Faculty of Biosciences, Fisheries and Economy
Norwegian College of Fishery Science

Marine food-web structure and community patterns in high-latitude marine ecosystems

- ecological responses to warming

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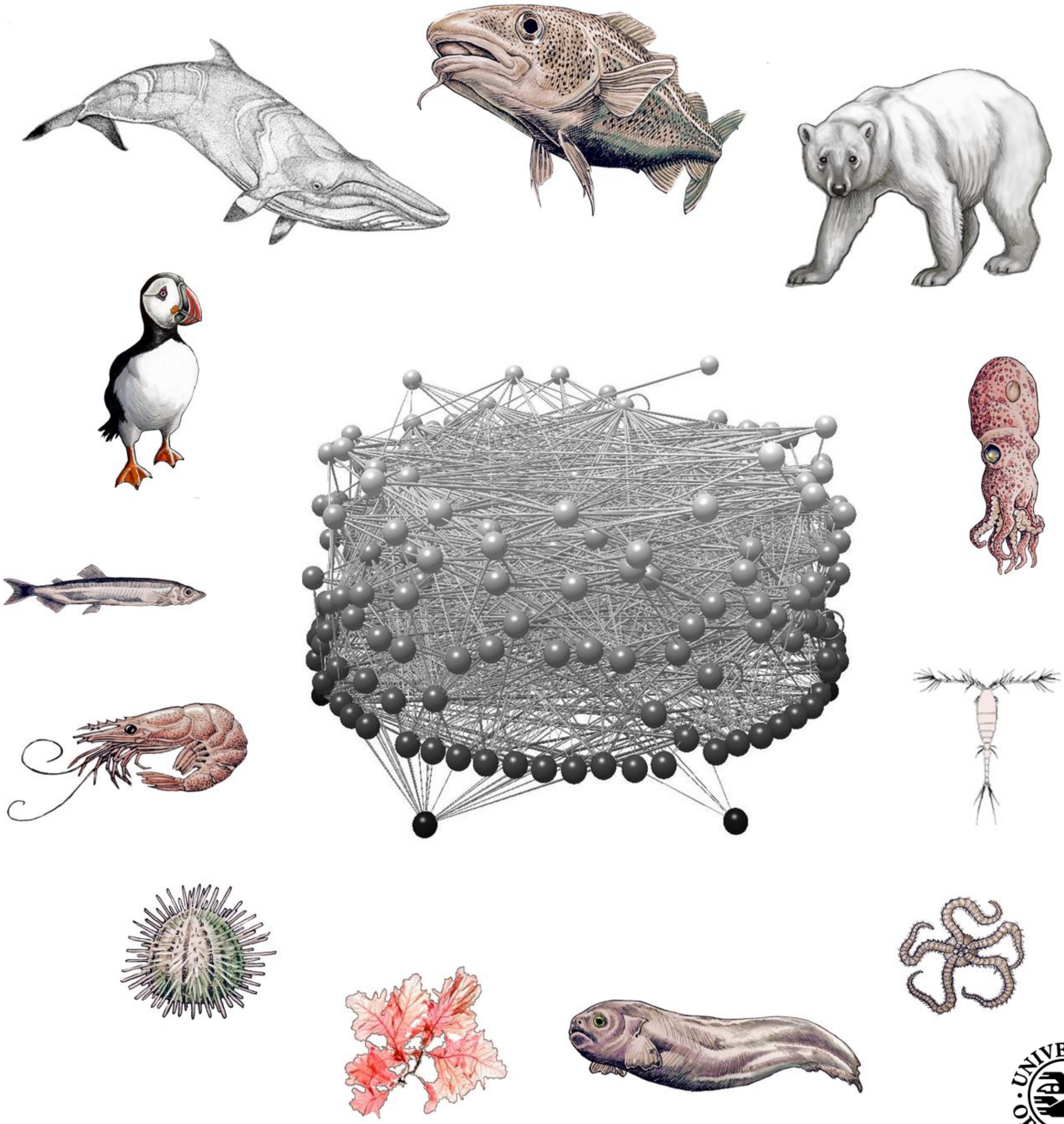
Susanne Kortsch

A dissertation for the degree of Philosophiae Doctor – April 2016



Front cover: Species drawings by Anna Laurine Kornum, except minke whale, copepod and red algae. The food web is illustrated in Network 3D.
Graphic design by Susanne Kortsch.

Marine food-web structure and community patterns in high-latitude marine ecosystems

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Thesis for the degree of Philosophiae Doctor

Tromsø, April 2016

UNIVERSITY OF TROMSØ

Supervisors

Prof. Michaela Aschan

Assoc. Prof. Raul Primicerio

The Norwegian College of Fishery Science
Faculty of Biosciences, Fisheries and Economics
UiT The Arctic University of Norway
Tromsø, Norway

For the love of the Ocean

The Temple of Nature

BY firm immutable immortal laws
Impress'd on Nature by the GREAT FIRST CAUSE,
Say, MUSE! how rose from elemental strife
Organic forms, and kindled into life;
How Love and Sympathy with potent charm
Warm the cold heart, the lifted hand disarm;
Allure with pleasures, and alarm with pains,
And bind Society in golden chains.

…

ORGANIC LIFE beneath the shoreless waves
Was born and nurs'd in Ocean's pearly caves;
First forms minute, unseen by spheric glass,
Move on the mud, or pierce the watery mass;
These, as successive generations bloom
New powers acquire, and larger limbs assume;
Whence countless groups of vegetation spring,
And breathing realms of fin, and feet, and wing.
…

Erasmus Darwin, 1802

Contents

List of papers

Paper 1 Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A.V., Aschan, M. (2015) Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists.
Proceedings of the Royal Society B, 282, 20151546

Paper 2 Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A.V., Planque, B. (Manuscript) Food-web structure changes along environmental gradients in a high-latitude marine ecosystem.
Intended for Global Ecology & Biogeography

Paper 3 Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P.E., Rodrigues, J., Lønne, O.J., Gulliksen, B. (2012) Climate-driven regime shifts in Arctic marine benthos.
Proceedings of the National Academy of Sciences, 109, 14052-14057

Appendix

Data paper

Planque, B., Primicerio, R., Michalsen, K., Aschan, M., Certain, G., Dalpadado, P., Gjøsæter, H., Hansen, C., Johannesen, E., Jørgensen L.L., Kolsum, I., Kortsch, S., Leclerc, L-M., Omli, L., Skern-Mauritzen, M., Wiedmann, M. (2014) Who eats whom in the Barents Sea: a food web topology from plankton to whales.
Ecological Archives E095–124, *Ecology* 95, 1430–1430

Co-author contributions

	Paper 1	**Paper 2**	**Paper 3**
Concept and ideas	**SK**, RP, MA, AVD	**SK**, RP, BP, MA	**SK**, RP, BG, FB
Study design and methods	**SK**, RP	**SK**, BP, RP	**SK**, RP, FB, BG
Data gathering	**SK**, MF, AVD, MA	**SK**, MA, AVD, SL	**SK**, BG, JR
Data analysis and interpretation	**SK**, RP	**SK**	**SK**, RP
Manuscript preparation and writing	**SK**, RP	**SK**	**SK**, RP
Inputs to the manuscript writing	**SK**, RP, MF, AVD, MA	**SK**, RP, BP, MA, AVD, SL	**SK**, RP, PER, FB, JR, OJL, BG

Name abbreviations of authors: Susanne Kortsch (SK), Raul Primicerio (RP), Michaela Aschan (MA), Benjamin Planque (BP), Andrey V. Dolgov (AVD), Maria Fossheim (MF), Sigrid Lind (SL), Frank Beuchel (FB), Paul E. Renaud (PER), João Rodrigues (JR), Ole-Jørgen Lønne (OJL), Bjørn Gulliksen (BG)

Summary

The rate and spatial scale at which we, technology-assisted humans, are altering the environment is unprecedented in history, causing major alterations and disruptions in ecosystem structure and function worldwide. Some of the most pronounced alterations are experienced in the Arctic, where temperatures have risen at twice the global rate and sea ice cover is declining rapidly due to climate warming. The Barents Sea, a bordering shelf sea of the Arctic Ocean, has experienced some of the most pronounced effects of climate warming within the Arctic, in particular along the marginal ice zone in the northeast, where sea ice is retracting fast and the open-water period is becoming prolonged. Climate-induced environmental alterations in habitats lead to distributional shifts of species, and to changes in productivity regimes and species abundance, which result in alterations in the structure and function of the ecosystem. While species-level responses to climate change are frequently reported, it remains a challenge to upscale these responses to structural changes at the community and ecosystem level. In this thesis, I use an empirical approach, combined with theoretical considerations, to study how structure changes along environmental and climatic gradients in the Barents Sea and how community structure changes as a response to climate warming.

In **Paper 1**, I characterized the structural differences of a warm-water, boreal, and cold-water, arctic, food web in the Barents Sea, and I evaluated the potential changes in arctic food-web structure due to poleward shifts of boreal fish. Together with colleagues from the Institute of Marine Research (Norway) and Knipovich Polar Research Institute of Marine Fisheries and Oceanography (Russia), I compiled a food web of who eats whom for the entire Barents Sea ecosystem. This information was used together with species distribution data to subsample regional food webs. The study revealed that the boreal Barents Sea food web is more connected and less modular than the arctic, and, in general, displays higher values of commonly reported metrics including loops. Food-web module analysis revealed that modules are associated with benthic and pelagic habitats and that cod and haddock are network connector hubs, linking strongly within and across food-web modules. Analysis of the average number of trophic interactions of the Barents Sea fish community revealed that a property of fish moving poleward is high generalism and that fish in the Arctic are more specialized in their diet. I compared the structure of the arctic food web with and without poleward-moving fish. Inclusion of boreal generalists increased the connectance and decreased the modularity in the arctic food web. As

food-web modules are associated with habitats, I hypothesized that the inclusion of these fish strengthens the couplings of energetic pathways between benthic and pelagic compartments with not only a potential for increased energy transfer, but also a potential for spread of perturbations across modules.

In **Paper 2,** I studied how food-web structure varies along environmental gradients in the Barents Sea. The analysis revealed that food webs within the Barents Sea display biogeographic regions with distinct food web characteristics. The five main food-web regions are: the Southwest (Boreal), the Northwest (Svalbard Archipelago), the Central Barents Sea (Mixed Water), the Southeast (Coastal), and the Northeast (Arctic). The main axis of spatial food-web variation (i.e. connectance and modularity) is associated with gradients in seawater temperature and sea ice coverage. The food webs within the Barents Sea with the most distinct food-web properties are the arctic food webs in the northeast. Another important dimension of food-web variation is associated with high environmental and topographic heterogeneity coinciding with high food-web complexity (i.e. high linkage density, high mean path length and high incidence of motif sub-structures) around Svalbard. The analysis of species participation in motifs revealed that generalist and pelagic fish are involved in looping structures i.e. mutual predation motifs and cannibalism. These structures are prevalent in the boreal food-web region but absent from the Arctic. This study contributes to further evidence that marine food-web structure is linked to broad-scale environmental gradients through environmental constraints on species traits, niche space and environmental filtering of species' spatial distributions.

In **Paper 3,** I studied the temporal development (1980–2010) in rocky-bottom community structure in Svalbard during a period of rapid warming and sea-ice decline. The study revealed an extensive and sudden shift in community structure in both fjords. The most striking component of the shift was a fivefold increase in macroalgal cover in Kongsfjord in 1995 and an eightfold increase in Smeerenburgfjord in 2000. Parallel changes in the abundance and composition of benthic invertebrates suggest that the benthic reorganization is community-wide. The abrupt nature of the community response, in particular the response of macroalgae, is indicative of an ecological regime shift and suggests that community responses to climate-driven effects can be abrupt, extensive and persistent. I hypothesized that the shifts was promoted by increased temperature and light availability changing the competitive abilities among macroalgae and calcareous algae, promoting positive feedback mechanisms that result in a regime shift. Novel interactions among macroalgae and invertebrates may have induced new feedbacks that may be responsible for maintaining the new macroalgae state.

Preface

Doing a PhD on food webs is much like entering the Amazon forest. "*Seen from the outside, the Amazonian forest seems like a mass of congealed bubbles, a vertical accumulation of green swellings; it is as if some pathological disorder had attacked the riverscape over its whole extent. But once you break through the surface-skin and go inside, everything changes: seen from within, the chaotic mass becomes a monumental universe.*" After a while, it feels like "*The forest ceases to be a terrestrial distemper; it could be taken for a new planetary world, as rich as our world, and replacing it. As soon as they eye becomes accustomed to recognizing the forest's various closely adjacent planes, and the mind had overcome its first impression of being overwhelmed, a complex system can be perceived.*" The quote is taken from a journey description by the structural anthropologist Claude Levi-Strauss when he was trekking in the Amazon in the 1930s (Levi-Strauss, 1955). My personal and scientific development during the four-year PhD process has been a bit similar to what Levi-Strauss describes. To begin with, I felt overwhelmed by the apparent disorder of the many species interactions in the Barents Sea food web, but, after a while, my mind started to recognize structure and patterns and I could slowly begin to perceive its complexity. Studying the relationships among species in front of a computer is a virtual and abstract affair, but it has been a great personal adventure and it has made me realize and appreciate even more the inter-connectedness of everything in life and nature.

Acknowledegments

This PhD project began in 2012 when I was thrown headfirst into the Barents Sea, without a life vest and any land in sight, to explore the relationships amongst the creatures living there. At times, it felt like I could have drowned in the waves of complexity of this vast Ocean, but I never gave up finding a rock or a *pattern* to hold onto. The truth is I never entered this virtual watery cosmos entirely on my own. There has been a bunch of people following me on my travel, saving me at times, when I needed a hand, a rest and some good advice. It is time to thank a few people without whom, I am not sure; I would have made this journey safely into land – not least, survived to tell this tale.

I am especially indebted to my two super-enthusiastic supervisors, Michaela Aschan and Raul Primicerio, who have bravely followed me all the way through this PhD process and who have stood by my side in times of joy, creativity and playfulness as well in times of frustration. I want to thank you both for your kindness, help, advices and your patience, and for sharing many memorable moments with me. Thank you for giving me the opportunity to do this PhD! Thanks also to the Troms Science Foundation for financial support. I want to thank Raul, in particular, for being an excellent and inspiring mentor in science; who was willing to share his knowledge and skills generously with me, and with other students, and not least for accepting me the way I am. Moreover - you did the almost impossible, you opened my eyes to ecology and even theoretical ecology, which was probably (out of ignorance) the last thing I dreamt about studying when I started out as a biology student. So thanks for that: Grazie mille! This PhD would not have been possible without you.

I am sincerely grateful to all my co-authors for collaboration, feedback and advice: Bjørn Gulliksen, Ole Jørgen Lønne, Frank Beuchel, Paul Renaud, João Rodrigues, Michaela Aschan, Raul Primicerio, Sigrid Lind, Maria Fossheim, Andrey Dolgov and Benjamin Planque. Many thanks to Benjamin for co-mentoring me during the last project of this thesis. I enjoyed and learned a lot from our conversations about marine biology and science in general. Thanks also to Ole Jørgen and Bjørn for being good supervisors during my master thesis. I want to acknowledge, Bjørn, in particular, for his endurance in collecting long-time series data in Svalbard long before most people were thinking about climate change in the Arctic. Your effort and passion for marine biology is truly inspiring and admirable – in times of rapid change, we could all learn from that; it takes time, patience and perseverance to collect good biological data. Essentially, it takes time to do good science!

This project would also not have been possible without the continuous support from the Institute of Marine Research (IMR, Norway) and the Polar Research Institute of Marine Fisheries and Oceanography (PINRO, Russia). I want to thank the IMR and PINRO for your joint effort to map the entire ecosystem and for your willingness to share the ecosystem data with me. There are many people working at the IMR here in Tromsø and in Bergen to whom I owe big thanks and admiration for their effort in processing the Barents Sea ecosystem data. Thanks to all the people working onboard the research vessels, collecting the data, classifying the species and weighing the organisms. Thanks for a wonderful ecosystem research cruise around Svalbard in 2012. The variety of organisms caught (app. 250 epibenthos and 75 fish) on this cruise was just amazing. I learned a lot about the diversity of the marine organisms in the Barents Sea during these two weeks. There are some people from IMR who deserve extra thanks and who have been instrumental for the completion of the food-web database and the species per polygon matrix, and hence for the completion of this PhD. Big thanks to: Padmini Dalpadado, Lis Lindal Jørgensen, Maria Fossheim, Edda Johannesen, Kathrine Michalsen, and Mette Skern-Mauritsen.

I want to thank the Santa Fe Institute (SFI) for accepting me to participate in the Complex Systems Science Summer School in 2013 and the University in Tromsø for supporting my travel to the US. The SFI is truly the perfect playground and meeting point for scientists from many different disciplines. Being a student at the SFI was fun, inspiring and deeply motivating. The stay at the SFI really boosted my admiration and fascination with complexity science and motivated me to develop my skills; I am deeply grateful. I want to thank Charles Novaes de Santana and Carlos Melián for inviting me to the Eawag Institute (Switzerland) and for many inspiring conversations about science during my one-week stay.

Finally, I want to thank my family and friends in Denmark (I miss you) and my good friends at work and outside work for continuous support. The list of *good friends* that deserve *special thanks* is so long that I stop by saying: You know who you are; I am deeply grateful to all of you for being there for me! I am looking forward to spend more time with you in good conversations, doing yoga, meditating, enjoying sauna and nature, watching movies, concerts and theatre, hiking and skiing. Finally, I want to thank my *Norwegian family* for saving me week after week with wonderful and funny Thursday dinners.

1. Introduction

Some scientist say that we are entering a new epoch described as the Anthropocene, in which human activities are increasingly re-shaping the Earth's ecosystems (Latour, 2014; Waters *et al.*, 2016). Overexploitation of natural resources and loss of habitats are among some of the most critical pressures pushing species to the brink of extinction and changing species distribution and abundance, which lead to alterations in ecosystem functioning (Ceballos *et al.*, 2015). This calls for appropriate management of natural resources. The realization that single species do not operate as isolated entities, but are linked to other species including humans in the ecosystem, has led to change in management perspectives. Ecosystem-based management, or the Ecosystem Approach to Management, including Integrated Ecosystem Assessment, has been adopted for many marine ecosystems worldwide, including the Barents Sea (Levin & Lubchenco, 2008; Levin *et al.*, 2009; Pitcher *et al.*, 2009; Anon, 2011). Integrated Ecosystem Assessment requires macroecological perspectives, which in turn require synthesis and integration of diverse biological and physical data. To inform decision and policy makers about ecosystem concerns, it is crucial to acquire appropriate and sufficient knowledge about how the ecosystem works: what its actual components are (i.e. the species) and how they interact with each other, and how they respond to perturbations from a changing environment. Such knowledge can then be coupled with social and economic thinking to construct the best possible policies to protect the environment, while sustainably exploiting it (Godfray & May, 2014).

Currently, the rate and spatial scale at which arctic marine ecosystems undergo structural changes are accelerating due to climate warming. Increasing seawater temperature and less sea ice modifies arctic marine habitats, with implications for the organisms living there. Recent meta-analyses indicate that species worldwide, including those in the Barents Sea, are moving towards the poles as a response to warmer seawater (Mueter *et al.*, 2009; Bates *et al.*, 2014; Fossheim *et al.*, 2015). The promptest responses to warming are altered migration patterns of opportunistic fish (Poloczanska *et al.*, 2013). Yet, knowledge about the impacts and implications of climate warming in marine systems is scarce compared to terrestrial systems (Rosenzweig *et al.*, 2008), in particular at the community and ecosystem level. Despite the difficulty in determining the outcome of species interactions, shifts in species distributions will inevitably change the structure of ecological communities. Novel interactions will establish, whereas former interactions may be lost. Since structure is closely linked to function, rewiring of food-web structure will necessarily have implications for food-web dynamics and overall ecosystem functioning.

Food webs are complex and composed of a myriad of species and their interactions, changing through space and time, and constantly developing and adapting. Owing to this complexity, species responses to environmental perturbations are complex too. The nature of these responses can be non-linear and unpredictable, involving indirect effects, positive and negative feedbacks, and regime shifts. This complexity renders future states of ecosystems hard to predict (Planque, 2016). However, observational studies documenting responses to climate warming in the Arctic are accumulating (Parmesan, 2006), but due to data constraints, these studies cannot document the nature of the response whether it is abrupt or gradual, nor how a response results in structural changes at the community or food-web level (Legagneux *et al.*, 2014). Despite the considerable interest in understanding how the structure of arctic marine communities and food webs changes as a response to increasing seawater temperature and rapid sea ice loss in the Arctic, few systematic long-term and few large-scale spatial studies in the marine Arctic have addressed these issues (Anderson & Piatt, 1999; Kortsch *et al.*, 2012; Kortsch *et al.*, 2015). Most evidence for regime shifts and community-wide shifts in the marine environments comes from lower latitudes (Hare & Mantua, 2000; Weijerman *et al.*, 2005; Hoegh-Guldberg *et al.*, 2007; Barceló *et al.*, 2015; Graham *et al.*, 2015). Nonetheless, empirical evidence for community-wide shifts in species abundance and distribution of high-latitude and arctic aquatic ecosystems has been accumulating for some time (Grebmeier *et al.*, 2006; Mueter & Litzow, 2008; Fossheim *et al.*, 2015), including evidence for abrupt regime shifts in arctic lakes and in subarctic rocky-bottom benthos (Smol *et al.*, 2005; Kortsch *et al.*, 2012).

