Species, B) Connectance, C) Links per Species, D) Mean Clustering Coefficient, E) Fraction of top species, F) Fraction of intermediate species, G) Generality SD, H) Vulnerability SD.



Note: Positive values represent higher values in the Arctic whereas negative values represent higher values in the Antarctic

Figure A.2: Differences between the Arctic and Antarctic food web properties throughout the random removal of 50% of the nodes in both webs. A) Fraction top species, B) Fraction intermediate species, C) Connectance, D) Links per species, E) Generality standard deviation, F) Vulnerability standard deviation, G) Clustering coefficient.

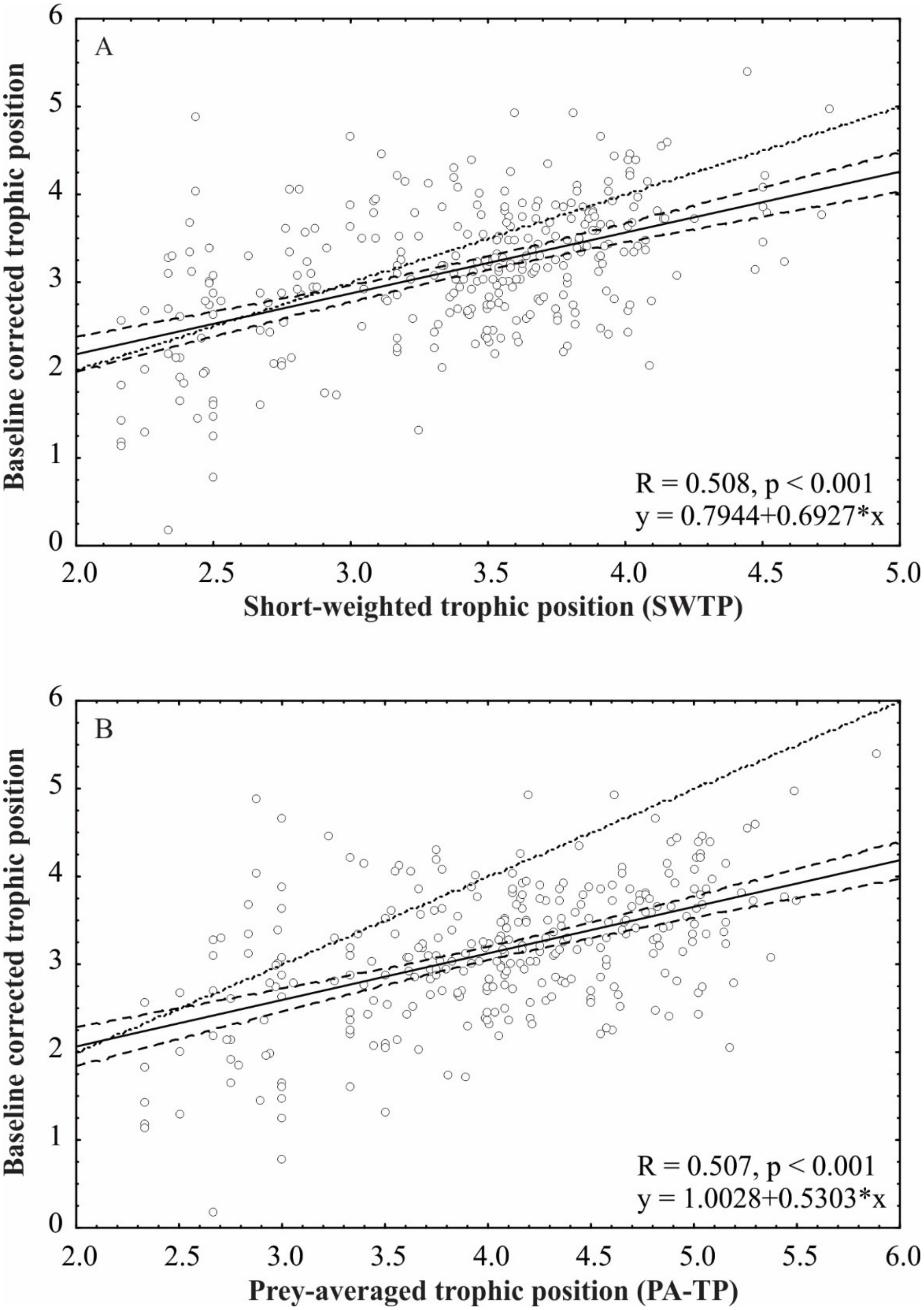


Figure A.3: Comparison of baseline corrected and binary estimates of trophic position for all 366 species. a) Baseline corrected trophic position (BCTP) compared to short-weighted trophic position estimates, b) Baseline corrected trophic position (BCTP) compared to prey-averaged trophic position estimates. Shown are the CI (± 0.95) and line of best fit (black).

