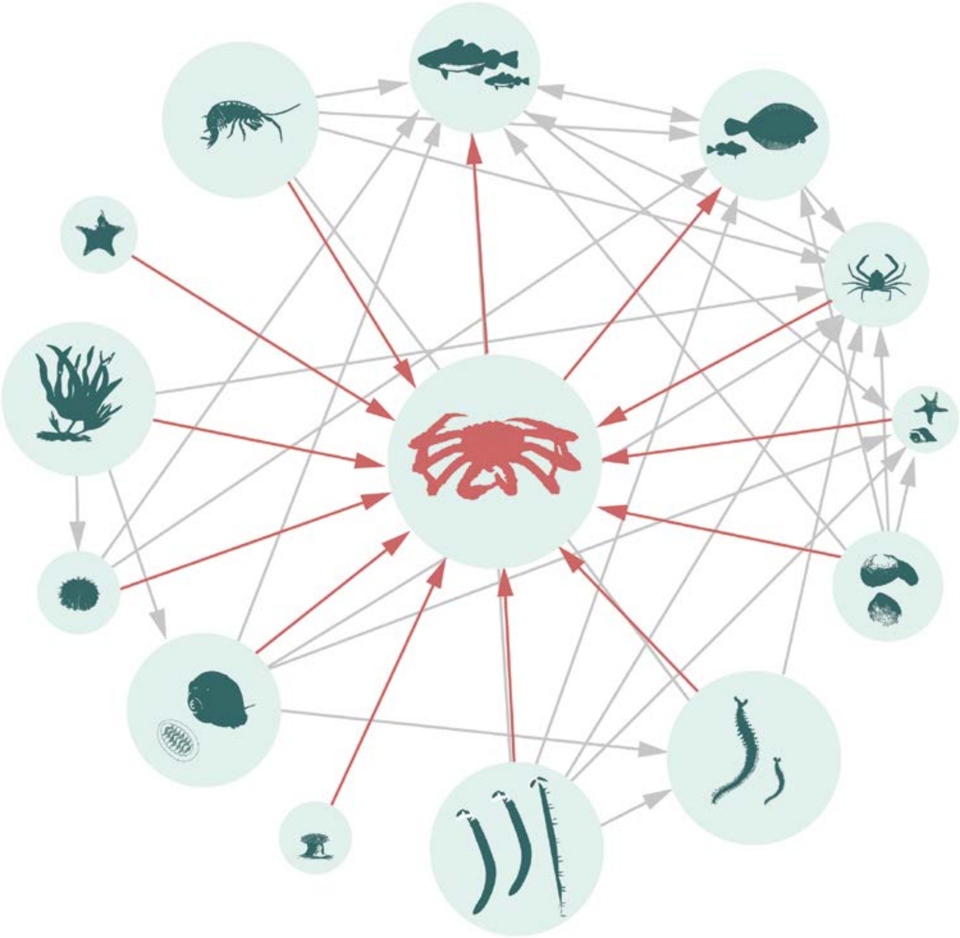
Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology

The role of the invasive red king crab in the food web of a high-latitude fjord

Studying macrobenthic communities and trophic control in Porsangerfjord, northern Norway

Mona Maria Fuhrmann
A dissertation for the degree of Philosophiae Doctor – July 2016



The role of the invasive red king crab in the food web of a high-latitude fjord

Studying macrobenthic communities and trophic control in Porsangerfjord, northern Norway

Mona Maria Fuhrmann

Thesis for the degree of Philosophiae Doctor

University of Tromsø

Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

July 2016

“My big fish must be somewhere.”