2. Aim and scope of the thesis

In this PhD thesis, I characterize and explain patterns of marine community and food-web structure and elucidate how patterns in food-web structure and arctic marine communities vary with environmental and climate variability through space and time. I use ecological theory to explain the potential mechanisms that generate the observed empirical marine community and ecosystem patterns.

The aims of this thesis are:

1) First, to characterize the temporal and the spatial structure of arctic benthic communities and Barents Sea food webs – from the species level to the ecosystem level and from the local scale to the regional scale.

2) Second, to study how community and food-web structure changes along environmental gradients and how structure changes as a response to climate warming.

Although this thesis has elements of description, it has been my ambition to explain the empirical observations and findings in light of ecological theory in order to construct a solid framework for ecological interpretation. Further, I have strived to evaluate the potential implications of the ecological findings for ecosystem functioning. The thesis consists of three main papers and a data paper. **Papers 1 and 2** address how spatial food-web structure varies along environmental gradients and among biogeographic regions in the Barents Sea. It has been my ambition to address the mechanisms generating food-web patterns by combining the spatial analysis of food-web structure with analysis of species roles. **Papers 1 and 3** specifically address how climate warming may alter the structure of arctic marine communities and food webs. **Paper 1** addresses the spatio-temporal development in fish community structure across the entire Barents Sea during a period of rapid warming in the past decade since 2004, and **Paper 3** addresses the temporal development of structure in arctic hard-bottom benthic communities during a 30-year period of warming from 1980 to 2010.

3. Background

3.1 Patterns and structure in ecology

"*In any general discussion of structure, relating to an isolated part of the universe, we are faced with an initial difficulty in having no a priori criteria as to the amount of structure it is reasonable to expect. We do not, therefore, always know, until we have had a great deal of empirical experience, whether a given example of structure is very extraordinary, or a mere trivial expression of something, which we may learn to expect all the time. ...*
Our preliminary exploration thus suggests that the completely disordered is unimaginable and that the known consists of a collection of relationships between temporarily unknown entities. If we are going to say anything at all, some structure is certain to be involved, but, as has already been indicated, the amount of structure per unit volume cannot be guessed in advance."
(Hutchinson, 1953)

Patterns are structural regularities widely observed in nature. As Hutchinson (1953) points out, we do not always know exactly how much structure and which kind of structure to expect *a priori*, but it is certain that structure will be involved in our observations. In fact, without patterns and complex structures in ecology, there would be nothing to explain (Lawton, 1996). Patterns are the emergent phenomenon of underlying ecological processes. Patterns, instinctively, appeal to the eye and induce a desire to learn about the mechanisms that shape them. Formalizing, quantifying and understanding the relationships between patterns, processes and functions goes right to the heart of science. In ecology, specifically, a main goal is to understand the relationship between ecological and evolutionary processes and patterns in complex ecological communities, and how these relate to ecosystem functioning (Levin, 1992). Nevertheless, the mechanisms, processes and functions that shape complex community patterns are still poorly understood (Godfray & May, 2014). One obvious reason for this difficulty rests in the complexity of the issue. Ecological communities are made up of hundreds or thousands of species, and a multitude of interactions and different interaction types with many intrinsic feedbacks and indirect effects. On the planet, there are about 9 million species of which 2.2 million are marine (Mora *et al.*, 2011), and although not every species connects to every other, everything in the ecosystem is somehow connected. Faced with this complexity, it is understandable that no single model or equation can explain all these mechanisms and processes in the natural world at once. Although, it is well established that underlying principles govern the complex structures and patterns that we observe, it does not imply a single explanation for every pattern. Most patterns are probably best explained by several contributory mechanisms and processes (Lawton, 1996). The quest in ecology then becomes not so much to find a single correct answer to every pattern, but rather to find several explanations and determine their relative contribution. To understand the causes and implications of ecological patterns and to understand the phenomenon that promote the co-existence of millions of interacting species, it is important to find ways to quantify how ecological patterns vary through space and time (Levin, 1992).

3. 2 Food-web ecology

3.2.1 Species interactions and food webs as binary networks

Many ecological patterns in nature are brought about by biotic interactions among species (MacArthur, 1955). A plethora of different interaction types can be found in ecological communities e.g. predation, parasitism, competition and mutualism, all of which are important for ecosystem functioning and evolutionary processes (Wootton, 1994). Through species interactions, species affect each other, positively or negatively, depending on the type of interaction and the relative strength of these interactions. Species may also affect each other indirectly mediated via a third species (Wootton, 1994). Indirect effects may be stronger than direct effects and are common in interaction structures such as intraguild predation, exploitative competition, apparent competition, and indirect mutualism. Of course, species may engage in several interaction types, be predators, competitors and mutualists at the same time, and therefore all these interaction types work in concert to shape communities. However, the most common, tangible and important interaction in terms of energy transfer is the trophic interaction, i.e. who eats whom (e.g. predation and parasitism). The trophic relationships among species can be represented with binary food webs, in which nodes represent species and the links represent the trophic interaction among species (Figure 1). See Figure 1b-f for illustrations of in- and out-degree and of selected interaction types.

Although binary food webs have been described as a caricature of nature (Pimm, 1982), they have also been described as the *road maps through Darwin's famous entangled bank* (Box 1) (Pimm *et al.*, 1991). Generalities in the network structure of food webs can be calculated via graph theory and network analysis, also referred to as topology of food webs (Box 2). A whole range of structural food-web properties can be calculated. The most basic topological properties are: the number of species, links per species and connectance i.e. the number of realized interactions out of all possible, but also properties such as path length, trophic level, number of basal species, number of top species, number of intermediate species, clustering and modularity are commonly reported metrics in food webs.

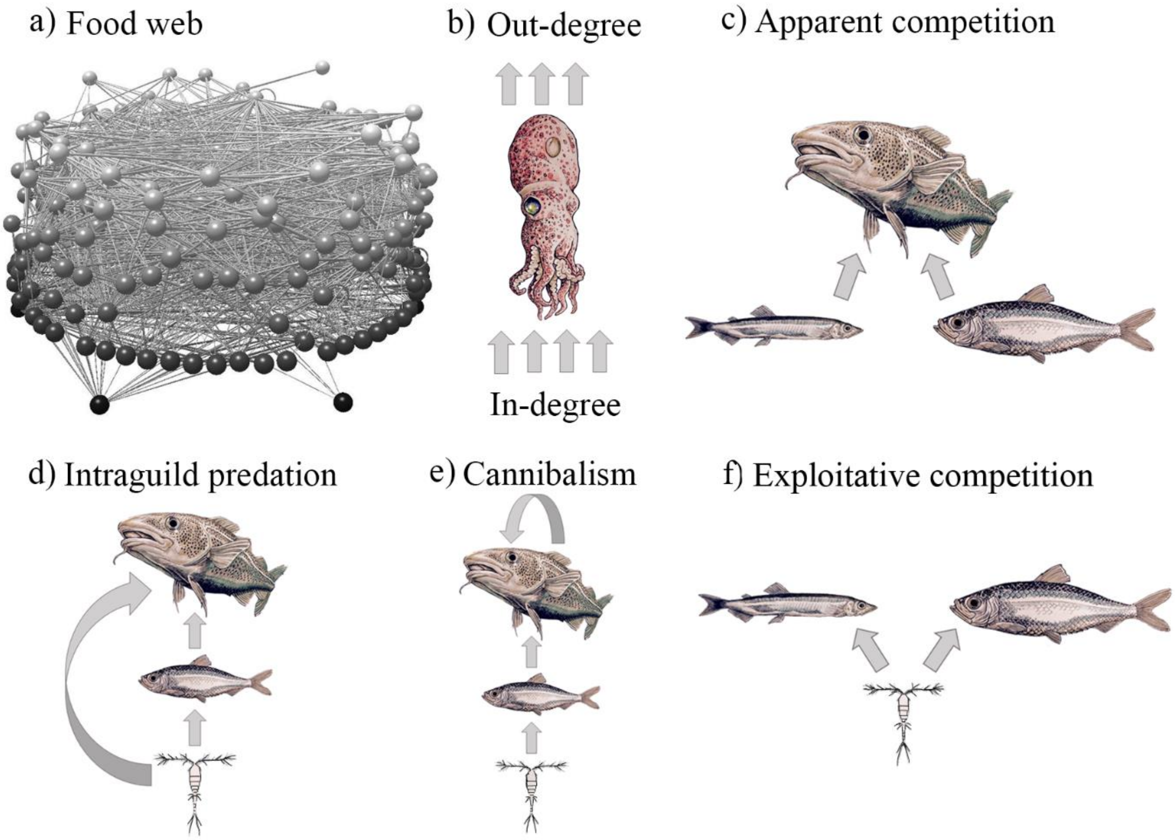
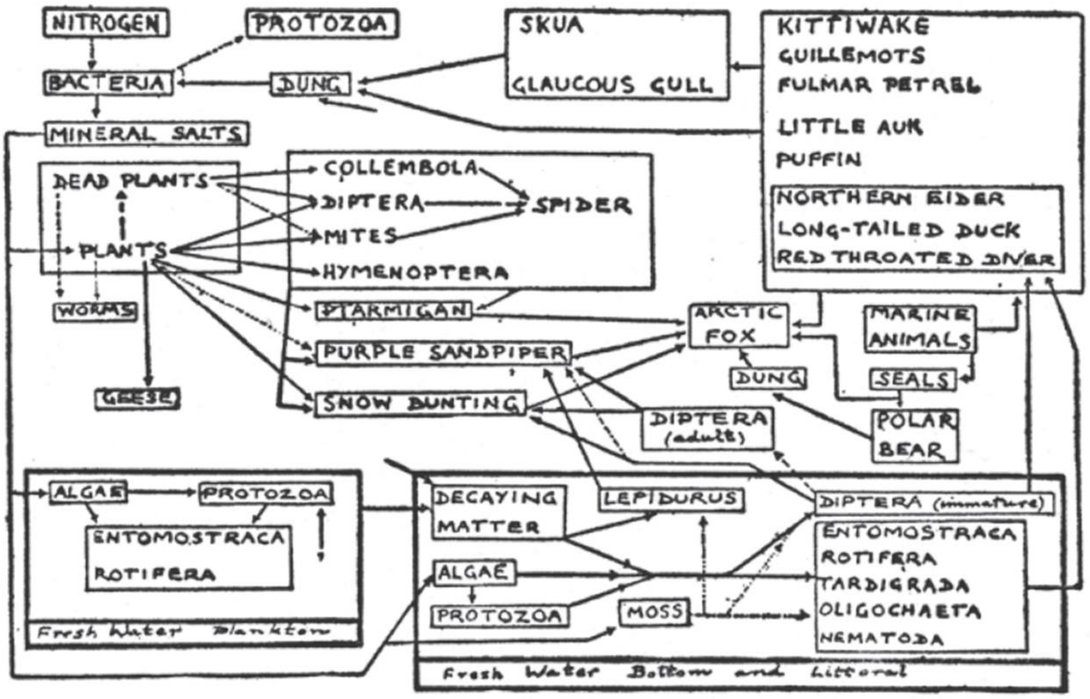


Figure 1. Schematic description of a binary food web and common interaction types. a) example of a binary food web, where the nodes represent the trophospecies and the links the trophic interaction, b) the trophic structure of a species is characterized by its in-degree i.e. its prey and its out-degree, i.e. its predators, c) apparent competition motif or shared predator, d) intraguild predation motif, e) cannibalism = self-loop, f) exploitative competition motif = shared resource. The food web was visualized in the Network3D software (Williams, 2010). The species drawings were made by Anna Laurine Kornum.

The debate about whether food webs display universal properties, or are context-dependent, is not resolved, one reason being that compilation and aggregation of species in food webs differ. However, once variability in compilation, diversity and connectance are taken into account, there seems to be at least coarse-grained imprints of universal patterns in food webs (Dunne, 2006). For example, a seemingly universal property in food webs is the relatively short mean path length i.e. taxa are on average two trophic links apart, indicating that species are relatively close neighbours (Williams *et al.*, 2002).

Box 1: Brief historical account of food-web ecology

The Bear Island food web, Barents Sea



Summerhays & Elton, 1923

Figure 2. Early version of a Barents Sea food web, and one of the first relatively detailed schematic representations of a food web ever to be depicted is of Bear Island by Summerhays and Elton in 1923. Bear Island is located at the western edge of the Barents Sea, between Norway and Svalbard. Elton called this food web a food cycle, and Bear Island a barren spot in the Arctic zone, south of Spitsbergen (Summerhayes & Elton, 1923).

Already in 1859, Darwin pointed out that: *"… plants and animals, most remote in scale of nature are bound together by a web of complex relations."* One of the first representations ever to depict the web of complex relations is the iconic Bear Island "food cycle" by Summerhays and Elton in 1923 (Figure 2) (Summerhayes & Elton, 1923). Bear Island is located at the westernmost edge of the Barents Sea. The food web was compiled by the famous ecologist Charles Elton and colleagues on a polar expedition to the Arctic, more precisely on their way to Spitsbergen, which is the largest island in the Svalbard archipelago (Southwood & Clarke, 1999). Thus, it happened that one of the first food webs ever to be illustrated comes from the Barents Sea. According to food web ecologist Jennifer Dunne, the Bear Island food web belongs to first-generation food webs (Figure 2). It is simple compared to contemporary food webs, but it is a pioneering study in food-web ecology. It represents the biological system as a complex system, i.e. a system of interacting components, and it emphasizes trophic relationships among species as a central organizing principle in nature. Elton was the first to use the term food chain, although Elton called his representation of connected food chains, a food cycle; his work led to the development of the concept of the food web (Pascual & Dunne, 2006).

Food webs are central topics of contemporary community ecology, but it was not until the late 1970s that the search for regularities in the network structure of food webs began (Pascual & Dunne, 2006). In 1978, Joel Cohen published the first collection of 30 binary (presence/absence) empirical food webs, transforming food-web ecology from the natural history of species to a quantitative science (Cohen, 1978). Cohen noticed that most food webs are interval and that the ratio of prey to predator (~ 3/4) is independent of the total number of trophospecies in the food web. In the beginning of the 1990s, Polis and Martinez took food web science to another level by publishing empirical food webs with even more detail (Martinez, 1991; Polis, 1991). These food webs belong to second-generation food webs. They are more detailed than first-generation food webs, but still lack some realism with respect to species resolution. Nonetheless, these food webs display regularities in their degree distributions, trophic structure, and mean path length (Williams *et al.*, 2002).

Contemporary food webs are becoming ever more detailed in the resolution of species and their interactions and belong to the third-generation (Figure 3). For instance, the Weddell Sea food web includes as many as 500 species and 16000 links (Box 2). Recently, fourth-generation food webs started to appear in the literature (Kortsch *et al.*, 2015; Wood *et al.*, 2015; Gilarranz *et al.*, 2016). These food webs are taking food-web research a step even further by also considering the spatial and temporal aspect of empirical food-web structure. The Barents Sea food webs, presented in this thesis in Papers 1 and 2, belong to fourth-generation webs. These food webs are highly resolved in terms of species and links and they show how food-web structure varies across an entire ecosystem. With increased resolution in species and their interactions combined with an accelerating development in theoretical food web ecology, food-web research is currently entering a golden age. A bibliographic analysis reveals an exponential growth in food-web studies since the 1970s (Ings *et al.*, 2009).

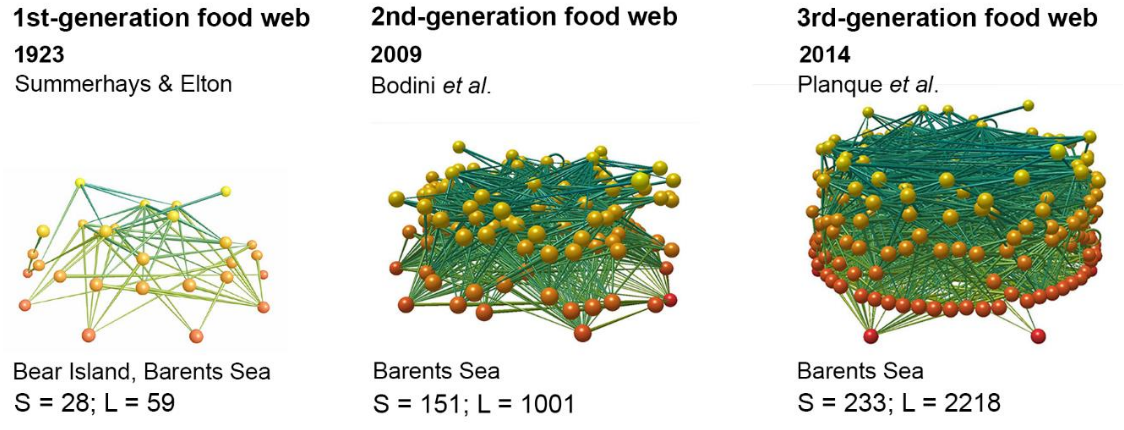


Figure 3. Development in the resolution of food webs in the Barents Sea from the earliest food webs to the current food webs presented in this PhD thesis. According to food-web ecologist Jennifer Dunne, food webs can be classified into first-, second- and third-generation food webs. The simple Bear Island food web from 1923 belongs to first-generation food webs. Food webs appearing in the beginning of the 1990s belong to second-generation food webs. The Bodini *et al*. (2009) Barents Sea food web also belongs to second-generation food webs. Contemporary food webs such as Planque *et al*. (2014) Barents Sea food web are highly resolved and belong to third-generation food webs. The spatial Barents Sea food webs presented in this study might even be called fourth-generation food webs due to the high spatial and taxonomic resolution**.**

The degree distribution of most food webs is either exponential or scale-free, and common to food webs is that a few species have many trophic interactions, while most species have few interactions (Dunne *et al.*, 2002b). The degree is a network analytical term of a species' total number of interactions. The degree distribution can be split into out-degree (Figure 1b), i.e. the generality distribution, or in-degree (Figure 1b), i.e. the vulnerability distribution, and informs about how specialized species are in a food web on average. Food webs are modular. Modularity refers to the existence of subgroups of species interacting more with each other than with other subgroups, and two marine studies have shown that food-web modules are associated with different marine habitats (Rezende *et al.*, 2009; Kortsch *et al.*, 2015). Modularity is believed to be of particular importance for the robustness and persistence of food webs as it may determine the degree to which perturbations will propagate through the food web or be retained within a module. Theoretically, perturbations will propagate faster within modules than between modules (Krause *et al.*, 2003), acting as buffer to perturbations at the level of the entire food web, and thereby promoting food-web persistence (Stouffer & Bascompte, 2011).

3.2.2 Food-web structure, dynamics and function

"*Why is network anatomy so important to characterize? ... Because structure always affects function*." (Strogatz, 2001).

Food-web patterns have implications for food-web dynamics and function, and vice versa (Bengtsson & Martinez, 1996). There is a reciprocal relationship between community and food web structure and function (Thompson *et al.*, 2012). For example, the behaviour and stability of ecological communities depend on the topology of the food web, influencing the transfer of energy and the spread of perturbations, and in turn, these dynamic features influence community structure (MacArthur, 1955; May, 1972; Paine, 1980). The traditional view held in ecology stated that (MacArthur, 1955; Elton, 1958), the more species in a community, the more stable the community. However, mathematical models showed that larger and more inter-connected communities were less stable (May, 1972). This finding clashed with the traditional view and spurred the famous *diversity begets stability debate*. May's mathematical food-web models were performed on random matrices, but species interactions and, hence, food-web structure in nature are far from random (Allesina *et al.*, 2015). The crucial point is that some non-random structures in the architecture of food webs allow species to co-exist and food webs to persist. Examples of non-random patterns in food webs are the degree distribution, modularity, path length, number of trophic levels and motif structures, i.e. submodule configurations. Explanations for recurrent patterns in food webs have successfully been related to constraints in energy flow, trophic level and species' body size (Williams & Martinez, 2000; Brose *et al.*, 2006; Eklöf *et al.*, 2013). Recent work has highlighted the role of trophic coherence, which measures how accurately species fall into distinct trophic levels, in stabilizing complex and large food webs (Johnson *et al.*, 2014). Trophic coherence can explain why food webs, at least mathematically, despite being species-rich and complex, could be stable after all. Measures such as trophic coherence, modularity, motifs and several other features highlight how important structure is for function, and how important it is to figure out which topological features specifically, unknown until known, provide food webs with their stability and persistence. Despite intensive pursuits to explain, both theoretically and empirically, the diversity–stability relationship, a general accepted theory for what promotes species co-existence and stability of species in food webs is still lacking. Once again, the difficulty in explaining the stability of food webs rests in the complexity of the many species interactions and interaction types, which yields a countless number of parameters, making it hard to calculate and simulate the system with sufficient generality to propose a general theory (Haerter *et al.*, 2016).