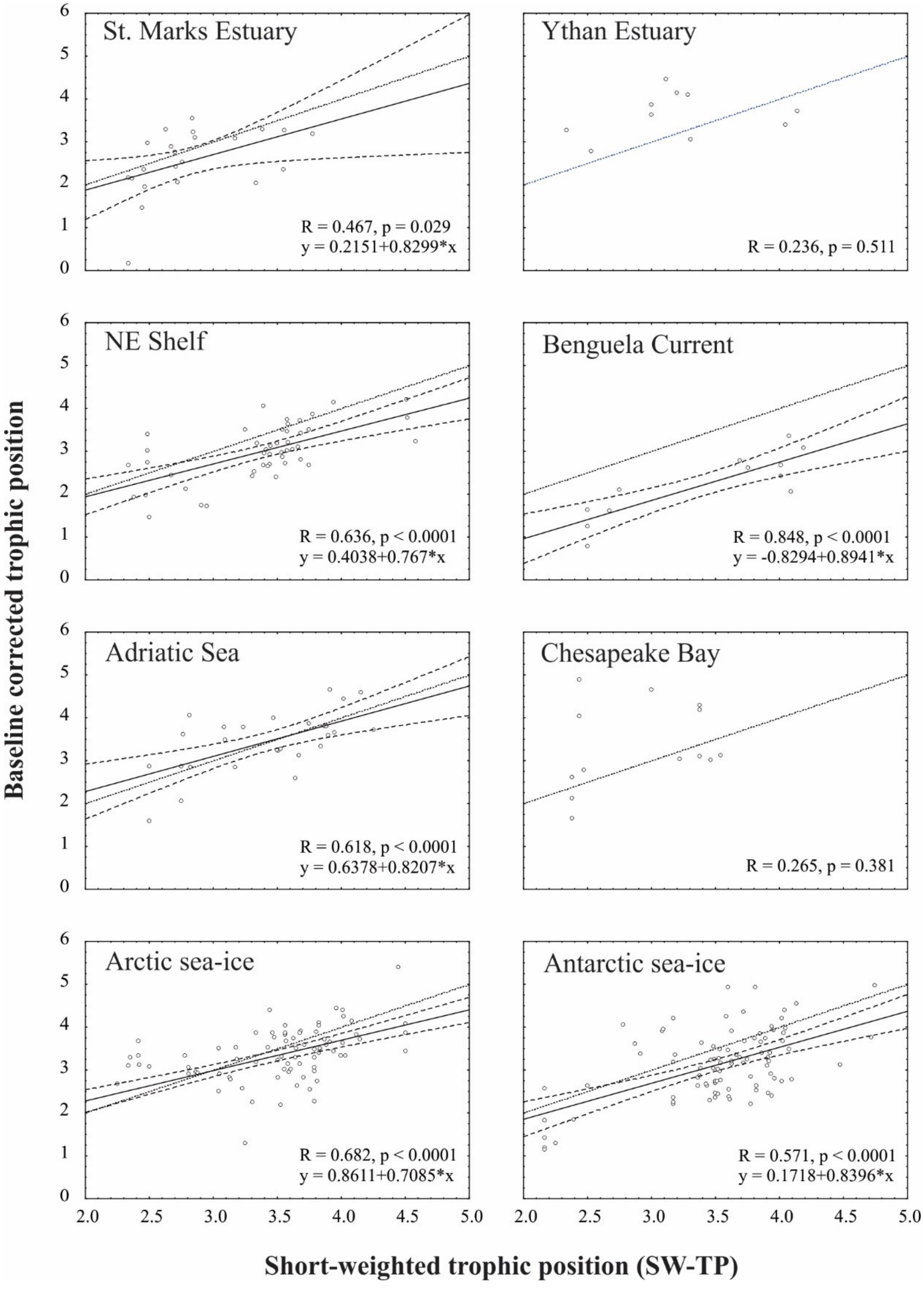


Figure A.4: Comparison of baseline corrected (BCTP) and binary estimates (SWTP) of trophic position for individual webs: St. Marks estuary, Ythan estuary, NE shelf, Benguela current, Adriatic sea, Chesapeake bay, Arctic sea-ice, and Antarctic sea-ice. Shown are the CI (± 0.95) and line of best fit (black)