— Ernest Hemingway

Contents

I. Acknowledgments 1

II. Summary 3

III. List of Papers 6

1 Introduction 8

1.1 Study background 8

1.2 In the wrong waters- alien invasive decapods 9

1.3 The red king crab – invasive history, management and research 11

1.4 The challenge of measuring an impact 14

1.5 Food web concepts and tools 15

1.6 Food web models 17

1.6.1 Ecopath with Ecosim (EwE) 18

1.7 Benthic secondary production at high latitudes 19

1.8 Main objectives 21

2 Approach 22

2.1 Porsangerfjord – an ecological laboratory 22

2.2 EwE modelling 24

2.3 Data collection 26

2.3.1 Red king crab distribution 27

2.3.2 Diet analysis 27

2.3.3 Environmental data 28

2.4 Estimation of benthic P/B and production 28

3 Summary of results 30

Paper I 30

Paper II 30

Paper III 31

3.1.1 Supplementary results to Paper III: Keystoneness of red king crab 32

4 Discussion 34

4.1 Eating and being eaten– feeding strategy and predation pressure 34

4.2 Predation impact 36

4.2.1 Direct predation impact on large, long-lived invertebrates 36

4.2.2 Benthic production and P/B 37

4.2.3 Predation on herbivorous echinoids 39

4.2.4 Keystoneness 39

4.2.5 Omnivory 40

4.3 Niche overlap and competitive effects 41

4.4 Applicability and limitations of this work 42

4.5 Conclusions and future perspectives 45

5 References 48

6 Papers 57

I. Acknowledgments

First of all, I wish to thank my UiT supervisors, Torstein Pedersen and Einar M. Nilssen, for their guidance along this difficult but extremely enlightening journey. Your expertise in ecology is impressive and your patience and trust in me is well appreciated. Thank you Torstein for your persistence, your encouraging optimism, your effort to improve my Norwegian skills, and also for never talking football with me! Thank you Einar for the nice company in the field and the many good tips on where to spend my holiday!

I would also like to thank my co-workers at the Institute of Marine Research (IMR): Lis L. Jørgensen, Jan Sundet, Maria Jenssen and Ann-Merete Hjelset for their contribution in many good discussions, workshops, and field work. Additional thanks to Jan, for the provision of extra funding. I hope to continue our collaboration in the future. I am very grateful for statistical advice and challenging exchange with my co-author Virginie Ramasco.

I would like to thank Eivind Oug (NIVA) for his enthusiasm to play with mud, for sharing his impressive taxonomic skills and his expertise in benthic ecology. I hope we will be able to finish the invaluable time series in inner Porsangerfjord.

A number of colleagues have contributed to this project through field and laboratory work, most importantly Emma Källgren. Thank you for your reliability, your organizational skills and all the good work you have done! My gratitude goes to the crew of R/V Johan Ruud for a great support during the cruises to Porsangerfjord. I would also like to thank Aivo Lepland (NGU) who has provided some of the video material used in Paper I and Marianne Nilsen who answered my questions regarding stable isotope analysis.

My special thanks go to Susanne Kortsch and my (former) office mates Nina Mikkelsen and Silje Ramsvatn. Not only have I valued your help and professional advice, but I am grateful your friendship over the past years. I also want to thank all my colleagues at the AMB for creating a very social working atmosphere and many enjoyable lunch and coffee breaks. Thanks go to Erin Kunisch who was willing to proofread this synopsis for English-language.

Michael Greenacre, Raul Primiciero, Mikko Vihtakari, Martin Mörsdorf and Andre Frainer have helped me to resolve some of the statistical issues in this thesis.

Last but not least I would like to thank all my friends, both here in Tromsø and in other places, for helping me to hang in there, survive the darkest winters, refill my energy with exciting outdoor activities, giving me wonderful holiday breaks, and by simply being there.

Finally I thank my dear family. Especially my Dad for nagging me to finish so I could get a proper job, Caro for always having my back, my Grandma for her optimism, and my Mom for helping me to not lose hope, listening to all my complaints, and supporting me in the best way possible.