3.2.3 Hubs, keystone species and ecosystem engineers

Species play different ecological, structural and functional roles in a food web. It is obvious that species at the base, i.e. primary producers, and at the top, i.e. top predators, play different roles with respect to energy transfer and food-web regulation. However, it is more intricate to determine exactly how species link to other species across the network, what their distinct roles are with respect to predator–prey interactions and competition. Network analysis can help to elucidate the more intricate roles that species embedded in large food webs play. In a network perspective, a species' role is a direct result of its position in the food-web network, its interaction with neighbouring species and their interactions (Kortsch *et al.*, 2015). In addition, the strength of these interactions is important for energy transfer and stability (Paine, 1966). Species with high structural impact may be called hubs, keystone species and ecosystem engineers. A hub is a network term and describes a species with many trophic interactions across the network. If a hub connects species highly across and within a module, it may be called a network connector hub (Guimera & Amaral, 2005; Kortsch *et al.*, 2015). In ecological terms, such species are generalists or super-generalists. These species may also be keystone species, but need not be, as keystone species do not necessarily need to have many trophic interactions to have a great structural impact. Keystone species play a disproportionately large role in keeping other species in check via predation or herbivory (Paine, 1966). To determine whether a species is really a keystone species in a food-web, it is essential to have information on the strength of its interactions with other species (Berlow *et al.*, 2004), as keystone predation has a disproportionately large impact on species abundance in a community which may promote a range of indirect effects. Keystone species and hubs are often positioned at higher trophic levels. Ecosystem engineers, in contrary, are often positioned at the base of the food web. Species such as macroalgae and trees can play a role as ecosystem engineers or foundation species, lending secondary structural support to other species, thereby facilitating the existence of other species e.g. epifauna or epiphytes which creates novel interactions and novel energetic pathways through which energy may flow. What hubs, keystone species and ecosystem engineers have in common is their important role as community-structuring organisms. If such species suddenly become more abundant or less abundant, the entire community structure may alter. Sometimes changes in abundance may even lead to regime shifts (Kortsch *et al.*, 2015). Owing to their structural importance, they also play an important functional role in the ecosystem, and their presence or absence may change ecosystem functioning substantially in terms of diversification and alteration of energetic pathways and the strength of these.

3.2.4 Motifs – substructures linking species roles to food-web structure

Motifs are recurrent functional substructures and patterns embedded in food-web networks (Figure 4 a&b). A motif substructure can take any number of nodes, but the most common motifs represented in food-web research are tri-trophic motifs i.e. substructures with three species' interactions (Figure 4b). Analyses of tri-trophic motifs provide an opportunity to link the trophic structure of individual species to food-web dynamics and to food-web structure (Stouffer, 2010; Stouffer *et al.*, 2012; Borrelli, 2015). In total, 13 possible and unique configurations of tri-trophic motif exist, of which the tri-trophic food chain (s1) is the most basic (Figure 4b). Other common and ecologically relevant food-web motifs are the intraguild predation (s2), the exploitative competition (s4) and the apparent competition (s5) motifs

(Figure 5b). Loops (s3) and several of the motifs containing mutual predation are often underrepresented when compared to permuted null-model networks. Motifs represent various interaction types in the food web e.g., competition for resources. Some of these interaction types, the intraguild predation motif and apparent competition motif, can also promote a range of indirect and cascading effects (Polis *et al.*, 1989; Wootton, 1994). Motifs with double links, i.e. mutual predation, are most common among stage-structured population such as fish that undergo ontogenetic niche shift (Stouffer *et al.*, 2007; Kortsch *et al.*, Paper 2 of this thesis). This type of structure may promote alternative equilibria and positive feedbacks, features that can potentially lead to regime shifts. Species also play different roles with respect to motif participation, and species with a high degree, i.e. many trophic interactions, will also participate in many motifs and may thus have a large impact on food-web dynamics and function (Stouffer *et al.*, 2012; Kortsch *et al.*, Paper 2 of this thesis).

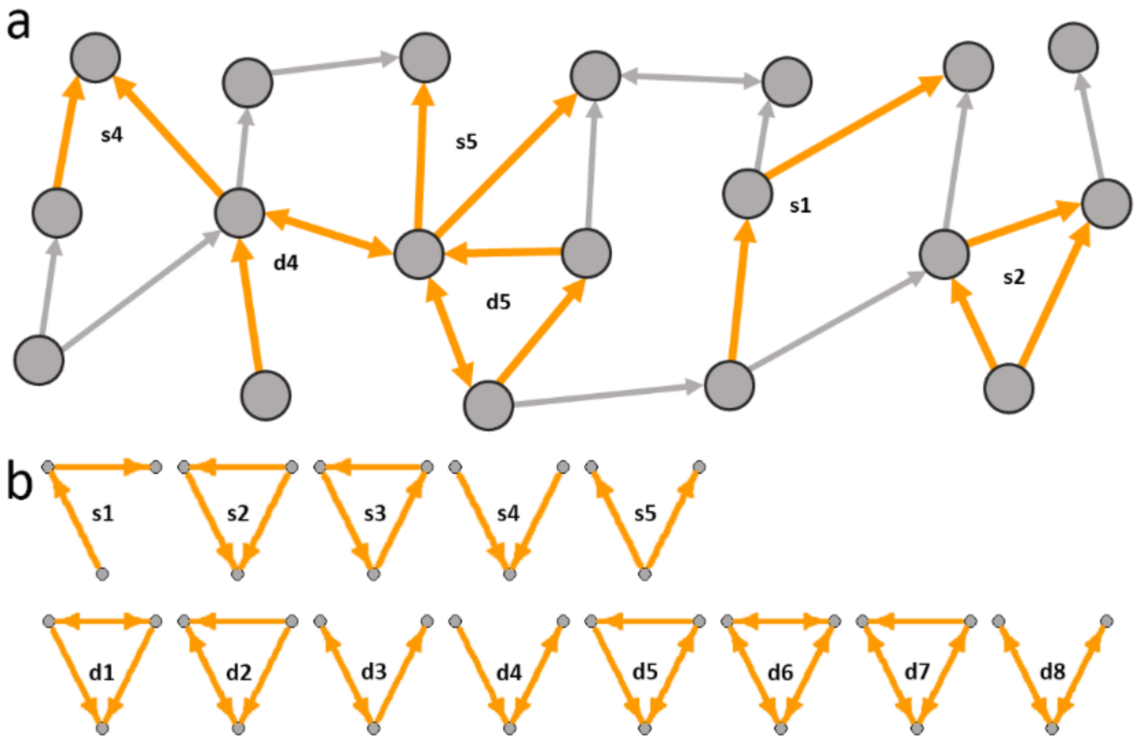


Figure 4. a) Illustration of tri-trophic motifs, i.e. submodules, embedded in the food-web network. Nodes (circles) represent species and edges (links) the trophic interaction. b) Only 13 unique tri-trophic motif configurations are possible. Apart from s3, the loop motif, which is rare, the single link motifs (s1 to s5) are the most common tri-trophic motif substructures in food webs. In particular, s1 = the chain motif; s2 = the intraguild predation motif; s4 = the exploitative competition motif (shared resource); and s5 = the apparent competition motif (shared predator). Double (d1 to d8) link motifs, i.e. motifs containing mutual predation, are often underrepresented in food webs when compared to null model outputs, apart from the d 1, d2 and d7 motifs that are overrepresented (Stouffer, 2010).

Box 2: Topology of marine food webs

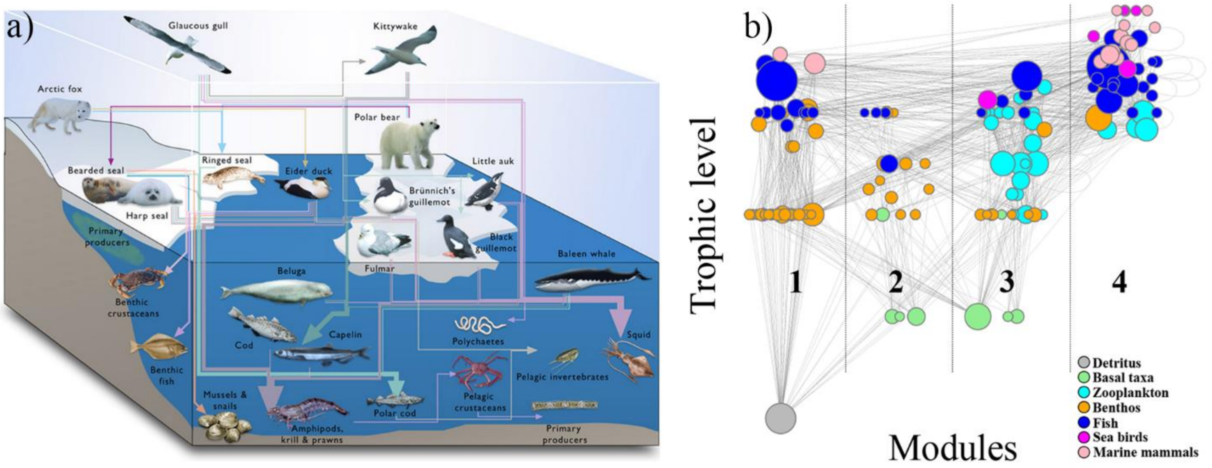


Figure 5. a) Simplified arctic Barents Sea food web and dominant pathways, the figure is adapted from the Arctic Climate Impact Assessment (ACIA, 2004). b) Representation of a complex arctic Barents Sea food web adapted from Kortsch *et al*. (2015).

Table 1. Comparison of structural properties among marine food webs. The Barents Sea, in the first column, is the food web compiled during this PhD project.

	Barents Sea	Southern Ocean	Weddell Sea Shelf	Caribbean large	Caribbean small	NE US Shelf	Benguela
No. of species	233	586	492	247	50	80	29
No. of links	2218	3989	16136	3196	535	1454	177
Link density	9.49	6.81	33.1	12.94	10.7	18.2	6.1
Connectance	0.04	0.01	0.07	0.05	0.21	0.22	0.21
Clustering	0.22	0.19	0.26	0.16	0.57	0.58	0.52
Modularity	0.27	0.46	0.33	0.24	0.18	0.13	0.13
FracOmni	0.69	0.40	0.87	0.87	0.84	0.95	0.68
LevelOmni	0.52	1.86	1.77	0.74	1.09	0.83	0.78
PredPrey	1.04	0.60	1.07	0.98	0.96	1.00	1.08
FracCannibals	0.11	0.04	0.04	0.04	0.42	0.31	0.21
FracBasal	0.03	0.54	0.07	0.02	0.04	0.04	0.07
FracTop	0.06	0.23	0.14	0.00	0.00	0.04	0.14
FracIntermediate	0.91	0.23	0.79	0.98	0.96	0.92	0.79
GeneralitySD	1.40	1.67	0.84	1.94	0.93	0.73	0.84
VulnerabilitySD	1.32	2.67	1.37	1.22	0.63	0.92	0.83
meanTL	3.16	2.81	7.01	3.67	3.92	2.9	3.7
meanPath	2.17	3.25	2.04	1.93	1.57	1.55	1.6
Reference	Planque 2014	Raymond 2011	Jacob 2005	Optiz 1996	Optiz 1996	Link 2002	Yodzis 1998

Food webs are becoming ever more detailed (Figure 5). Some of the most highly resolved food webs are marine. The Southern Ocean and the Weddell Sea food webs are the most resolved, with around 500 species and up to 16000 links. Table 1 shows that marine food webs vary in size and that food-web structure varies with scale (Riede *et al.*, 2010). For example, small webs are more clustered than larger ones. The number of links increases with the number of species (Riede *et al.*, 2010). Mean path length, which is a relatively conserved property in food webs, ranges from approximately 1.5 to 3 among these marine webs, which means species are 1 to 3 links apart. What distinguishes the Southern Ocean food web from the other marine food webs in Table 1 is that 50% of the species are contained at the base of the food web, whereas high numbers of intermediate species characterize most marine food webs. Most food webs are biased towards higher trophic levels. The Southern Ocean case illustrates well that comparing food webs across systems without considering how they were compiled, i.e. which selection criteria were used to select the species and their interactions, can be tricky because food webs display different degree of bias towards certain group of species or different aggregation level. Yet, many food-web studies compare food webs across systems without considering this aspect thoroughly. Early criticism of food-web studies even went as far as to say that differences between food webs reflected differences in the investigators' cultures and minds (May, 1983). However, food webs are getting ever more resolved, thus cultural differences and biases might be less of a problem in contemporary webs; but, still, most food webs contain a certain degree of bias that should be taken into account when comparing and interpreting empirical food webs across systems. The selection criteria of species and their interaction for the Barents Sea foods presented in this thesis are thoroughly described in the Planque *et al*. 2014 database paper in the appendix of this thesis. The strength of the food-web comparisons in Papers 1 and 2 of this thesis is that aggregation and compilation are identical among the food webs; therefore, differences in structure should be attributed to differences in species composition and link configuration among the Barents Sea regions.

3.2.5 Biogeography of species food-web networks

Evolutionary (e.g. selection and drift) and ecological processes (e.g. migration and dispersal) manifest as distinct macroecological and biogeographical patterns at large spatial scales (Brown, 1995). It is well established that diversity and species distributions vary along environmental gradients but it is uncertain how and why. One of the most fundamental broad-scale patterns concerning life on earth is the increase in diversity from the poles to the equator (i.e. along latitude); however, diversity within latitudinal bands also varies across altitude and depth, may depend on island size or archipelago structure, and is affected by the degree of isolation, habitat heterogeneity and productivity regime (Gaston, 2000). Owing to these features, some local biogeographic regions embedded within larger regions constitute biodiversity hotspots (high diversity) and others coldspots (low diversity). Whereas diversity patterns and their predictors are relatively well-established in terrestrial systems, well-documented global biodiversity patterns in marine systems are scarce and still under debate.

Recently, a study showed that although latitudinal gradients in marine diversity are not clear-cut among all groups of taxa and phyla, temperature is the environmental predictor most significantly related to marine diversity, in particular in coastal systems and for fish, which was the group of taxa driving most of the diversity patterns in this study (Tittensor *et al.*, 2010). The highest coastal marine diversity was found around the islands in Southeast Asia close to the equator. Tittensor *et al.* (2010) hypothesized that higher temperature (i.e. higher kinetic energy) increase metabolic rates that, in turn, increase speciation rates and hence result in higher diversity. Recently, a study showed that temperature, out of 45-candidate variables, was the dominant predictor of trophic dynamics in northern-hemisphere marine systems (Boyce *et al.*, 2015b). Temperature patterns were correlated with the average phytoplankton size and the degree of omnivory – features that may induce a range of direct and indirect effects on trophic dynamics and bottom-up versus top-down control (Boyce *et al.*, 2015b). Both of the above studies concluded that, based on their findings, changes in ocean temperature may have strong consequences for distributions of marine species and trophic dynamics in marine systems (Tittensor *et al.*, 2010; Boyce *et al.*, 2015b). Whereas temperature seems to be one of the most important drivers predicting large-scale distributions and diversity patterns of marine organisms worldwide, it is less clear how the structure of species interactions varies across environmental and climatic marine gradients through space and time. Out of data scarcity, few studies following interacting species through space and time have managed to integrate network theory and biogeography; however, this field of study is growing and new papers are published frequently (Baiser *et al.*, 2012; Baiser *et al.*, 2015; Cirtwill *et al.*, 2015; Morris *et al.*, 2015; Trøjelsgaard *et al.*, 2015; Hattab *et al.*, 2016; Kortsch *et al*., Paper 2 of this thesis). Integrating network theory, biogeography and metacommunity ecology combined with functional trait information of species may be a promising step towards addressing and answering fundamental ecological questions related to how evolutionary and ecological processes together shape ecological community patterns.

3.3 Climate warming and ecological responses

3.3.1 Community-wide regime shifts

Ecosystem responses to perturbations and climate change can be unpredictable and come as surprises. If shifts in community structure are abrupt, extensive and persistent, the behaviour of the shift may be indicative of a regime shift and of the existence of alternative stable states

(Scheffer *et al.*, 2001). A regime is characterized by its own set of governing processes, species composition and relationships among species, i.e. interaction types. The concept of alternative stable states can be illustrated with the analogy of ball-and-cup landscape (Figure 6). The most well-known and alluring examples of regime shifts in marine systems occur in coastal systems such as coral reefs and kelp forests. It has been frequently reported that coral reefs become overgrown by macroalgae due to increased nutrients inputs and overfishing of herbivore fish, favouring macroalgal growth over corals. The existence of regime shifts is closely linked to altered positive feedback loops and loss of resilience (Figure 6). The trophic interaction between fish and macroalgae, and the commensalistic interaction between fish and corals, keeps the coral reef in a "healthy" regime. However, when overfishing pushes herbivore fish to the verge of local extinction, redundancy of the grazer function decreases (i.e. less species performing the grazer role), and, like rivets popping out of the wings of an airplane, the coral regime loses resilience.

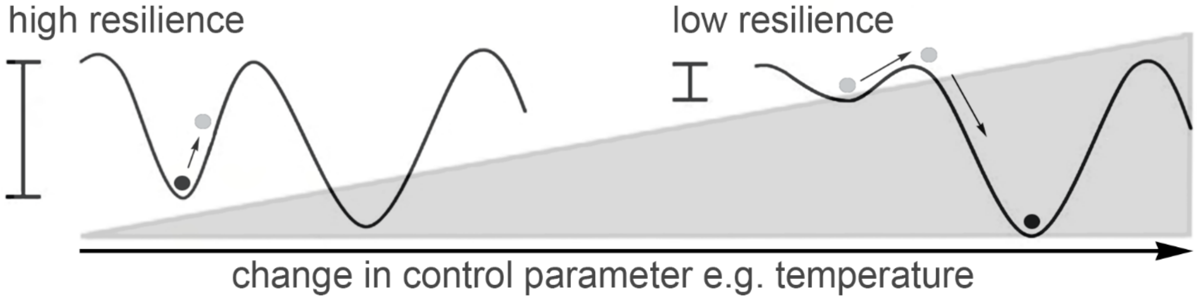


Figure 6. The concept of a regime shift can be illustrated with the analogy of a cup-and-ball landscape. The landscape represents a collection of possible states of the system. The black ball represents the current state and position of the system, while the cup represents the basin of attraction. The resilience of the system refers to the size of the basin of attraction, i.e. the size of the cup, and represents how much perturbation the system can absorb without changing its structure and function. Changes in climate or overfishing may modify the shape of the basin of attraction, i.e. change the resilience of the system. The basin of attraction may shrink, losing resilience. Further perturbations or shifts in control parameters, e.g. temperature or light, may then cause the ball, i.e. the system, to move away from its equilibrium. Because of a shallow basin of attraction, i.e. little resilience, the ball easily moves out of its equilibrium and into a new state. This phenomenon is called a regime shift.

At a given threshold, when the grazing function is sufficiently repressed, the regime switches from coral-dominated to macroalgae-dominated inducing new internal feedbacks, interactions and processes. Recently, further evidence for climate-driven regime shifts in coral reefs due to bleaching has been provided (Graham *et al.*, 2015). Other examples of regime shifts in marine systems come from major shifts in fish communities and from marine systems where cod is a dominant structuring species (Hare & Mantua, 2000; Frank *et al.*, 2005; Weijerman *et al.*, 2005). Although regime shift may occur in distinct systems, a commonality between the systems, and a key ingredient in all the regime shifts are alterations in positive feedback loops.

3.3.2 Ecological responses to climate warming

A key question in arctic ecology is how climate change will affect biological community structure. The past decade's climate warming has accelerated with greatest changes recorded in the Arctic. Temperatures have risen at twice the global rate and sea ice has declined by 30% (Figures 7a and 7b) (Hansen *et al.*, 2006; Comiso *et al.*, 2008; Comiso, 2012), resulting in a retraction of the marginal ice zone with consequences for the whole ecosystem (Carmack *et al.*, 2015). Changes in habitat characteristics may induce substantial food-web reorganizations via regional gains and losses of species, altering interactions among species and community structure. Recently, poleward movements of boreal species and substantial shifts in species distributions have been documented in the Arctic and in the Barents Sea (Mueter & Litzow, 2008; Fossheim *et al.*, 2015). Although much work has focused on the single-species responses to changes in abiotic factors, e.g. temperature, more recent work shows that the outcome of biotic interactions is important for determining the ecological responses to climate change, in particular at higher organizational levels such as the community level (Gilman *et al.*, 2010; Brose *et al.*, 2012; Post, 2013). Linkages among species may either buffer or amplify effects from climate change (Figure 8) (Urban *et al.*, 2011). Due to the complexity in the outcome of species interactions, it is hard to predict exactly how species' abundance and distribution will change over time. Will communities absorb or strengthen perturbations induced by climate change through negative or positive feedback loops, or will regime shifts occur? Despite considerable effort to explain and predict community responses to perturbations, the functions controlling the mechanisms are still poorly understood, not least because the very same functions and parameters used to model these responses are undergoing changes due to evolutionary processes (Godfray & May, 2014). For this reason, observational long-term studies tracking species' interactions through time and space may prove more valuable than ever. However, only a few systematic long-term time series exist for systems in the Arctic (Forchhammer *et al.*, 2002; Meltofte *et al.*, 2008; Wassmann *et al.*, 2011), of which the two benthic time series presented in this study are among the few marine examples (Kortsch *et al.*, 2012).