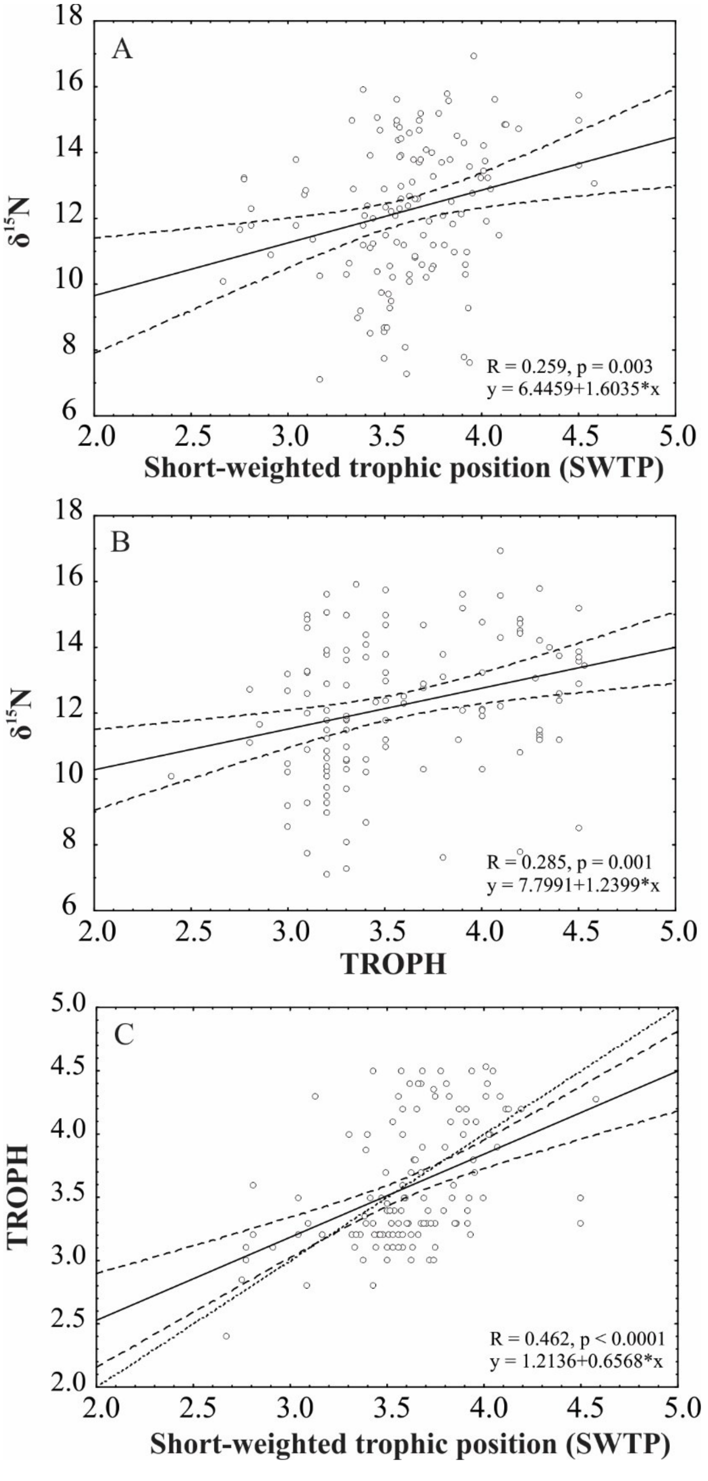


Figure A.5: Separate comparisons of flow-based and binary estimates of trophic position for each of the four webs used in this analyses. a) $\delta^{15}N$ values versus binary trophic position (SWTP), b) $\delta^{15}N$ values versus *TROPH* estimates from FishBase.org, c) relation between *TROPH* and binary trophic position estimates (SWTP). Shown are the CI (± 0.95) and line of best fit (black).

Appendices B Supplementary Materials

This information is available from Dalspace.

Supplement S1

Complete reference list for species diets for the Arctic and Antarctic sea-ice food webs used in Chapter 2.

Supplement S2

Trophic position database showing name of web, habitat type, taxa grouping, common and species name, prey-averaged TP, short-weighted TP, shortest chain length, $\delta^{15}N$ estimate, and baseline corrected $\delta^{15}N$ for species with TP>2, species used for baseline correction, and references.

Supplement S3

Species lists, species ID numbers, short-weighted trophic position, prey-averaged trophic position, mean stable isotope values, and baseline corrected trophic positions, for the Arctic and Antarctic used in Chapter 3.

Supplement S4

Complete reference list for species lists, species ID numbers, short-weighted trophic position, prey-averaged trophic position, mean stable isotope values, and baseline corrected trophic positions, for the Arctic and Antarctic used in Chapter 3

Appendices C Licenses

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