II. Summary

Biological invasions are one of the many challenges facing coastal waters of the ocean and with increased human activity and a changing climate, increasingly threaten high-latitude environments. The red king crab, one of the world's largest decapods, was introduced into the Barents Sea in the 1960s. It has since become a valuable fishery resource in Russian and Norwegian waters, and is continuously expanding its distribution range along the coastline. In the early 2000s, red king crabs entered Porsangerfjord, which now holds one of the largest densities of king crabs along the northern Norwegian coast. Along with the invasion of red king crabs, Porsangerfjord has also experienced extensive down-grazing of kelp by sea urchins and a decline in coastal cod abundance. Because of these factors, the Porsangerfjord ecosystem provides a unique ecological laboratory of scientific studies. A shallow sill separates the inner fjord from the outer fjord and crabs have only recently entered this new area, which is characterized by year around cold bottom temperatures and a complex topography.

The red king crab is a predator of various benthic invertebrates in a range of soft- and hard bottom habitats. Benthic invertebrates perform numerous important functions in marine ecosystems. Macrobenthic secondary production comprises a crucial component of the energy flow in ecosystems, supporting higher trophic level species such as cod. With prospective management in mind, it is crucial to assess the significance of the red king crab as a benthic predator, by integrating dynamic processes and energy flow in food web studies. Therefore, the major objectives of this thesis were to assess macrobenthic communities and their secondary production in Porsangerfjord, and, together with information on the trophic niche, asses the role of the red king crab in the food web and its predation and competitive impacts through Ecopath with Ecosim mass balance models (EwE).

Results from this thesis reveal heterogeneity in benthic communities along the fjord (**Paper I**), likely a result from different environmental conditions and possibly predation effects by the red king crab. Polychaetes dominated community structure and we found high total soft bottom macrobenthic biomass and production in the inner fjord, despite cold temperatures and lower production to biomass ratios (P/B). A generalistic, opportunistic feeding strategy makes the crab a successful invader and its diet included a variety of prey items including mollusks, polychaetes and echinoderms. Larger and long-lived species are suggested to be indicative of predation (**Paper I**, **III**) and those were more scarce in the outer fjord, i.e. in areas with high king crab densities (**Paper I**), raising the community P/B ratio in these areas. Stable isotope

analysis revealed no distinct ontogenetic niche shift in the red king crabs, with both adults and juveniles feeding at approximately trophic level 3. However, distinct distribution of size groups pointed to differences in habitat and resource use between crabs during their life cycle (**Paper II**). Trophic niches of red king crab in Porsangerfjord overlapped with a few other native benthic predatory invertebrates such as other decapod crabs, sea stars and predatory snails, and bird groups, while most fish fed at higher trophic levels and/or used pelagic pathways (**Paper II and III**). The red king crab had an important top-down role in the ecosystem, with a high overall impact. The crab itself was of low significance for other predators, impacting other species groups mostly through direct predation (**Paper III**). Supporting results from **paper I**, EwE modelling showed that impacts were high on large, long-lived benthic invertebrates, often serving as prey and competitors at the same time. Predation by the red king crab on different trophic levels raised system omnivory, with unknown consequences for stability and resilience. Predation by the crabs possibly lead to a change in size structure in the benthic compartment, raising P/B ratios and leading to a faster turnover in biomasses. Increasing densities of red king crabs may also mediate regrowth of macroalgae by predation on sea urchins in some areas of the fjord, but this needs further investigation.

Word cloud of the synopsis in this thesis

III. List of Papers

1. Fuhrmann MM, Pedersen T, Ramasco V, Nilssen EM (2015) Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab. *J Sea Res* 106:1-13.

2. Fuhrmann MM, Pedersen T, Nilssen EM. Trophic ecology of the invasive red king crab (*Paralithodes camtschaticus*) in a native benthic food web. Manuscript submitted to *MEPS*

3. Pedersen T, Fuhrmann MM, Lindstrøm U, Nilssen EM, Ivarjord T, Ramasco V, Jørgensen LL, Sundet JH, Sivertsen K, Källgren E, Hjelseth A-M, Michaelsen C, Systad G, Norrbin F, Svenning MA, Bjørge A, Steen H, Nilssen KT (2016). Modelling ecosystem structure and trophic control by the invasive red king crab in Porsangerfjord, northern Norway. Manuscript