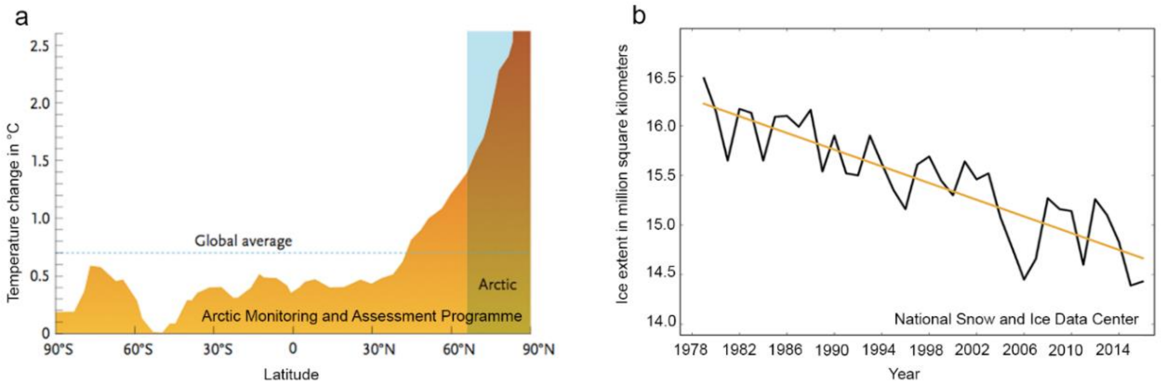


Figure 7. a) The average increase in surface temperature since the 1951–1980 reference period with respect to latitude. In the Arctic, the warming has been more than twice the global average. b) Monthly sea-ice extent in March for the 1979–2016 period, showing a decline of 42100 square kilometres per year corresponding to 2.7% per decade. Images are from the Arctic Monitoring and Assessment Programme (www.amap.no) and from the US National Snow and Ice Data Center (www.nsidc.org).

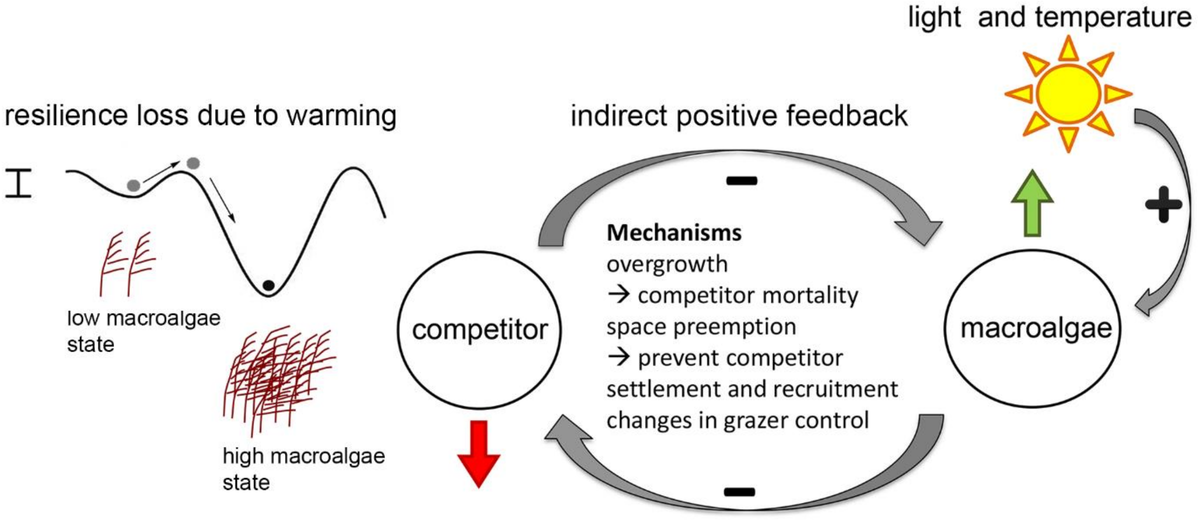


Figure 8. The conceptual model illustrates the importance of biotic interactions involved in ecological responses to climate warming. Biotic interactions may determine the outcome of the response and induce positive feedbacks that may amplify the response. In this particular case, macroalgae competes for substrate space against a space competitor, calcareous algae. Under low light and low temperature conditions, calcareous algae are the dominant space occupiers on arctic rocky shores. With increasing light and temperature availability due to warming, the calcareous algae state loses resilience and macroalgal growth and recruitment is benefitted. Macroalgae competitive abilities are promoted, which changes the strength of the linkages between the two competitors. Because macroalgae is the stronger competitor, the negative – negative direct effects of interference competition for space results in a positive indirect net effect on macroalgae abundance.

4. Main questions asked in the three papers

The overall objective of this thesis has been to increase our understanding of the temporal and spatial structure of arctic benthic communities and Barents Sea food webs. The following questions were asked for each paper:

Paper 1

In Paper 1, I compared the topological structure of boreal and arctic food webs.

I. What are the structural differences between boreal and arctic food webs of the Barents Sea?
II. What roles do different taxa play with respect to modularity?
III. How are the ongoing poleward shifts of boreal fish affecting the structure of arctic marine food webs?

Paper 2

In Paper 2, I compared 25 sub-food webs across the Barents Sea.

I. Do food-web properties display clear spatial patterns along biogeographic regions in the Barents Sea?
II. Is habitat heterogeneity associated with food-web complexity?
III. Which species contribute most strongly to the tri-trophic motif structures?

Paper 3

In Paper 3, I compared the temporal development in community structure of two hard-bottom benthic communities of two subarctic fjords in Svalbard, in the northwestern Barents Sea.

I. How did the community structure of arctic benthic communities develop during a 30-year period (1980–2010) of rapid climate warming?
II. Which processes and mechanisms can trigger ecological regime shifts in arctic benthic communities?

5. Materials and methods

5.1 The study region – Barents Sea and Svalbard

The Barents Sea is the largest marginal shelf sea of the Arctic Ocean located between Norway and Russia, and Svalbard, Franz Josef Land and Novaya Zemlya (Figure 9). It is one of the most productive oceans worldwide, supporting some of largest commercial fisheries (Michalsen *et al.*, 2013). Recently, the cod stock has increased to record high levels (Kjesbu *et al.*, 2014). The Barents Sea is composed of biogeographically distinct regions with respect to hydrography, topography and species distributions. The boreal region in the southwest is highly influenced by the inflow of warm atlantic water (T>3°C, S >35 ‰). The arctic region in the north and northeast is influenced by cold arctic water masses (T<0°C, 34.3 ‰ ≤ S ≤ 34.8 ‰) and seasonal sea-ice cover. The polar front region, where the atlantic and arctic water masses meet, is very productive. The exact position of the polar front varies from year to year and is most variable in the east, depending on the strength of the atlantic water inflow (Loeng & Drinkwater, 2007). Currently, the marginal ice zone in the northeast is one of the regions worldwide undergoing some of the largest changes with respect to climate warming (Carmack *et al.*, 2015).

The Svalbard archipelago is located in the northwest of the Barents Sea. This region is characterized by relatively high habitat heterogeneity and environmental variability due to mixing of atlantic and arctic water masses, and due to the proximity to the coast and to the deep shelf slopes in the west. The fjords along the western coast of Svalbard are influenced by a mixture of atlantic, arctic and glacial melt water. The two study sites in Svalbard – Kongsfjord and Smeerenburgfjord – are located along the west coast, Smeerenburgfjord being located a bit further north than Kongsfjord (Figure 9). Owing to easy access and due to open waters, the Barents Sea and the Kongsfjord are some of the best-studied regions in the Arctic with respect to marine biology as well as hydrology (Hop *et al.*, 2002; Wassmann *et al.*, 2011). During the last decade, the Barents Sea and Svalbard have experienced rapid warming and the smallest ice extent recorded with less than 30% of the Barents Sea ice-covered annually (Figure 10 a&b) (Årthun *et al.*, 2012). Around the Svalbard archipelago the sea-ice contraction has been greatest during the winter, and the loss of sea ice north of Svalbard is close to 10% per decade since the 1980s (Figure 10 a&b) (Onarheim *et al.*, 2014; Onarheim *et al.*, 2015)

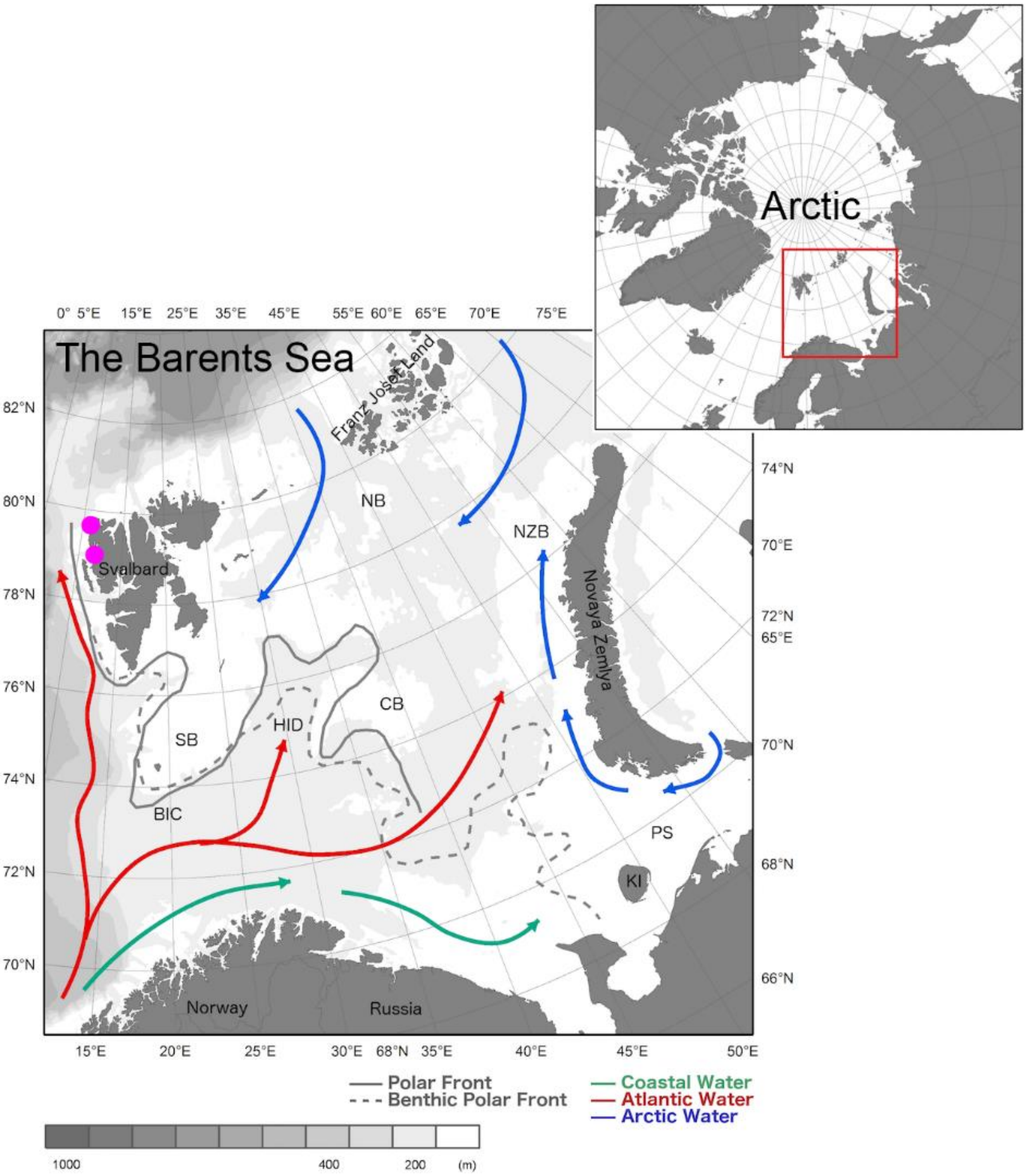


Figure 9. Map of the Barents Sea and its location within the Arctic. Bottom depths are indicated with the grey gradients. The direction and flow of the atlantic and arctic ocean currents are indicated with red (Atlantic) and blue (Arctic) arrows. The Polar Front, separating atlantic and arctic water masses is indicated with a grey line. The Svalbard archipelago is located in the northwest corner of the Barents Sea. The two pink dots indicate where the benthic sampling stations (in Paper 3) are located along the west coast of Svalbard. The figure is reprinted with permission from Renate Degen and the journal *Marine Ecological Progress Series* (Degen et al., 2016).

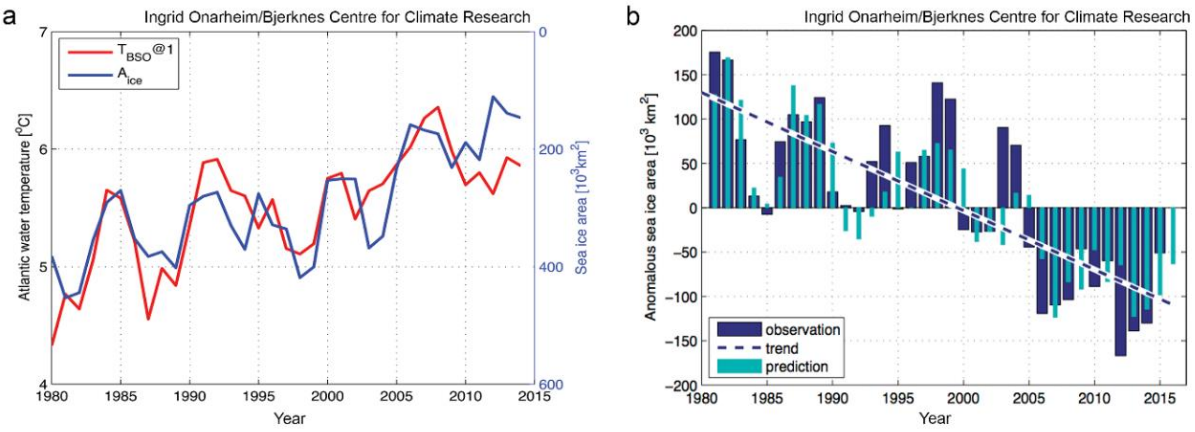
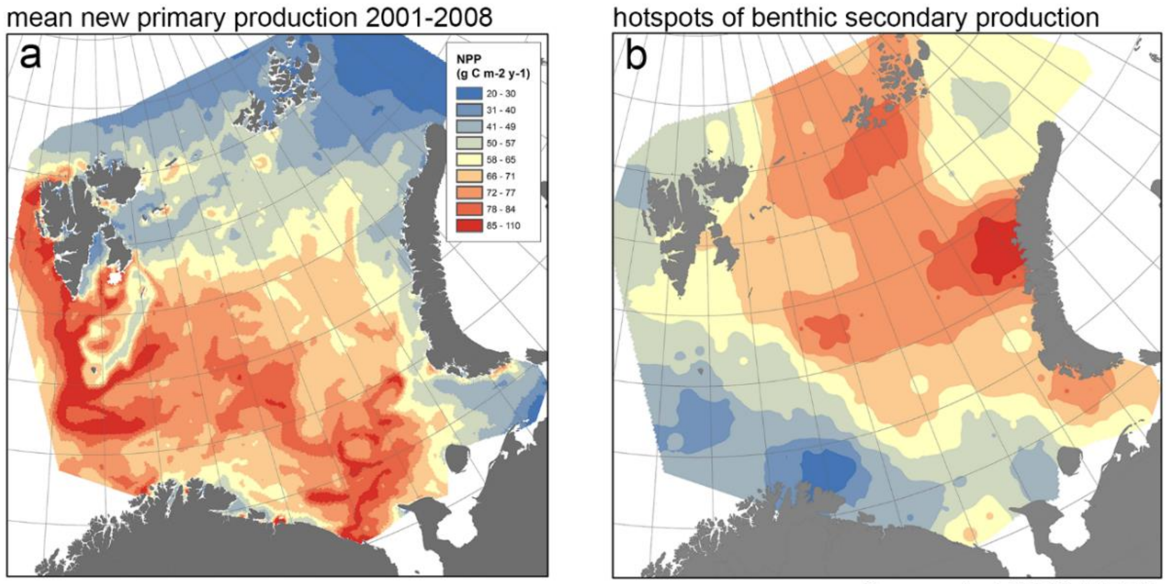


Figure 10. a) shows the increase in atlantic water temperature within the Barents Sea from 1980 to 2015 and the corresponding reduction in the sea ice; and b) shows the observed and predicted winter sea ice anomalies in the Barents Sea from 1980 to 2010. Since 2005, the observations have been below the average for the period.

5.1.1 Biology of the Barents Sea and Svalbard

The main ecological zones in the Barents Sea are the Boreal, the Arctic, the Polar Front (central), the Svalbard Archipelago and the Southeast (Kortsch et al., Paper 2 of this thesis). The boreal region in the southwest is influenced by the inflow of relatively warm and saline atlantic water. The mean annual primary production is highest in the boreal region influenced by nutrient-rich atlantic waters and declines towards the northeast (Figure 11a) (Reigstad *et al.*, 2011; Degen *et al.*, 2016), but short-term production along the marginal ice zone and retreating ice edge in the northeast can be very high during a relatively short time window of productivity in the spring. In the arctic region, large amounts of this primary production, including ice algae (53%), is transported directly to the ocean floor. For comparison approximately 28% of primary production sinks out in the boreal region (Reigstad *et al.*, 2011). The flux of carbon to the seafloor in the northeast Barents Sea is responsible for high benthic secondary production and diversity (Jørgensen *et al.*, 2015). Recently, a study showed that benthic secondary production was significantly higher in the ice-covered northeastern Barents Sea compared to the southwest (Figure 11b) (Degen *et al.*, 2016). While benthic biodiversity is high in the northeast Barents Sea, pelagic fish diversity is low. Polar cod is the only real arctic pelagic fish in these waters, but recently capelin, a dominant pelagic fish species in the Barents Sea, has increased in abundance in the northeastern parts of the Barents Sea (ICES, 2014), whereas polar cod abundance has declined (ICES, 2014). The largest diversity and turnover of fish can be found in the Svalbard archipelago and surrounding waters (Certain & Planque, 2015), but also the boreal region in the southwest harbours a high diversity and biomass of fish (Johannesen *et al.*, 2012).



Degen *et al*. 2016 *MEPS*

Figure 11. a) Map of mean new primary production in the Barents Sea for the period 2001 to 2008 derived from the SINMOD model (see Wassmann *et al.*, 2006), and b) map of hotspot analysis of secondary production of epibenthos in the Barents Sea. Red indicates significantly higher values than mean, and blue lower than mean. The figures were reprinted with permission from Renate Degen and the journal *Marine Ecological Progress Series*.

5.2 Compilation of the food webs

The first step towards understanding ecosystem structure lies in extensive collection of good ecosystem data. Together with colleagues from the Institute of Marine Research (Norway) and from the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (Russia), I compiled the Barents Sea food web meta-web, which ranks among the most resolved marine food webs in the world. The compilation of species interaction was based on extensive literature review of gut content analysis of the respective species in the food web. Compilation methodologies and species-selection criteria are thoroughly described in the data paper in the appendix of this thesis. We used the food web meta-web combined with species-distribution data from the joint Russian–Norwegian ecosystem survey to assemble sub-webs specific to certain sub-regions in the Barents Sea in **Papers 1 and 2** (see Box 3).

Box 3: The ecosystem survey and the food webs

Ecosystem survey data

Since 2004, the joint Russian–Norwegian Barents Sea Ecosystem Survey has sampled taxa from the entire water column and sea floor (except for benthic infauna) in a joint effort to map the whole ecosystem (Planque *et al.*, 2014). The survey takes place in August/September each year when sea ice is at its minimum. The species distribution data used to construct the local food webs in this thesis are therefore representative for the late summer period of the year. Each year approximately 300–700 ecosystem survey stations are sampled throughout the Barents Sea (Figure 12a) (Olsen *et al.*, 2011). Multiple sampling methodologies are deployed to gather information on epibenthos, fish, sea birds and marine mammals. The species distribution data at station level is most resolved for epibenthos and fish. Sea birds and marine mammals are observed along transect and were located to polygons for the use of assembling food webs in this study.

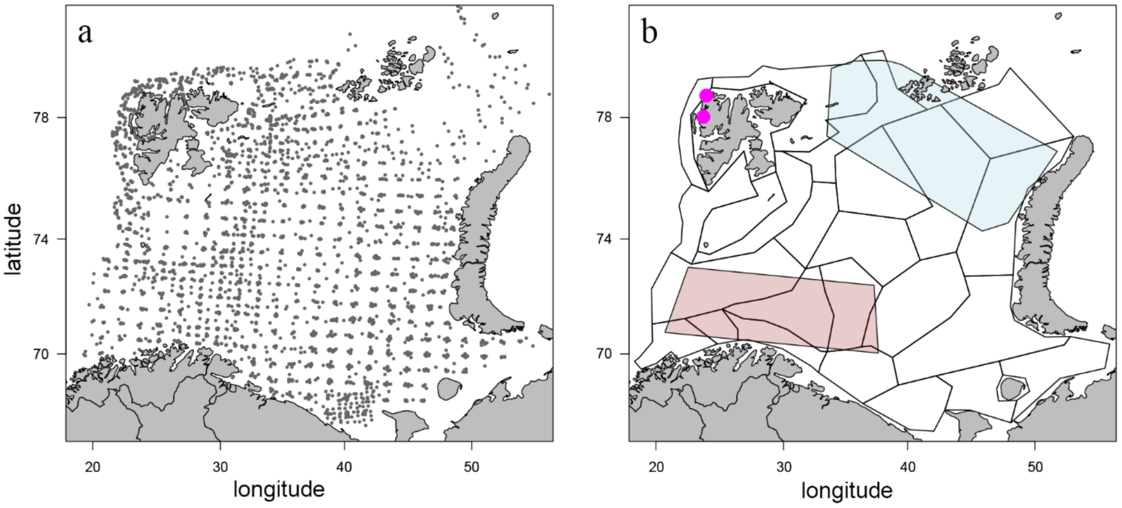


Figure 12. a) Map of the Barents Sea and the ecosystem survey sampling stations indicated with the grey points on the map. b) Map of the boreal (red) and arctic (blue) study regions defined in Paper 1 and map of the 25 polygons, sub-food web regions, defined in Paper 2. The two pink dots along the west coast of Svalbard are the two rocky-bottom sampling localities in Paper 3.

The food-web meta-web

The food webs in this thesis are the most resolved food webs of the Barents Sea. Furthermore, the methodology, i.e. species and interaction selection criteria, is transparent and the data source explicit (Planque *et al.*, 2014). The food-web meta-web represents the most common taxa from the seafloor to the surface for the whole Barents Sea, comprising 233 trophospecies and 2218 feeding links. The food web includes detritus and bacteria, 8 basal taxa, 43 zooplankton, 79 benthic, and 77 fish, as well as 9 sea birds and 15 marine mammals. A detailed description of the criteria used to compile the meta-web can be found in the data set paper in the appendix of this thesis. The food-web files can be downloaded from the *Ecological Archives* website (Planque *et al.*, 2014). The meta-web includes taxa from the entire Barents Sea ecosystem ranging the boreal and arctic regions. Taxa inhabiting different parts of the Barents Sea do not spatially overlap and will therefore not interact. To account for the varying spatial distribution of species and distinct realized local interactions, we used species-distribution information from the ecosystem survey data combined with the information from the meta-web to compile local sub-food webs.

Regional sub-food webs

To study how the structure of contrasting regions within the Barents Sea differs, we compared boreal arctic food webs in Paper 1. We chose areas southwest and northeast of the polar front, the main hydrological demarcation separating boreal and arctic biogeographic regions in the Barents Sea. The southwest region is influenced by relatively warm seawater, whereas seasonal ice cover and cold seawater influence the northeast. To study how food webs vary along environmental gradients in the Barents Sea, we constructed 25 sub-food webs by choosing subsets of taxa specific to predefined sub regions (polygons). The sub-regions are defined as geographical units in the Atlantis model, a numerical end-to-end ecosystem model, currently under development and implementation for the Barents Sea (Fulton *et al.*, 2011). The polygons (Figure 12b) are defined according to habitat characteristics such as oceanography, climatic conditions and bottom structure, and result in internally, relatively homogenous sub-regions with respect to the environment (Certain & Planque, 2015).

5.3 Photographic analysis of arctic hard-bottom benthos

In 1980, permanent benthic monitoring stations were established – in Kongsfjord and in Smeerenburgfjord at 15 m depth along the west coast of Svalbard (Figure 9). Photographs of the two benthic transects, consisting of five adjacent quadrates (0.5 m x 0.5 m) were taken annually in late August or early September since 1980. The photographic sampling is non-destructive and therefore suitable for performing long-term studies. At both study sites, one transect was manipulated in 1980 via a pulse perturbation by clearing off all organisms; the other transect was kept undisturbed. In **Paper 3**, counting benthos and estimating the spatial coverage of species within the benthic communities was carried out via digital image analysis in the *Adobe Photoshop CS4 extended* software program.

5.4 Statistical tools and techniques

In this PhD thesis, I have applied several techniques and tools provided by network and graph theory (**Papers 1 and 2**) and multivariate statistics (**Papers 1, 2 and 3**). Network analysis offers an integrative framework to assess the relationship between structure, dynamics and function in food webs, and the potential to assess the impacts of perturbations, e.g. losses and gains of species, on food-web structure. Multivariate statistics are valuable tools for summarizing and highlighting main trends in multidimensional ecosystem data as in multispecies communities and food webs. I also applied null models for statistical inference in **Papers 1 and 2.**

In both **Papers 1 and 2**, I calculated commonly reported food-web metrics for each food web using graph theory. In **Paper 1**, I focused, specifically, on the role of modularity in boreal and arctic food webs and on the role that species play with respect to modularity i.e. the within and between module-connecting role. In **Paper 1**, I also estimated the food-web in- and out-degree distributions and the spatial mean degree centrality of the fish community. These maps were plotted stationwide in the Barents Sea and compared among years to elucidate how the mean degree centrality, i.e. the degree of generalism or specialism changed spatially from 2004 to 2012. In **Paper 1**, multivariate linear discriminant analysis (LDA) was used to estimate the significance of the association among modules and food-web habitats. In **Paper 2**, I focused on how food-web metrics and the proportion of motifs change spatially along environmental gradients in the Barents Sea using graph theory. I also estimated the incidence of species participation in the motifs. The association among food-web metrics, motifs and environmental variables were assessed using multivariate principal component analysis (PCA). In **Paper 3**, changes in temporal community structure was assessed via multidimensional scaling (nmMDS) and a multivariate regression tree analysis. The likelihood of a regime shift in the macroalgal time series was assed via a Bayesian break point analysis.

5.5 Environmental variables

In all three papers (**Papers 1, 2 and 3),** abiotic variables were collected to illustrate the temporal and spatial changes in abiotic divers in the Barents Sea and around Svalbard. In **Paper 1**, the changes in the days with sea-ice cover were indicated in the spatio-temporal degree centrality maps of fish. In **Paper 2**, environmental data was retrieved for each polygon (n=25): mean water column temperature (surface layer to bottom), mean water column salinity (surface layer to bottom), mean days with sea-ice cover, and mean depth. I also calculated a proxy for habitat heterogeneity by using the standard deviation of bottom depth and temperature within polygons. In **Paper 3**, sea surface temperature and number of ice-free days were calculated for a defined region along the west coast of Svalbard during a 30-year time period from 1980 to 2010 (Maslanik & Stroeve, 1999; Cavalieri *et al.*, 2004; Meier *et al.*, 2006).

6. Results, discussion and conclusions

6.1 Main findings

Paper 1

Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A., Aschan, M.

Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists (2015)

Proceedings of the Royal Society Biological Sciences, 282: 20151546

We showed that structural properties and link configuration between boreal and arctic food-web regions in the Barents Sea differed despite similar number of taxa present in the food webs. We found that the arctic food web was more modular and less connected than the boreal, whereas the boreal food web contained higher values of all commonly reported food-web metrics, except for modularity. The boreal food web contained several super-generalist such as cod. Because of their many trophic interactions and module-connecting role, super-generalists influence the network structure substantially, in particular, linkage density, the degree of compartmentalization, clustering, and percentage of species in loops. Boreal fish species are migrating poleward into the northeastern part of the Barents Sea to forage during late summer. We showed that a main characteristic of the boreal fish moving poleward is high generalism, a property that increases connectance and reduces modularity of the arctic food web. Our results provided further evidence that food-web modules form natural boundaries for marine habitat, i.e. pelagic and benthic. We showed that cod and haddock act as network connector hubs, linking energetic pathways across trophic levels and modules. The presence of cod and haddock also increases the number of loops in the marine arctic food web. Owing to this, we posited that the recent poleward shift of boreal generalists might alter arctic marine food-web structure and function substantially.

Paper 2

Kortsch, S., Primicerio, R., Aschan, M., Lind, S., Dolgov, A., Planque, B.

Marine food-web structure changes along environmental gradients in the Barents Sea

Intended for Global Ecology & Biogeography

Based on our analysis, Barents Sea food-web structure displays distinct biogeographic patterns. We could divide the Barents Sea food webs into five main food-web clusters: the Southwest (Boreal), the Northwest (Svalbard,) the Mid (Mixed Water), the Southeast (Coastal), and the Northeast (Arctic). Specifically, we find that the main axis of spatial food-web variation (connectance and modularity) is associated with gradients in seawater temperature and sea-ice coverage. Metrics associated with higher seawater temperature are: connectance, percentage of cannibals, and a high proportion of intraguild and mutual predation motifs. Metrics associated with cold seawater and sea ice are: modularity and a high proportion of shared resource motifs. Another important dimension of food-web variation is associated with high food-web complexity (e.g. connectance) coinciding with high environmental and topographic heterogeneity. Food-web metrics associated with high environmental habitat heterogeneity are: number of species, number of links, number of motifs, high mean path length, and high mean trophic level. Motif participation revealed that pelagic and generalist fish are contributing most strongly to the intraguild motifs and looping structures, i.e. mutual predation and cannibalism. Our study provides empirical evidence that food-web structure in the Barents Sea can be linked to broad-scale environmental gradients through environmental constraints on species' traits, niche space and environmental filtering of species' spatial distributions.

Paper 3

Kortsch, S., Primicerio, R., Beuchel, F., Renaud, P. E., Rodrigues, J., Lønne O. J.,

Gulliksen, B.

Climate-driven regime shifts in Arctic marine benthos (2012)

Proceedings of the National Academy of Sciences, 109: 14052-14057

We documented extensive and rapid structural changes in the rocky-bottom communities of two arctic fjords from 1980 to 2010 during a 30-year period of gradually increasing seawater temperature and decreasing sea-ice cover in Svalbard. The most striking component of the structural reorganization was an abrupt fivefold increase in macroalgal cover in 1995 in Kongsfjord and an eightfold increase in 2000 in Smeerenburgfjord. Simultaneous changes in the abundance of benthic invertebrates suggest that the macroalgae play a key role in structuring benthic rocky-bottom communities. The abrupt, substantial and persistent nature of the change in macroalgae abundance and benthic community structure is indicative of an ecological regime shift. The mechanisms behind the regime shift are thought to be driven by climate warming inducing changes in the competitive abilities among macroalgae and calcareous algae, and a change in positive feedback mechanisms. We hypothesize that macroalgal growth, recruitment and competitive abilities are benefitting from increased seawater temperature and light availability, inducing a shift from a calcareous algae-dominated to a macroalgae-dominated seafloor with community-wide consequences due to a range of altered feedback mechanisms between macroalgae and benthic invertebrates.

6.2 Discussion and conclusions

6.2.1 Systematic patterns in spatial food-web structure across the Barents Sea

It is well established that species diversity varies along environmental and climatic gradients, separating biogeographic regions (Mora *et al.*, 2011). However, it is less clear how structural patterns of food webs vary across space and along environmental and climatic gradients. A handful of empirical studies have demonstrated that topological properties change along environmental gradients. Most of these studies are performed on bipartite food-web networks (Trøjelsgaard & Olesen, 2013; Morris *et al.*, 2014; Kissling & Schleuning, 2015; Morris *et al.*, 2015; Trøjelsgaard *et al.*, 2015). Only a few are performed on unipartite aquatic food webs (Thompson & Townsend, 2005; Wood *et al.*, 2015; Gilarranz *et al.*, 2016), of which two are marine and reasonably highly resolved (Wood *et al.*, 2015; Gilarranz *et al.*, 2016). This thesis provides empirical evidence that food-web structure varies along environmental and climatic gradients in the Barents Sea and that structure displays distinct biogeographic patterns (**Papers 1 and 2**).

The two most contrasting regions in the Barents Sea are the boreal in the southwest and the arctic in the northeast (**Papers 1 and 2**). The boreal region in the southwest is influenced by warm, saline and nutrient-rich seawater, whereas cold and relatively fresh arctic seawater and seasonal ice cover influence the arctic region in the northeast. The arctic food webs in the northeast display the most distinctive topological food-web properties compared to the remaining food webs in the Barents Sea (**Paper 2**). Although the arctic food-web region defined in **Paper 1** and the three arctic food-web regions in **Paper 2** differ in size and in the number of species, the region in **Paper 1** being larger and more species-rich, the topological results from the two studies lend support to each other. Taken together, these studies suggest that size of food-web region and number of species are not the main determinants for the topological characteristics of the arctic food webs, although food-web metrics have been demonstrated to scale with numbers of species (Riede *et al.*, 2010). **Papers 1 and 2** also show that, despite similar number of species in the food webs, food webs of similar size can display different topological features. These findings lead me to conclude that rather than the number of species *per se*, specific attributes of the species in a given region, their trophic structure and participation in food-web configurations (i.e. interaction type and frequency of participation in, e.g., motifs and loops) determine food-web structure.

Papers 1 and 2 of this thesis pay special attention to the role of fish in the marine food webs for several reasons. The fish group is taxonomically highly resolved and the fish distribution data is among the most detailed, with 300–700 annual sampling stations in the Barents Sea (Olsen *et al.*, 2011). Fish also constitute an important functional group in the marine food web as intermediate network connectors of the basal taxa i.e. primary and secondary producers and the top predators, as well as being connectors of food-web compartments (**Paper 1**). For this reason, much of the present discussion involves the role of fish in the marine Barents Sea food webs. Species traits such as body size, metabolic category and motility have been successful in predicting and explaining food-web structure (Eklöf *et al.*, 2013). Average body size and average motility of fish differ between the boreal and arctic food-web regions of the Barents Sea. (**Paper 1**). At the community level, the average arctic fish is smaller and more stationary than the average boreal, whereas the average boreal fish grows larger and is more motile (Wiedmann *et al.*, 2014). Fish with arctic affinities often live in association with the seafloor and are more specialized in their diet (**Paper 1**) (Fossheim *et al.*, 2015), whereas fish with boreal affinities are more generalist and pelagic in their diet (**Papers 1 and 2**). Major differences in fish traits between the boreal and the arctic region of the Barents Sea will inevitably manifest as structural differences at the food-web level. At the global food-web level, structural differences between boreal and arctic food webs are best explained by differences in connectance and degree of modularity (**Paper 2**). Some of these differences may be attributed to the presence of diet and habitat generalists in the boreal food web. With their many interactions, diet and habitat generalists increase connectance considerably, while decreasing modularity. In general, the boreal food web contained higher values of all the commonly reported structural food-web properties (e.g. higher clustering, higher trophic level, more cannibals and more species in loops) compared to the arctic food web, apart from modularity (**Paper 1**).

6.2.2 Modularity and habitats

Paper 1 focused on modularity as an important structural property in food webs and our analysis provided further evidence that food-web modules are associated with ecosystem habitats, (see also Rezende *et al.*, 2009). According to our analysis, food-web modules are associated with pelagic and benthic habitats. We also showed that the degree of modularity depends on how strongly species connect energetic pathways between modules. When we added poleward-moving super-generalists to the arctic food web modularity decreased substantially because these species connect to other species across modules, which, according to our analysis, is similar to linking energetic pathways across habitats. In **Paper 1**, we therefore posited that the increasing presence of cod and haddock in the Arctic during the late summer enhances energetic couplings between benthic and pelagic food-web modules. Connecting pathways across compartments will inevitably have implications for food-web dynamics and stability, but it is uncertain how. We posited that transfer and exchange of energy and matter between benthic and pelagic compartments might increase in the arctic food web via novel energetic pathways and because large fish such as cod actively seek prey between compartments. Further, modularity is believed to buffer perturbations by retaining them within the affected food-web module, a feature that may increase food-web persistence (Stouffer & Bascompte, 2011). Therefore, in a more connected arctic food web with lower modularity, perturbations might spread more rapidly across the entire network and, in particular, across benthic and pelagic food-web compartments. In this manner, overall food-web stability could decrease in the Arctic. However, a common feature among generalists is their ability to switch prey and to couple slow (detritivore-driven) and fast (pelagic-driven) resource channels, features that may enhance ecological stability in food webs (Murdoch, 1969; McCann *et al.*, 2005). The fact that cod moves further northeast in the Barents Sea to forage on species, such as capelin and hyperiids that have also expanded their distribution and abundance northeast in the Barents Sea (ICES, 2014), could therefore also stabilize food-web dynamics in the arctic region (Orlova *et al.*, 2013; Eriksen *et al.*, 2016). Answering questions about the stability and persistence of arctic food webs and their capacity to absorb perturbations is a complex issue that needs further investigation, consideration and model development.

6.2.3 The relationship between food-web complexity and habitat heterogeneity

In line with our *a priori* expectation, we found that the Svalbard archipelago food webs were the most complex in terms of number of species, links and food-web configurations compared to the remaining food webs in the Barents Sea (**Paper 2**). In light of previous findings and classic ecological theory on *the habitat heterogeneity hypothesis*, suggesting that habitat heterogeneity enhances aquatic food web connectivity and species diversity (MacArthur & MacArthur, 1961; MacArthur & Wilson, 1967; Thompson & Townsend, 2005), we hypothesized that habitat heterogeneity (i.e. high variability in environmental characteristics) within the Barents Sea would increase structural food-web complexity. The heterogeneity hypothesis assumes that habitat heterogeneity leads to higher diversity and structural complexity because structurally complex habitats provide a greater diversity of niches and environmental resources (MacArthur & MacArthur, 1961; MacArthur & Wilson, 1967; Tews *et al.*, 2004). In the Barents Sea, habitat heterogeneity is most pronounced around the Svalbard archipelago (**Paper 2**). Habitats around Svalbard are diverse and range from shallow rocky shores along the coast to deep habitats along the continental shelves. The hydrography around Svalbard is highly variable and includes atlantic, arctic, and coastal water masses and melt water and river runoff, influencing hydrographic processes such as mixing, transformation and advection (Cottier *et al.*, 2005). Habitat complexity and hydrographic variability affect productivity and species composition, and, indeed, recently a comparative study on fish diversity across the entire Barents Sea indicated that fish diversity and turnover rates are highest around the Svalbard archipelago in the Barents Sea (Certain & Planque, 2015). Our food-web analyses support this conclusion and contribute to further evidence that food-web complexity increases with habitat heterogeneity (**Paper 2**). **Paper 3** and other investigations of rocky-bottom benthos in Svalbard also indicate that substrate complexity due to habitat-forming species such as macroalgae may increase benthic biodiversity and alter community structure (Kortsch, 2010; Weslawski *et al.*, 2010). Erect habitat-forming macroalgae increase resource and niche availability by providing a secondary substrate for epifauna and epiphytes, nursery habitats for fish and refuges for grazers, as well as being a food resource.

6.2.4 Linking species to food webs via motifs

In **Paper 1**, we hypothesized that the lack of loops in the arctic food web could be explained by the lack of mutual predation links. This hypothesis was confirmed in **Paper 2**, where motif analysis showed that the arctic food web contained no mutual predation motifs, whereas the boreal food webs contained the highest proportion of mutual predation structures compared to the remaining food webs in the Barents Sea. The most frequent form of mutual predation in marine systems is due to ontogenetic reversal of predation because of ontogenetic niche shifts in fish (Polis *et al.*, 1989). Ontogenetic niche shift and reversal in stage-structured predation are common among pelagic fish. Indeed, motif participation analysis showed that the species involved in these structures are pelagic and generalist fish. Because the arctic region in the Barents Sea contains few arctic pelagic fish, they lack mutual predation structures. This example illustrates well how life histories and niche traits of species manifest as distinct interaction structures at the food-web level. It also illustrates how linking the analysis of food-web structure along environmental gradients with the analysis of species' structural roles in the food web provide insights into the potential mechanism that generates a given structure. It is important to note that our food webs do not capture all sources of mutual predation in the food webs, e.g. reversal in predation between fish larvae and zooplankton. Given that structure affects dynamics and function (DeAngelis 1992), mutual predation versus no mutual predation in a food web will necessarily affect dynamics and ecosystem functioning; the question remains as to how.

To answer this question, it is important to consider the potential dynamic implications of mutual predation, intraguild predation and cannibalism. Although this thesis deals with the static structure of empirical food webs and therefore does not address the dynamics of food webs, I believe that structural components may provide some insights as to what type of dynamics may be at play in a community (**Paper 2**). Looping structures and intraguild predation can be fast and strong energy-transfer pathways with direct and indirect feedbacks and strong regulating mechanisms (via density dependence) of fish populations (Bjørnstad *et al.*, 1999), since the abundance of one species via predation directly influences the abundance of the other, and vice versa. In **Paper 2**, we show that the fish involved in the looping structures are pelagic and generalist. Maintaining fast growth, high motility and high competition and predation pressures requires sufficient energy supply at the base of the food web. In the boreal region, where these looping structures are prevalent, primary production is at its highest in the Barents Sea (Figure 12a), and, combined with high levels of secondary production and advection of secondary production from the Norwegian Sea, this may indeed support these fast pelagic energy-demanding food-web channels in the southwestern region of the Barents Sea (Reigstad *et al.*, 2011). However, arctic regions are seasonally ice-covered and subjected to a long period of darkness during the winter, where primary production ceases. Moreover, seawater temperature close to freezing point constrains growth, metabolism, body size and motility of fish, favouring less motile smaller bottom-dwelling fish species over motile and fast-growing pelagic and generalist fish. The absence of these looping structures from the arctic food webs could therefore be due to the combined effects from temperature constraints on growth and metabolism of fish and strong seasonality in primary production.

Mutual predation is common in stage-structured pelagic fish populations in temperate marine systems, including in the boreal region of the Barents Sea (**Paper 2**). Theory predicts that systems with stage-structured populations are prone to alternative stable states, because of contrasting dominance patterns between stages in intraguild predation and mutual predation (Schreiber & Rudolf, 2008). Well-known empirical examples of marine systems containing stage-specific predation and that went through regime shifts come from Nova Scotia and the Baltic Sea (Casini *et al.,* 2009). In both systems, cod populations collapsed and changes in feedback mechanisms are thought to have prevented their recovery (De Roos & Persson, 2002; Van Leeuwen *et al.*, 2008). The relatively high occurrence of mutual predation motifs in the boreal food web may suggest that catastrophic population collapses may be an intrinsic property of the food webs in the southwestern parts of the Barents Sea. Indeed, in the past, populations of cod and capelin have undergone several collapses in the Barents Sea (Gjøsæter *et al.*, 2009; Gjøsæter *et al.*, 2015). Although widespread in marine food webs, marine ecology and fisheries research has paid little attention to the prevalence of these intricate looping structures and their importance for maintaining regimes and dominance patterns in marine food webs (Irigoien & de Roos, 2011).

6.2.5 Super-generalist, ecosystem engineers and community structure

Papers 1, 2 and 3 show that species play different roles in the food-web network depending on their position, the number of interactions they have with other species, and the incidence and type of interaction that they are involved in. **Papers 1 and 3** also show how certain species and taxonomic groups play a disproportionately important structuring role in the ecosystem with implications for community dynamics, e.g. regime shifts and function, e.g. feedback mechanisms. Among these species, cod has been a highly successful species in terms of its high abundance, a wide distribution and a major structuring role across distinct marine ecosystems in the northern hemisphere. In **Papers 1 and 2,** we provide further evidence that cod plays an important structuring role in marine food webs. With its 128 feeding links, Atlantic cod is by far the most super-generalist species in the Barents Sea. In **Paper 1**, we showed that cod is a network connector hub, linking species across pelagic and benthic food-web compartments with a strong effect on the degree of modularity and on other common food-web metrics. In **Paper 2**, we showed that cod is frequently involved in motif structures, in particular in competitive motifs and mutual predation motifs with potential consequences for food-web dynamics. Another group of marine taxa that show a disproportionally important structuring role in marine coastal systems worldwide is macroalgae (Scheffer, 2009). In **Paper 3,** we provide evidence that macroalgae are important ecosystem engineering and community-structuring species in the coastal Arctic. Both types of taxa, super-generalist fish and ecosystem engineering macroalgae, are involved in community-wide regime shifts in various ecosystems around the world (Alheit *et al.*, 2005; Barange *et al.*, 2008; Mumby & Steneck, 2008; Norström *et al.*, 2009; Frank *et al.*, 2011). Which niche traits, life-history attributes and biotic interaction structures characterize these species? To answer this question, it is important to consider the reciprocal nature of the relationship between structure and function in a species and in a community.

The key ingredients to creating alternative stable states and maintaining dominance patterns are positive feedbacks driving the system to a given state (Scheffer, 2009). Although cod and macroalgae are very different types of taxa with distinct trophic positions and biotic interactions, they both induce a range of positive feedbacks within their respective communities that may explain how they maintain their dominance regimes. As mentioned before, cod induces potential positive feedbacks by feeding on certain size classes of prey, driving the size structure of their prey into a favourable range or by inducing cascading effects in multiple channel feeding, two mechanisms that fuel resource availability for further growth and recruitment of cod (De Roos & Persson, 2002; McCann *et al.*, 2005). In **Paper 2**, we also show that cod is involved in exploitative and apparent competition motifs, structural mechanisms by which they may directly and indirectly control their competitors, but also enhance co-existence of species by preying on species competing for resources. One of the most important interaction types inducing positive feedbacks, in ecology, is facilitation (Scheffer, 2009). Facilitation is an interaction type common in plants such as macroalgae. In **Paper 3**, we hypothesize that macroalgae via competition and facilitation induce a range of positive feedbacks in the benthic communities promoting and reinforcing the abrupt benthic regime shift observed along the rocky shores of Svalbard and maintaining the new macroalgal state (see Box 4).

6.2.6 Community responses to climate warming

Papers 1 and 3 provide empirical evidence that structural components of arctic communities are changing due to climate warming. Some of the promptest responses to climate warming worldwide are altered migration patterns of opportunistic fish (Poloczanska *et al.*, 2013; Fossheim *et al.*, 2015). In the Barents Sea, poleward expansion of boreal fish generalists has been documented (Fossheim *et al.*, 2015), and in **Paper 1** we show that the characteristic of the fish moving poleward is high generalism, a feature that has great impact on food-web structure. For example, connectivity between benthic and pelagic compartments in arctic marine food webs may increase, while modularity may decrease. Establishing new energetic pathways between food-web compartments will most likely have implications for ecosystem functioning (Figure 13).

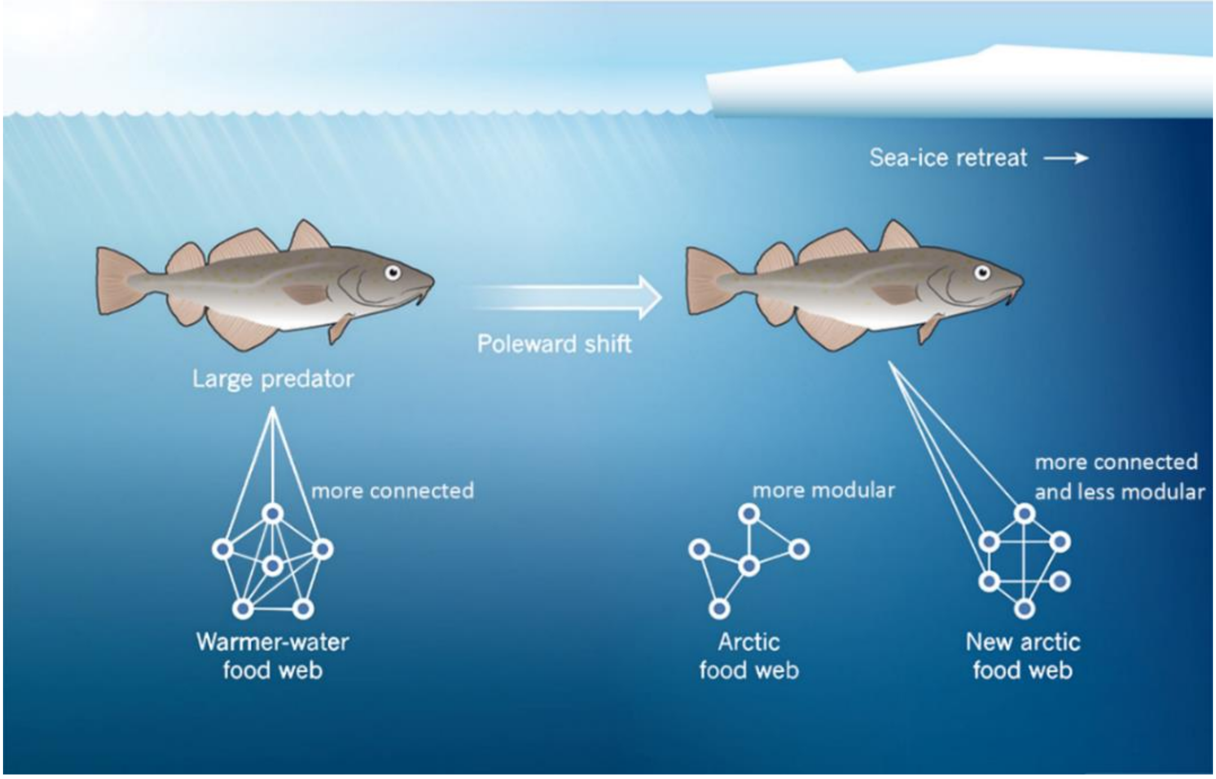


Figure 13. Boreal warm-water food webs are more connected and less modular than cold-water arctic food webs. Due to poleward movement of boreal generalists such as cod, arctic marine food-web structure is changing. The presence of cod, a super-generalist species, in the marine Arctic introduces new feeding links to the arctic food web, increasing its overall connectance. Because cod consumes many prey from different habitats, and because habitats form natural boundaries for food-web modules, cod couples energetic pathways between pelagic and benthic food-web modules, decreasing overall modularity of new arctic food web. A slightly modified version of this figure is reprinted with permission from the journal *Nature*. The figure first appeared in a News & Views article by Julia Blanchard about Paper 1 (Blanchard, 2015).

Species from different compartments will become closer neighbours in the food-web network, resulting in not only matter and energy but also perturbations potentially spreading further and more rapidly across the arctic marine ecosystem. Responses to climate change are expected to be abrupt, but few studies can document the nature of a community shift, simply because long-time series tracking species temporal development are missing. In **Paper 3,** we document regime shifts in arctic benthic communities (Figure 14). The mechanisms thought to drive the regime shifts are caused by changes in light availability and increased temperature due to climate warming, benefitting the competitive abilities of macroalgae over calcareous algae and other sessile space competitors. See Box 4 (Figure 15) for an explanation of the potential positive feedbacks induced by macroalgae that may have promoted the regime shift and that may explain some of the mechanisms by which the new macroalgal state is maintained. A commonality between the systems described above and a key ingredient in all the regime shifts is alterations in positive feedback loops (Scheffer, 2009)

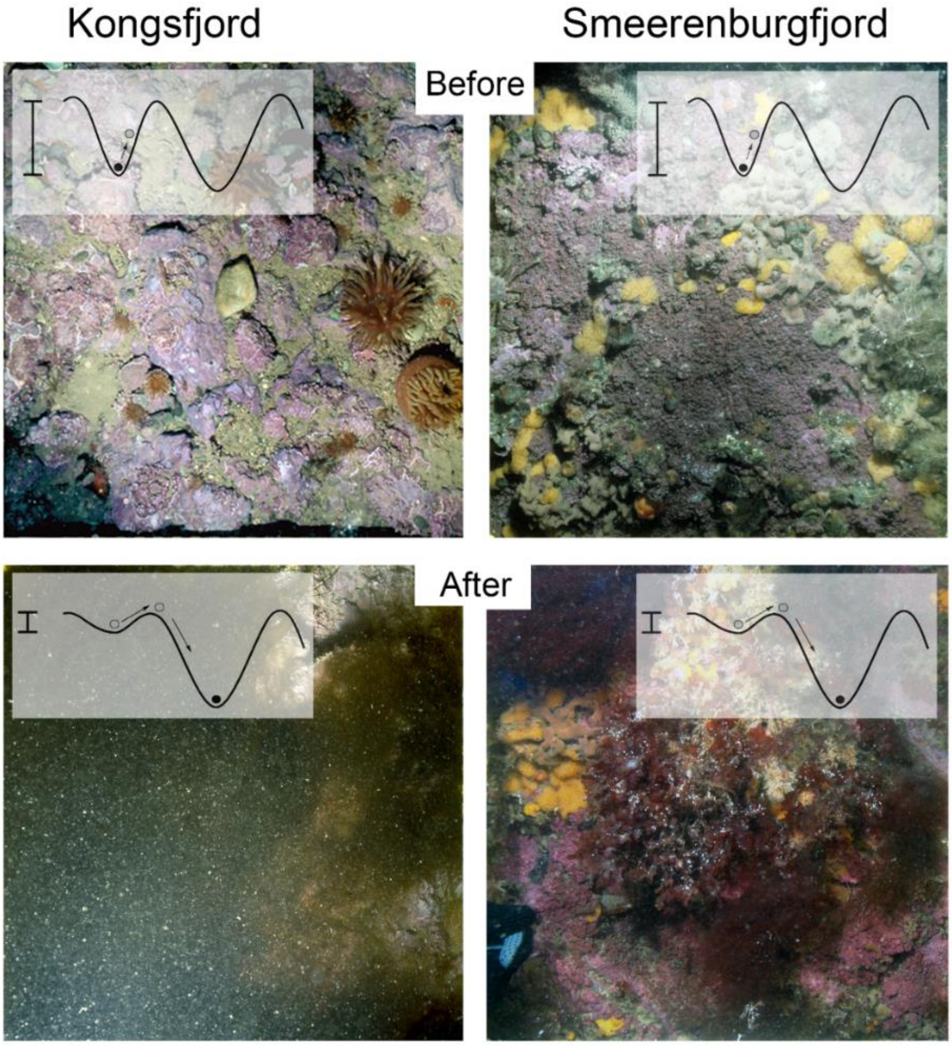
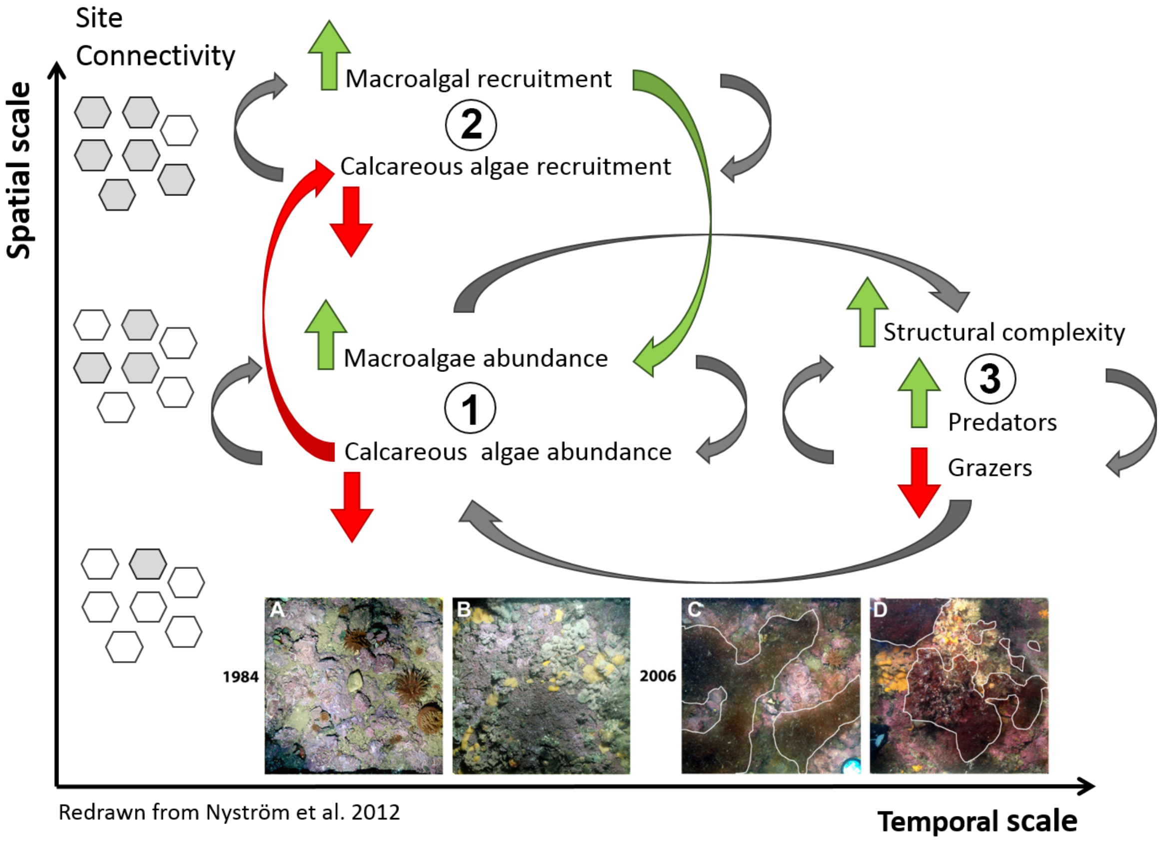


Figure 14. Photographs of the rocky-bottom communities in Kongsfjord and Smeerenburgfjord in Svalbard before and after the regime shift in 1996 and in 2000. The 1980s were characterized by a calcareous algae-dominated state in both fjords with patchy assemblages of sessile invertebrates. In 1996, there was a fivefold increase in macroalgae in Kongsfjord and in 2000 an eightfold increase in Smeerenburgfjord. Parallel shifts in the community structure of invertebrates suggests that the regime shift was community-wide.

Box 4: Conceptual diagram of potential feedbacks in Svalbard hard-bottom communities



Redrawn from Nyström et al. 2012

Figure 15. Schematic illustration of potential reinforcing feedbacks in the hard-bottom benthic communities in two arctic fjords of the west coast in Svalbard. Climate warming can generate feedbacks that materialize through the outcomes of local competitive interactions between macroalgae and calcareous algae. 1) The feedbacks are generated between two algae competing for space and nutrients. As seawater and light availability increases, macroalgae will have competitive advantages over calcareous algae. 2) increased macroalgae abundance enhances macroalgae recruitment, whereas calcareous recruitment diminishes with decreasing abundance. As the abundance and biomass of macroalgae increase, connectivity between macroalgae-dominated sites increases, promoting regional macroalgae recruitment further. 3) Over time, these feedback may be strengthened further, if grazers on macroalgae decline due to increasing abundance of predators. Increased abundance of structuring macroalgae may lead to increased structural complexity because macroalgae act as ecosystem engineers, providing a secondary substrate for epifauna and epiphytes as well as shelter and refuge for grazers, but also increased abundance of predators. The new macroalgal state is maintained by these feedback loops that act over temporal and spatial scales. Increased nutrient inputs due to enhanced degradation of organic material from macroalgae may be another positive feedback mechanism strengthening the macroalgal state. Also nutrient provision by epifauna on macroalgae, e.g. bryozoans and hydroids, may act as positive feedbacks promoting macroalgal growth further (Hepburn & Hurd, 2005; Bracken *et al.*, 2007).

7. Methodological constraints and future work

One of the main limitations of our topological food-web descriptions is that they are static representations of species' trophic interactions, while, in nature, food webs are dynamic and configurations change through time and space. Species shift their diet with life stage and season (Johannesen *et al.*, 2015), and mobile species may shift their diet between foraging regions. Trophic configurations may change with resource availability, habitat size and with temperature (Sentis *et al.*, 2014; McMeans *et al.*, 2015). To account for changes due to diet because of ontogenetic niche shifts, it would be necessary to split the nodes into juveniles and adults. Integrating stage-specific nodes would change the structure and corresponding feedbacks in the food web. For pragmatic reasons, we ignored diet plasticity and assumed that species connected in the meta-web would also be connected in the sub-webs i.e., local food-web regions. I fully acknowledge the limitation of this assumption, but I would still argue that our analyses, although relatively simple, might give a good idea about how the potential interactions and configurations of the arctic food web could change owing to the poleward movement of boreal generalists. I also acknowledge that plasticity of species interaction is important for food-web dynamics and may either increase or decrease food-web persistence, depending on the type of rewiring (Valdovinos *et al.*, 2010; Ramos-Jiliberto *et al.*, 2012; Gilljam *et al.*, 2015). Plasticity in diet was not covered in our papers and development of this aspect could be an avenue for future work.

The two arctic food webs (Arctic I and Arctic II) in **Paper 1** should be interpreted as representations of potential realized interactions in the Barents Sea before and after the poleward expansion of boreal fish generalists. Realized interactions can, empirically, only be assessed via stomach content or isotope analysis, which are laborious operations considering the vast area that we are studying. Nonetheless, stomach content analyses have been undertaken recently in the Barents Sea by the Institute of Marine Research, indicating that cod stomachs were filled with a greater variety of prey species than previously (Johannesen *et al.*, 2015), which lends support to their role as food-web network connectors, linking across trophic levels and habitats. Theoretically, one way to assess potential interactions in a food web is via probabilistic food-web modelling, combining food-web data with species abundance data and trait information (Pellissier *et al.*, 2013; Morales-Castilla *et al.*, 2015; Poisot *et al.*, 2015). Information on abundance would allow us to assess the probability of an interaction. For example, if interacting species are abundant in a region, the probability of interaction is high, whereas if both species are rare, the probability of interaction is correspondingly low.

Another limitation of our binary food webs is the lack of interaction strength. The structure of food webs is not only determined by the way species are linked, but also by the strength of interactions. However, it is not a straightforward procedure to add the interaction strengths among species, as the effect of one species upon another is empirically not known for most species. Theoretical studies have approached this problem via body-size information and allometric scaling laws (Emmerson & Raffaelli, 2004; O'Gorman *et al.*, 2010). Integrating information of body size for each species is the next natural step in developing the Barents Sea food webs. Body-size information combined with data on species traits, distribution and abundance can be used to predict quantitative food-web structure across the Barents Sea. Theoretically predicted interaction strengths among species would allow for dynamic assessments of the flow and transformation of energy via, e.g., bio-energetic food-web models (Yodzis & Innes, 1992; Bascompte *et al.*, 2005). Dynamic modelling of quantitative food webs is essential for testing complexity-stability relationships, robustness and persistence of the food-web structure to perturbations (Otto *et al.*, 2007; Gilarranz *et al.*, 2016), which is a crucial step in developing proper resource-management plans. Such types of modelling should be prioritized in future work on Barents Sea food webs. Combining food web data with information on species' traits (in particular body size), abundance, and interaction strength would allow for the testing of a range of ecological hypotheses (Brown, 1984; Slatyer *et al.*, 2013). For example, whether the degree of specialism increases with temperature in actively hunting invertebrates (Binzer *et al.*, 2016), or perhaps decreases?

Another common limitation in food web research, including in the Barents Sea food webs, is the missing homogeneity in taxonomic resolution among ecological groups. Our food webs are systematically biased towards higher trophic levels. While fish, sea birds and marine mammals are represented at the species level, primary producers are represented as aggregated groups, because of incomplete species and diet information and poor sampling of basal species. Lumping phytoplankton species into one group results in a group of species spanning a size range of a magnitude similar to the size range between mice and elephants (Boyce *et al.*, 2015a). I acknowledge that a better resolution at the basal level would improve the representation of the complexity in marine food webs. Incorporating a more highly resolved representation at the basal level would have consequences for food-web structure, e.g. trophic level, chain length and connectivity. As predator–prey interactions among basal groups are determined almost entirely by size relationships (Boyce *et al.*, 2015a), a size-based approach could be developed to connect phytoplankton and secondary producers in the food web, resulting in a more realistic food-web structure. However, a strength of our food-web comparison is that unlike most comparative food-web studies, the levels of trophospecies aggregation between the study regions are identical (**Papers 1 and 2**). Therefore, dissimilarities between food-web regions in the Barents Sea should not be attributed to differences in the classification and aggregation of trophospecies; rather, they should be attributed to differences in species composition and link configuration among the regional food webs.

7.1 Future prospects for the Svalbard time series: merging interaction types

Trophic interactions are the most central organizing principle in ecosystems because they represent the flow of energy. Therefore, trophic interactions have received much attention in ecology; but also non-trophic interactions, such as mutualism and competition, are very important for the co-existence of species and for promoting and maintaining community structure. Actually, competitive outcomes may constrain trophic interactions before predation-related traits (Allesina & Levine, 2011). For example, in lake ecosystems, competition between brown trout and arctic charr may induce a diet (niche) shift in arctic charr from generalism to specialism (Langeland *et al.*, 1991). Since various interaction types, trophic and non-trophic, work in concert to shape communities, they should ideally be integrated into one framework and analysed jointly. Facilitation (e.g. mutualism or commensalism), which is a widespread interaction type in ecosystems, is particularly common among plant communities and their interactions, e.g. among plant–plant, plant–insect or plant–invertebrate. Recently, a few studies have begun to investigate the network structure of non-trophic interaction in intertidal communities (Kéfi *et al.*, 2012; Kéfi *et al.*, 2015), and yet another study has investigated the effects of combining trophic and non-trophic interactions into one framework, investigating what consequences this has for ecological interpretation (Sander *et al.*, 2015).

Paper 3 of this thesis deals with non-trophic interactions such as competition and facilitation and their importance for structuring hard-bottom benthic communities in Svalbard. Analysis and interpretation of the Svalbard time series of rocky-bottom benthos could be developed further by investigating the network structure of trophic and non-trophic interactions within these communities. The trophic and non-trophic interaction types may be combined into one framework and, due to the temporal information provided by the time series, the temporal development of these various types of interactions may be explored. This would also allow us to assess the structure of biotic interactions, trophic and non-trophic, before and after the regime shift, which might further allow to the identification of changes in feedback mechanisms that could have promoted the regime shifts. Temporal analyses, combining trophic and non-trophic interactions, are rare and would be extremely valuable to advancing our basic ecological understanding of how biotic interactions develop trough time and how they maintain structure and function in ecological communities.

7.2 Humans as part of the food web

The human footprint on the planet is growing. There are 7 billion people on the planet currently, and this number is estimated to reach more than 9 billion by 2050, all in need of food and shelter (Godfray *et al.*, 2010; Béné *et al.*, 2015). Yet, most studies of highly resolved ecological food webs do not include humans as a node in the network, except for a newly published paper that looked at the role of hunter-gatherers in the Sanak food web, a North Pacific marine food web (Dunne *et al.*, 2016). Only Pacific cod with 124 interactions had more interactions than hunter-gatherers, with 122 interactions. Not surprisingly, they found that humans are super-generalists and highly omnivorous. Although hunter-gatherers played an important structural role in the Aleutian marine system, this theoretical approach suggested that the presence of limited technology-assisted hunter-gatherers did not lead to species' long-term extinction. On the contrary, the role that humans played as generalists, with their ability to switch prey, potentially promoted stability and biodiversity (McCann *et al.*, 2005). However, modern humans, assisted by advanced technology, can exploit resources that would otherwise be out of reach; this has a huge impact on ecosystem structure and function. Owing to the advances in technological development, the rate and spatial scale at which modern *Homo sapiens* are altering the environment through agriculture, fisheries, clearing of forests, habitat fragmentation, pollution, and CO2 release is unprecedented in history (Sala *et al.*, 2000; Duraiappah *et al.*, 2005; Levin & Lubchenco, 2008), causing major alterations in ecosystem structure and function (Barnosky *et al.*, 2012). To understand, how robust (or vulnerable) ecosystems are to environmental human-induced degradation and how much capacity the ecosystem has to withstand human impact, we should also include humans as a node in our food web analysis. It might directly enhance our understanding of how activities, for example, fisheries may alter the structure of food webs and how potential feedbacks in ecosystems are changed. For example, a recent study showed that marine food webs close to human settlements were less persistent than food webs further away from human influence (Gilarranz *et al.*, 2016).

8. Considerations for conservation and ecosystem management

"To protect Nature, we must have some understanding of her complexities, for which the food web is the basic description." (Pimm, 1982)

Why should we care about the trophic structure of food webs? First, because structure always affects dynamics and function of ecosystems! The degree of modularity, the number of loops or the length of food chains are all factors that might influence how communities will respond to environmental change (Pimm, 1982). Structure is of great importance to food web stability and persistence and needs to be considered when studying the effects of environmental changes. Second, because ecological community structure is currently disrupted worldwide by unprecedented species loss and distributional changes of species, such as a poleward shift across all major ecosystems and by invasions of species across ecosystems (Barnosky *et al.*, 2012). Because food webs are the road maps of trophic interactions through *Darwin's entangled bank* and indicate how energy flows among species, the network approach provides an opportunity to reconcile ecosystem structure and function (Thompson *et al.*, 2012). Food web analysis is a powerful framework with which to elucidate how perturbations propagate through the ecosystem (Dunne *et al.*, 2002a; Curtsdotter *et al.*, 2011), and facilitate the identification of the structural roles that species play in maintaining configurations important for stability and ecosystem functioning.

Papers 1 and 2 of this thesis suggest that topological features of the empirical food webs are a result of species-specific attributes and their trophic structure, and not a result of the number of species and links *per se*. This has implications for the way we should think about species management. While species loss is of vital concern, it may be just as important to identify the consequences of interaction types lost or added to an ecosystem (Mougi & Kondoh, 2012; Stouffer *et al.*, 2012). Traditional ecological research assesses the abundance, biomass and distribution of species. Although informative, analyses that treat a species as independent units tell us nothing about the trophic and non-trophic structure of a species, i.e. its relationships to neighboring species, and the effects that species have on each other. Throughout this PhD synthesis, I argued that a species' trophic structure has community-wide implications for food web persistence, robustness and functioning (Stouffer & Bascompte, 2011). This is because removing a species from the food web or adding a species will affect not only the species removed or added but also the trophic structure of other species, and will propagate through the entire food-web network.

Whereas probably no single management index works for all food webs and ecosystems, the point raised in recent papers is that prioritizing management based on network-wide indices could improve conservation outcomes to overall food-web persistence compared to single-species management (Levin & Lubchenco, 2008; Gilarranz *et al.*, 2016; McDonald-Madden *et al.*, 2016). While being just a first attempt to map the trophic structure of marine Barents Sea communities at the regional to the ecosystem level, this thesis contributes in this direction. Combining data sets of species-distribution data with data on trophic interactions, as performed in this PhD thesis, coupled with functional trait information of species and sound dynamic multispecies modelling, as planned in future work on Barents Sea food webs, may pave the way for an integrated ecosystem-based assessment for the Barents Sea. This could potentially generate better solutions to conservation and ecosystem management. Having said this, it is worth mentioning that ecosystem science "*is not rocket science; it is far more complex*"(Game et al., 2014). Complexity emerges from the myriad of interacting living elements that constantly evolve and adapt. To deal with this complexity is a great challenge and one must not be naïve; *there is no escaping the magnitude of this endeavour* (Brown, 1995).

However, in my view, if we want to act responsibly and face ourselves with the reality of nature, including our own nature, we are left with no other choice than to embrace, respect and appreciate nature's complexity. Although this outlook may seem daunting, there are reasons to be optimistic because the dynamics of the ecological and evolutionary processes are constrained by the nature of its components and the kinds of interactions among them, i.e. by the structure of the system (Brown, 1995). These constraints produce recognizable patterns at higher organizational scales. Patterns that are captivating and fascinating, so the good take-home message here is; that, it is precisely in nature's complexity that beauty and mystery dwells, and thinking about it; who would like to live a life without beauty and mystery.

9. What is new?

My PhD thesis contributes to development in basic food web ecology and marine biology. The findings are also relevant for applied marine ecology and management considerations in the Barents Sea. My work provides empirical evidence that food-web structure changes along environmental and climatic gradients in the Barents Sea and that structural components of arctic marine communities are changing as a response to warming. In light of ecological theory, I have tried to explain the mechanisms behind some of the observed community patterns. One of my papers (**Paper 3**) provides empirical evidence that responses to warming may be abrupt, extensive and persistent, indicative of a regime shift. This is the first time that empirical evidence for a potential regime shift has been indicated for arctic marine hard-bottom communities. The detection of an abrupt community shift was possible thanks to the long-time series, underscoring the importance of collecting long-term data for documenting the nature of species responses and community development to past conditions.

The main body of this PhD focuses on marine food webs in the Barents Sea. To my knowledge, this is the first time that differences in topology of highly resolved empirical marine food webs have been analyzed along environmental gradients for such a large area; though see a newly published paper by Gillaranz *et al.* for another study of spatially reasonably highly resolved marine food webs (Gilarranz *et al.*, 2016). Analysing food webs at the regional scale was facilitated by combining two data sets; species-distribution data and information of species interactions via a meta-web. Combining data-sets to subsample local food webs is instructive and allows for comparing species across regions in the ecosystem. We documented that boreal fish species moving poleward as a response to climate warming in the Barents Sea are characterized by high generalism, a property that has a strong impact on overall food-web structure, in particular on modularity. Although we do not have knowledge of the exact realized interactions between cod and its preys in the Arctic, the potential interactions suggested a rather drastic alteration in the arctic marine food-web structure with super-generalists such as cod included. **Paper 2** is one of the few studies to date documenting how food-web structure and motifs vary along environmental gradients on a biogeographic scale. **Paper 2** further illustrates how linking the analysis of food-web structure along environmental gradients with the analysis of species' structural roles in the food web provides insights into the potential mechanisms that generate a given structure. Developing this aspect further and digging deeper into how motifs vary along environmental gradients combined with species-trait information may contribute to the long-sought reconciliation between structure and function or pattern and process in ecological communities.

Acknowledgements

In this synopsis, I reprinted several figures. I would like to thank Renate Degen and the journal *Marine Ecological Progress Series* for permission to reprint figures. Thanks to Ingrid Onarheim at the Bjerknes Research Centre for permission to reprint figures. Thanks to the journal *Nature*, the National Snow and Ice Data Center and the Arctic Monitoring and Assessment Programme for permission to reprint figures. Thanks to the journals *Proceedings of the National Academy of Sciences* and *Proceedings of the Royal Society B* for permission to reprint Papers 1 and 3 of this thesis. I would also like to thank Louise Harnby and André Frainer for proof reading a previous version of this synopsis. Many thanks to my friend Anna Laurine Kornum for making nice drawings of some of the most important and conspicuous species in the Barents Sea ecosystem.

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Appendix
Data paper

Who eats whom in the Barents Sea: a food web topology from plankton to whales

Benjamin Planque, Raul Primicerio, Kathrine Michalsen, Michaela Aschan, Grégoire Certain, Padmini Dalpadado, Harald Gjøsæter, Cecilie Hansen, Edda Johannesen, Lis Lindal Jørgensen, Ina Kolsum, Susanne Kortsch, Lise-Marie Leclerc, Lena Omli, Mette Skern-Mauritzen and Magnus Wiedmann

Ecology, 95, 1430

Ecology, 95(5), 2014, p. 1430

Who eats whom in the Barents Sea: a food web topology from plankton to whales

Ecological Archives E095-124

Benjamin Planque,[1,6] Raul Primicerio,[2] Kathrine Michalsen,[3] Michaela Aschan,[2] Grégoire Certain,[1] Padmini Dalpadado,[3] Harald Gjøsæater,[3] Cecilie Hansen,[3] Edda Johannesen,[3] Lis Lindal Jørgensen,[1] Ina Kolsum,[2] Susanne Kortsch,[2] Lise-Marie Leclerc,[2,4] Lena Omli,[5] Mette Skern-Mauritzen,[3] and Magnus Wiedmann[2]

[1] *Institute of Marine Research, P.O. Box 6404, 9294 Tromsø, Norway*
[2] *Faculty of Biosciences, Fisheries and Economics, University of Tromsø, 9037 Tromsø, Norway*
[3] *Institute of Marine Research, P.O. Box 1870, 5817 Bergen, Norway*
[4] *Department of Environment, Government of Nunavut, P.O. Box 377, Kugluktuk, Nunavut NU X0B0E0 Canada*
[5] *Institute of Marine Research, Nye Flødevigveien 20, 4817 His, Norway*

Abstract. A food web is an ecological network and its topological description consists of the list of nodes, i.e., trophospecies, the list of links, i.e., trophic interactions, and the direction of interactions (who is the prey and who is the predator). Food web topologies are widely used in ecology to describe structural properties of communities or ecosystems. The selection of trophospecies and trophic interactions can be realized in different manners so that many different food webs may be constructed for the same community. In the Barents Sea, many simple food webs have been constructed. We present a comprehensive food web topology for the Barents Sea ecosystem, from plankton to marine mammals. The protocol used to compile the data set includes rules for the selection of taxa and for the selection and documentation of the trophic links. The resulting topology, which includes 244 taxa and 1589 trophic links, can serve as a basis for topological analyses, comparison with other marine ecosystems, or as a basis to build simulation models of the Barents Sea ecosystem. The data set consists of three related tables: (1) the list of taxa, (2) the list of pairwise interactions, and (3) the list of bibliographical references.

Key words: *benthos; birds; fish; mammals; plankton; trophic interactions.*

The complete data sets corresponding to abstracts published in the Data Papers section of the journal are published electronically in *Ecological Archives* at http://esapubs.org/archive (the accession number for each Data Paper is given directly beneath the title).

Manuscript received 13 June 2013; revised 17 January 2014; accepted 31 January 2014. Corresponding Editor: W. K. Michener.

[6] E-mail: benjamin.planque@imr.no

Who eats whom in the Barents Sea: a food web topology from plankton to whales

Ecological Archives **E095-124-D1**

Benjamin Planque, Raul Primicerio, Kathrine Michalsen, Michaela Aschan, Grégoire Certain, Padmini Dalpadado, Harald Gjøsæter, Cecilie Hansen, Edda Johannesen, Lis Lindal Jørgensen, Ina Kolsum, Susanne Kortsch, Lise-Marie Leclerc, Lena Omli, Mette Skern-Mauritzen, and Magnus Wiedmann . 2014. Who eats whom in the Barents Sea: a food web topology from plankton to whales. *Ecology* 95:1430.http://dx.doi.org/10.1890/13-1062.1

UPDATED METADATA (ADDED AUGUST 2015, SEE PAGE 13)

METADATA

CLASS I. DATA SET DESCRIPTORS

Abstract: A food web is an ecological network and its topological description consists of the list of nodes, i.e., trophospecies, the list of links, i.e., trophic interactions, and the direction of interactions (who is the prey and who is the predator). Food web topologies are widely used in ecology to describe structural properties of communities or ecosystems. The selection of trophospecies and trophic interactions can be realized in different manners so that many different food webs may be constructed for the same community. In the Barents Sea, many simple food webs have been constructed. We present a comprehensive food web topology for the Barents Sea ecosystem, from plankton to marine mammals. The protocol used to compile the data set includes rules for the selection of taxa and for the selection and documentation of the trophic links. The resulting topology, which includes 244 taxa and 1589 trophic links, can serve as a basis for topological analyses, comparison with other marine ecosystems, or as a basis to build simulation models of the Barents Sea ecosystem. The data set consists of three related tables: (1) the list of taxa, (2) the list of pairwise interactions, and (3) the list of bibliographical references.

Key words: *benthos; birds; fish; mammals; plankton; trophic interactions.*

Data files

`SpeciesList.txt`

`PairwiseList.txt`

`References.txt`

CLASS II. RESEARCH ORIGIN DESCRIPTORS

A. Overall project description:

A.1. Identity:

This data set was compiled as part of the project entitled BarEcoRe: Barents Sea Ecosystem Resilience under global environmental change

A.2. Originators:

The project was coordinated by Benjamin Planque at the Institute of Marine Research, Norway, benjamin.planque@imr.no. The construction of the topology was initiated during a workshop, held in Bergen and Tromsø on the 8–9 June 2011.

A.3. Period of study:

BarEcoRe started in June 2010 and ended in May 2013. The food web topology data set was assembled during that period. The topology does not refer to a period in particular but is based on documentation and observations throughout the 20th and early 21st century.

A.4. Objectives:

The main objective of BarEcoRe was to evaluate the effects of global environmental change on the future structure and resilience of the Barents Sea ecosystem. The food web topology was constructed in order to investigate the structural properties of the Barents Sea food web and how these may be related to ecosystem resilience.

A.5. Abstract:

BarEcoRe aimed to evaluate the effects of global environmental change on the future structure and resilience of the Barents Sea ecosystem. This was studied by investigating the effects of past changes in climate and fisheries on the Barents Sea ecosystem, by developing indicators of ecosystem resilience, diversity and structure, and by forecasting the possible future states of the Barents Sea ecosystem under particular environmental and fisheries scenarios. The key questions addressed by the project were: (1) What are the key characteristics of past temporal and spatial variations in fish and benthos communities and how are these related to past climate variability and fishing pressure? (2) How does climate variability and change propagate through the Barents Sea ecosystem and influence species interactions? (3) How can the combined effects of fisheries and climate modify the spatial distribution of plankton, benthos, and fish species in the Barents Sea? (4) What determines vulnerability or resilience of the Barents Sea ecosystem and how will these be affected by possible future changes in climate and fisheries regimes? (5) Can we detect early warning signals and can we evaluate management strategies with regards to ecosystem resilience? These questions were studied through a number of approaches which included: process studies of trophic interactions, retrospective analysis of plankton, benthos, and fish communities' structure and ocean climate, predictive models of ocean climate, population spatial distribution models under climate and biological constraints and ecological network analysis. This data set is the basis for the network analysis.

A.6. Sources of funding:

BarEcoRe was funded by the Norwegian Research Council (NFR-grant 200796/41), the Institute of Marine Research, Norway, and the University of Tromsø, Norway. Additional funding for the construction of this data set was received from the Tromsø Research Foundation.

B. Research motivation

The study of food webs has been a topic of ecological research for many decades. The growing interest in the study of complex systems and the use of graph theory to investigate properties of large networks has vitalised food web research and the analysis of food web structures or topologies (Dunne 2009, Petchey et al. 2010). A food web consists of throphospecies (one or more species sharing predators and prey) and the feeding links between them (Yodzis 1988).

Early work on the comparison of food webs between areas and ecological systems was fostered by the ECOWeB data bank, a compilation of food webs (Cohen 1989). However, such compilations suffered from lack of resolution and great disparities in the methods used to assemble food webs from different systems. This led to specific recommendations for improving food web construction (Cohen et al. 1993). Re-analyses of the original ECOWeB data revealed that incomplete food web topologies led to inaccurate conclusions (Goldwasser and Roughgarden 1997). To be useful for comparative analyses, food webs must be constructed using a clearly described methodology (Jordán 2003). Currently, many food webs exist for the Barents Sea (see, e.g., , Sakshaug et al. 2009). However these are usually restricted to few taxa (typically less than 20), with a particular focus on few groups (e.g., , fish and mammals) and their method of construction is poorly documented. The largest food web topology for the Barents Sea was recently assembled by Bodini et al. (2009) for the purpose of investigating secondary extinctions. It contains 254 species, of which 151 have one or more trophic links. The method and data sources used to construct this topology are not documented and it is therefore uncertain if such a data set can be used to derive reliable ecological conclusions on the functioning of the Barents Sea ecosystem, although this has already been attempted (de Santana et al. 2013). The motivation for compiling the current data set is to provide the first comprehensive food web topology for the Barents Sea for which the methodology is transparent and the data source explicit. We are aware of the large body of relevant references in Russian that have only partly been included in the present work. Future revisions of this topology will likely expand on the number of nodes, links and bibliographic references.

C. General methodology:

C.1. System definition

The food web topology is defined for the ecosystem of the Barents Sea from plankton to sea mammals. The topology consists of 3 elements: nodes, i.e., trophospecies, links, i.e., trophic interactions, and directions, i.e. who is the predator and who is the prey.

C.2. Spatial and temporal coverage

The spatial coverage of our data set extends over the Barents Sea, limited by Novaya Zemlya in the East. The Barents Sea is a shelf sea situated north of Norway and Russia extending from 68.5°N to 82.58°N and from 8.0°E to 68.5°E. It covers an area of 1.6 million km^2 with an average depth of 230 m (Carmack et al. 2006). The temporal coverage of the data set is set by the literature review and available data and covers the period 1927–2012, although half of the references used are from the last two decades (1994–2012).

C.3. Data sources

There are three primary sources for the data set: (1) peer reviewed publications; (2) gray literature and institutional reports; (3) inference on the basis of knowledge on similar species or comparable regions. Norway and Russia have, through the last 25 years, collected an extensive amount of fish-stomach data from the Barents Sea that was used to document links between fish and their prey. No surveys were conducted within the BarEcoRe project. The references used to support the inclusion of the trophic links, are provided in the data set (see section C.5.d).

C.4. Nodes, trophospecies

Nodes in the food web topology correspond to trophospecies. A trophospecies is one or more species sharing predators and prey. When possible, individual trophospecies correspond to taxonomic species. Yet, these can sometimes refer to larger taxonomic groups (e.g., , genus, family, class) or to specific stages (larvae, juveniles, adults). By default, a trophospecies is given with reference to the adult stage.

C.4.a: selection criteria

Trophospecies selection was done using four criteria: (1) there is information on trophic interactions, i.e., prey and/or predator/s are known; (2) the spatial extent of the species exceeds 5% of the total Barents Sea area; (3) the temporal extent is sufficient, i.e., the trophospecies has been observed in several instances over several years or seasons; (4) if the trophospecies has not been observed in the Barents Sea, but its distribution can expand into the area due to climate change (e.g., , mackerel *Scomber scombrus*) it can also be included.

C.4.b: grouping and splitting

When taxonomic identification was not conducted to species level, trophospecies may refer to larger groups such as genus, family, or class. There are few instances where different taxon levels result in overlap in the data set:
Oikopleura sp.,*Pagurus* sp., *Astarte* sp., *Sebastes*_sp, *Ammodytes*, Actinaria, and Porifera. Detritus forms a group which has no taxonomic identity. Many marine organisms undergo ontogenetic metamorphosis and/or changes in size that may span over several orders of magnitude. In such cases, the trophic links (relevant prey and predators) can vary greatly during the lifetime of the organisms. A group of fish eggs and larvae is therefore defined.

C.4.c: seasonal and spatial variations

The spatial distribution of many trophospecies is limited to specific regions of the Barents Sea and these can vary with seasons and years. As a result, all trophospecies listed in this topology do not necessarily meet. The resulting topology is a reference for all Barents Sea species, but analyses of the food web structure must take into account when and where prey and predators actually interact.

C.4.d: phylogenetic information

For each trophospecies listed in the data set, we provide additional information on order, class and phylum or sub-phylum. The information is derived from the World Register of Marine Species (WoRMS: http://www.marinespecies.org/) and Fish Base (http://www.fishbase.us/).

C.4.e: naming of trophospecies

Naming of trophospecies was done using the latin names for genus and species, when applicable. For higher systematic taxa, the latin name for genus, family, order, class, or phylum was used. For specific stages or groups that did not correspond to a taxon, a self-explanatory english name for the trophospecies was chosen (e.g., , detritus).

C.5. Links and directions, trophic interactions

Food web links are trophic interactions between two trophospecies. The relationship is directional from the prey to the predator. In case of cannibalism, the prey and predator is the same trophospecies. Basal species are trophospecies without prey. Top predators are trophospecies without predators. In the present data set, each trophospecies has at least one link towards a prey or a predator, due to the selection criteria (*C.4.a,* 1).

C.5.a: selection criteria

In the present data set only the effective trophic links were reported by specifying prey and predator names, i.e., there is no information to support the absence of trophic links. A trophic link between two trophospecies was included in the data set when there was information available to support the link. The information could come in various forms, from published material in peer reviewed journals, survey reports, institutional databases, expert knowledge or inference on the basis of knowledge on similar species or comparable regions. The information supporting individual links was qualified using a 1–4 scale, as detailed in section C.5.c.

C.5.b: seasonal and spatial variations

When a link is documented, it indicates that a specific prey is known to be eaten by a specific predator. As the spatial distribution of prey and predators can vary temporally within the Barents Sea, it does not imply that prey and predator are interacting everywhere and at all times. As a result, all trophic links listed in this topology can be used as a reference for the Barents Sea in general, but specific analyses of the food web structure must take into account when and where prey and predators may actually interact. This information is not provided in the current data set.

C.5.c: data source and qualification

The quality of the information used to document trophic links was graded from 1 to 4, '1', being the most reliable sources of information, and '4' being the least reliable sources of information (Table 1.).

TABLE 1. Coding nomenclature for the trophic links.

Code	
1	Link documented by quantitative data and published in peer-reviewed literature
2	Link documented by quantitative data available in databases or published in gray literature
3	Link reported from other sources of information (personal observations, fishermen's report, etc.)
4	Plausible link. It has not been observed but it can be inferred from other observations on related species or other geographic areas

The link was coded '1',when peer reviewed literature was the primary source of information documenting the trophic link between two trophospecies, and when this information was originating from a dedicated observation protocol (e.g., , stomach sampling). The link was coded '2', when the information was not reported in the peer-reviewed literature, but originated from gray literature, e.g., , reports from research institutes or databases based on a dedicated observation protocol. The link was coded '3', if no dedicated observation protocol was used, but the link was reported in several instances (e.g., , personal observations by scientists or fishermen).

The link was coded '4', if no primary source of information could be found, but it was thought to be plausible based on observations in other oceanic regions, or of organisms of the same group (e.g., , other species of the same genus).

D. Data limitations and potential enhancements

D.1. Definition of nodes

D.1.a. geographical and temporal selection criteria

The selection of taxa to be included in the data set relies on selection criteria (section *C.4.a.)* which include presence of the taxa in the Barents Sea over at least a minimum time and geographic extent (5% of the area). It was often not possible to access robust quantitative data on the spatial and temporal distribution of taxa so therefore uncertainty remains in the node selection process. Given past changes in the distribution and abundance of many species in the Barents Sea and expected future variations due to climate change, the list of taxa to be included in the topology should be revised and updated in the future.

D.1.b. taxonomy

Taxonomy is an active field of research and the name of all taxa listed in this data set may not remain fixed over time. We have used the WoRMS taxonomy terminology. The inclusion of different taxonomic levels in the same food web is problematic when conducting analysis of the topology. We have provided phylogenetic information so that it is possible to eliminate overlapping taxa when desired. Ultimately, a higher taxonomic resolution could be used to remove taxa above species level.

D.1.c. lower trophic levels

The current topology does not expand to trophic groups below meso-zooplankton, with the exception of diatoms, macroalgae, and mixotrophs. This may be expanded in the future.

D.2. Definition and coding of links

D.2.a: coding nomenclature

The coding nomenclature defines the reliability (section C.5.c) of the trophic link. Yet, some of the links need to be revised. To be successful, future attempts to build or complement a topology constructed with the present protocol should ensure sufficient scientific discussion (e.g., , in a workshop) to ensure consensus among the experts involved so that the protocol is well understood and followed.

D.2.b: bias towards predators

Studies on prey–predator interactions are often derived from observation on the predator, typically by conducting stomach analyses. Therefore the reported trophic links are biased towards predatory groups that are well studied, such as commercial fish species, as well as well-studied birds and mammals. For less well studied groups, e.g., , benthic invertebrates, the number of nodes and trophic links may be under-reported.

D.3 Exhaustiveness

Although we have tried to compile a food web topology that is as exhaustive as possible, the current data set is necessarily limited by the joint expertise of the authors. It is expected that the dissemination of the current data set will lead to feedback and improvement through corrections and additions from scientists active in this field.

CLASS III. DATA SET STATUS AND ACCESSIBILITY

A. Latest update: xxx.

This is the first version of this data set. There is currently no archiving procedure or repository for this data set other than the current publication.

B. Latest metadata update:

This is the first version of the metadata.

C. Copyright or Proprietary Restrictions:

This data set is freely available for non-commercial scientific use, given the appropriate scholarly citation.

D. Contact person:

Kathrine Michalsen. Institute of Marine Research, PO Box 1870, 5817 Bergen, Norway, kathrine.michalsen@imr.no.

CLASS IV. DATA STRUCTURAL DESCRIPTORS

A. Data set files

There are three data files. The first contains the list of trophospecies, the second the list of links and the third the list of literature references. All files are in ASCII format, where each line contains an individual record and each column an individual descriptor. Lines are separated by carriage return (CR) and columns are separated by tabulations (TAB). The first line of each data table contains the column headers.

A.1. List of trophospecies: SpeciesList.txt

A.1.a. file format and size

244 records (rows), 7 descriptors (columns), and headers in the first row.

A.1.b. fields

TROPHOSPECIES: Name of the taxa, in Latin.

ABBREVIATION: Shortened Latin name.

PHYLUM_SUBPYLUM: Taxa phylum or sybphylum

CLASS: Taxa class, if applicable

ORDER: Taxa order, if applicable

FAMILY: Taxa family, if applicable

GROUP: Practical grouping identifier (plankton, benthos, fish, birds, mammals)

A.2. List of trophic links: PairwiseList.txt

A.2.a. File format and size

1589 records (rows), 4 descriptors (columns) and headers in the first row.

A.2.b. Fields

PREY: Name of the prey taxa

PREDATOR: Name of the predator taxa

CODE: qualification code for the trophic link (see section *C.5.c*)

REFERENCE: Author and year of publication. When several references are provided, they are separated by a semicolon (;). This field can be empty.

A.3. Literature references: References.txt

A.3.a. File format and size

182 records (rows), 2 descriptors (columns), header in the first row.

A.3.b. Column headers

AUTHOR_YEAR: Author and year of publication

FULL_REFERENCE: Full bibliographic reference

B. Relational fields

The data tables in the three files constitute a relational database. The relations between fields in different tables are as follows:

[SpeciesList.txt] TROPHOSPECIES : [PairwiseList.txt] PREY

[SpeciesList.txt] TROPHOSPECIES : [PairwiseList.txt] PREDATOR

[PairwiseList.txt] REFERENCE : [References.txt] AUTHOR_YEAR

CLASS V. SUPPLEMENTAL DESCRIPTORS

A. Comparison between topologies at different quality level

The total number of taxa in this topology is 244, but the number of links to be retained depends on the link quality level. The acceptable level must be defined by users of the topology on a case-by-case basis. When all quality levels are considered (1–4), there are 1589 links out of a possible theoretical total of 2442 = 59536, giving a connectance of 0.027 (the connectance is the ratio of the number of observed links over the number of possible links). When only peer reviewed publications are considered, the total number of links is 621 and 52 orphan species (i.e., no prey and no predator link) are left. The connectance declines to 0.017. The effects of considering various qualification levels are summarized in Table 2.

TABLE 2. Descriptors of the food web topology (rows) for different levels of data quality. 1–4: all quality levels are considered; 1–3: the first 3 quality levels; 1–2: the first 2 quality levels; 1: only quality level 1.

Quality of links	**1–4**	**1–3**	**1–2**	**1**
Total number of taxa	244	244	244	244
Total number of taxa with 1+ link	244	225	220	192
Total number of links	1589	1065	1033	621
Cannibalistic links	15	11	10	8
Connectance 1 (all taxa)	0.027	0.018	0.017	0.010
Connectance 2 (taxa with 1+ link)	0.027	0.021	0.021	0.017

B. Comparison with existing food web topologies

In the past, several topologies have been published. However, there has not been detailed documentation on how the data was collected and validated. We report on two topologies that have been used in the past (Table 3). The topology presented by Dommasnes et al. (2001) was used as the basis for the construction of a combined Ecopath model for the Barents Sea and Norwegian Sea. It is a simplified topology where many nodes correspond to large species groups. This topology contained 30 taxa and 29 trophic links. More recently, Bodini et al. (2009) constructed a more comprehensive topology to study the cascading effects of species removal in a food web, a phenomenon described as secondary extinctions. The topology data set is not publicly available but it was kindly provided by the first author. Out of the 254 taxa listed by the authors, 151 had at least one connection to a prey or a predator, which resulted in 1001 trophic links. We found the connectance in the Dommasnes et al. (2001) topology to be much higher (0.201) than in that of Bodini et al. (0.044) and in the present study (0.026).

TABLE 3. Descriptors of the food web topology (rows) for the current food web (all quality levels), the food web published by Bodini et al. (2009) and the food web published by Dommasnes et al. (2001).

Topology	**Present study**	**Bodini**	**Dommasnes**
Total number of taxa	244	254	30
Total number of taxa with 1+ link	244	151	29
Total number of links	1589	1001	619
Cannibalistic links	15	1	4
Connectance 1 (all taxa)	0.027	0.016	0.188
Connectance 2 (taxa with 1+ link)	0.027	0.044	0.201

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UPDATED METADATA (ADDED AUGUST 2015)

Who eats whom in the Barents Sea: a food web topology from plankton to whales. *Ecology* 95:1430.http://dx.doi.org/10.1890/13-1062.1

Data set version 2

1. Introduction to the revision of the data – August 2015

This second version of the food web topology for the Barents Sea was compiled and quality checked by Susanne Kortsch (susanne.kortsch@uit.no) and Benjamin Planque (benjamin.planque@imr.no).

The information provided in the original publication of the metadata remains valid with the exception of the points highlighted below.

The revised food web topology for the Barents Sea includes revision of the list of trophospecies, revision of the list of pairwise trophic interactions, revision of the list of references, addition of a new table to link pairwise interactions to bibliographic references and modification of the files structure. New automated data qualification procedures were constructed and run to ensure consistency within and between files.

2. Revision of the species list

Taxa were carefully reviewed to ensure that they matched the selection criteria. Taxa that were not in the original data set have been included, such as the abundant polychaete *Myriochele heeri*, while rare species e.g., *Chimaera monstrosa* have been deleted. Species that are taxonomically misidentified at sea e.g., *Dipturus batis*, species that are not found in the Barents Sea e.g., *Calanus helgolandicus* and species with a more coastal distribution e.g., *Mytilus edilus* have been deleted. Species have also been deleted when it was not possible to find diet information, e.g., *Stylocheiron maximum*. Some trophospecies have been aggregated from species level to genus, because of their morphological similarity and the difficulty to distinguish them when sampled and counted at sea. The revised species list consists of 233 taxa.

3. Revision of the pairwise list

The pairwise list has been revised by adding new trophic links and carefully checking the quality coding of individual links. The revised pairwise list consists of 2218 trophic links.

4. Revision of the reference list

New references have been added to better document links that were previously reported or to document links that have been added in the revised data set. The revised reference list consists of 236 bibliographic references.

5. Modification of the files structure

The original data set consisted of three tables: the *species list,* the *pairwise list* and the *reference list*. The updated version contains four tables: the *species list*, the *pairwise list,* the *pairwise2reference* list and the *reference* list. We added the*pairwise2reference* list because the original format did not allow for matching between the *reference* field in the pairwise list and the *author_year* field in the reference list. There can be one, several or no bibliographic references attached to a single pairwise interaction. To account for this, the pairwise list was separated into two related files; the *pairwise* list that contains every single pairwise interactions and the *pairwise2references* list that contains a line for every pair of trophic interaction and reference. The structure of these files, and the relational fields that connect them, are described in the sections below.

6. Automated data qualification procedures

The following criteria were checked automatically and corrections were applied where required

- Species are unique (i.e., listed only once) in the species list
- Pairwise trophic interactions are unique (i.e. listed only once) in the pairwise list
- All species listed in the species list are found at least once in the pairwise list, either as prey or as predator
- All species listed in the pairwise list, either as prey or as predator, are found in the species list

- All pairwise interactions (PWKEY) in the pairwise2reference table are found in the pairwise list
- All references (AUTHOR_YEAR) listed in the pairwise2reference table are found in the reference table
- All references (AUTHOR_YEAR) listed in the reference table are found in the pairwise2reference table
- In the reference table, names of the first author in the AUTHOR_YEAR field and in the FULL_REFERENCE field match.

7. Data set files

There are four data files. The first contains the list of trophospecies, the second the list of trophic links, the third the list of associations between individual trophic links and references and the fourth the list of literature references. All files are in ASCII format, where each line contains an individual record and each column an individual descriptor. Lines are separated by carriage return (CR) and columns are separated by tabulations (TAB). The first line of each data table contains the column headers.

7.1. List of trophospecies: SpeciesList.txt

7.1.a. file format and size

233 records (rows), 7 descriptors (columns), and headers in the first row.

7.1.b. fields

TROPHOSPECIES: Name of the taxa, in Latin. (Primary key for this table)

ABBREVIATION: Shortened Latin name.

PHYLUM_SUBPYLUM: Taxa phylum or sybphylum

CLASS: Taxa class, if applicable

ORDER: Taxa order, if applicable

FAMILY: Taxa family, if applicable

GROUP: Practical grouping identifier (plankton, benthos, fish, birds, mammals)

7.2. List of trophic links: PairwiseList.txt

7.2.a. File format and size

2218 records (rows), 4 descriptors (columns) and headers in the first row.

7.2.b. Fields

PWKEY: Pairwise identification Key- (Primary key for this table). This is constructed by joining the abbreviations of the predator and prey species

PREY: Name of the prey taxa

PREDATOR: Name of the predator taxa

CODE: qualification code for the trophic link (see section *C.5.c in the original metadata description*)

7.3. trophic interaction & references: Pairwise2References.txt

7.3.a. File format and size

2126 records (rows), 2 descriptors (columns), header in the first row.

7.3.b. Column headers

PWKEY: Pairwise identification Key (note that this is not a primary key for this table)

AUTHOR_YEAR: Author(s) and year of publication

7.4. Literature references: References.txt

7.4.a. File format and size

236 records (rows), 2 descriptors (columns), header in the first row.

7.4.b. Column headers

AUTHOR_YEAR: Author(s) and year of publication

FULL_REFERENCE: Full bibliographic reference

7.5. Relational fields

The data tables in the three files constitute a relational database. The relations between fields in different tables are as follows:

[SpeciesList.txt] TROPHOSPECIES : [PairwiseList.txt] PREY

[SpeciesList.txt] TROPHOSPECIES : [PairwiseList.txt] PREDATOR

[PairwiseList.txt] PWKEY : [Paiwise2References.txt] PWKEY

[Paiwise2References.txt] AUTHOR_YEAR : [References.txt] AUTHOR_YEAR

8. Comparison with the original food web topology

The total number of taxa in this topology is 233. The number of links to be retained for a particular analysis depends on the link quality level. The acceptable level must be defined by users of the topology on a case-by-case basis. When all quality levels are considered (1–4), there are 2218 links out of a possible theoretical total of 233^2 = 54289, giving a connectance of 0.041 (the connectance is the ratio of the number of observed links over the number of possible links). When only peer-reviewed publications are considered, the total number of links is 1258 and 10 orphan species (i.e., species without any trophic link link) are left. The connectance declines to 0.026. The effects of considering various qualification levels are summarized in Table 1.

TABLE 1. Descriptors of the food web topology (rows) for different levels of data quality. 1–4: all quality levels are considered; 1–3: the first 3 quality levels; 1–2: the first 2 quality levels; 1: only quality level 1. The upper part of the table repeats information provided in the original metadata file. The lower part of the table indicates update for the revised food web topology.

Original data set (version 1)				
Quality of links (Data V1)	1–4	1–3	1–2	1
Total number of taxa	244	244	244	244
Total number of taxa with 1+ link	244	225	220	192
Total number of links	1589	1065	1033	621
Cannibalistic links	15	11	10	8
Connectance 1 (all taxa)	0.027	0.018	0.017	0.010
Connectance 2 (taxa with 1+ link)	0.027	0.021	0.021	0.017
Revised data set (version 2)				
Quality of links	1–4	1–3	1–2	1
Total number of taxa	233	233	233	233
Total number of taxa with 1+ link	233	226	224	223
Total number of links	2218	1672	1601	1258
Cannibalistic links	26	22	21	16
Connectance 1 (all taxa)	0.041	0.031	0.029	0.023
Connectance 2 (taxa with 1+ link)	0.041	0.032	0.032	0.026