Contributions

	Paper I	**Paper II**	**Paper III**
Concept and idea	MF, EN, TP	MF, TP, EN	TP, MF, UL, EN
Study design and methods	MF, TP, EN	MF, TP	TP, MF, UL, EN, TI, VR, LJ, JS, KS, EK, AH, CM, GS, FN, MS, AB, HS, KN
Data gathering	MF, EN	MF, TP, EN	TP, MF, UL, EN, TI, VR, LJ, JS, KS, EK, AH, CM, GS, FN, MS, AB, HS, KN
Data analysis and interpretation	MF, TP, VR, EN	MF, TP, EN	TP, MF, UL, EN, TI, VR, LJ, JS, KS, EK, AH, CM, GS, FN, MS, AB, HS, KN
Comments and input to manuscript	MF, TP, VR, EN	MF, TP, EN	TP, MF, UL, EN, TI, VR, LJ, JS, KS, EK, AH, CM, GS, FN, MS, AB, HS, KN
Manuscript preparation writing	MF, TP, VR	MF, TP	TP, MF,UL

Authors: Mona M. Fuhrmann (MF), Torstein Pedersen (TP), Einar M. Nilssen (EN), Virginie Ramasco (VR), Ulf Lindstrøm (UL), Trond Ivarjord (TI), Lis L. Jørgensen (LJ), Jan H. Sundet (JS), Knut Sivertsen (KS), Emma Källgren (EK), Ann-Merete Hjelset (AH), Christer Michaelsen (CM), Geir Systad (GS), Fredrika Norrbin (FN), Martin Svenning (MS), Arne Bjørge (AB), Henning Steen (HS), Kjell T. Nilssen (KN)

1 Introduction

1.1 Study background

Since its deliberate introduction into the Barents Sea, the red king crab (*Paralithodes camtschaticus;* Tilesius, 1815) has been discussed in the public eye, being both a valuable fishery resource and a potential threat to native biota. The crab has now resided in Norwegian waters for over 35 years and can be seen as a permanent component of benthic life along the northern coast. In the light of this, surprisingly little evidence evaluating its cumulative effect has emerged in the scientific literature. So far, only one empirical, peer reviewed study has been published addressing the impact of the red king crab in Norwegian waters (Oug et al. 2011). The study provides an excellent time series, but measures static components only, namely abundance and biomass of benthic invertebrates. A food web approach investigating the potential consequences of altered trophic interactions has not been done until today.

The Institute of Marine Research (IMR), together with other partner institutions, initiated a program entitled, Ecological Processes and Impacts Governing the Resilience and Alternations in the Porsangerfjord and the Hardangerfjord, or EPIGRAPH in 2008. The program was aimed at supporting future management plans and provides, among other objectives, a framework for studies on benthic biodiversity, production, and red king crab interactions in the focus area of Porsangerfjord. This thesis was part of the above-mentioned research activities, focusing on macrofaunal production and the role of the red king crab in the ecosystem.

In this introduction I will give an overview of the invasive history and biology of the red king crab and the role of invasive decapods in other systems. Since the ”impact” of the red king crab is frequently discussed throughout this thesis, I explain the concept and identify challenges when trying to measure an impact, and how food web models (such as Ecopath) can assist in the evaluation of impacts. I will give a brief introduction to benthic macrofauna as important contributors to energy flow in high latitude systems. Finally, I will present the major objectives of this thesis.

For the first time, I present the red king crab in the context of food webs, with all its trophic interactions, and provide quantification of energy flow in the benthos. Descriptive elements of Paper I and II are brought together in Paper III, presenting direct and indirect community-wide impacts of this invasive decapod. The trophic niche and feeding strategy of the red king crab, its impact on other groups and the overall ecosystem, as well as limitations of this work are discussed at the end of this synopsis. Data gathered in this thesis can serve as a groundwork for future monitoring in Porsangerfjord and other areas in the Barents Sea undergoing red king crab invasion, and open the way towards an ecosystem-based approach in red king crab management.

1.2 In the wrong waters- alien invasive decapods

Human activity has allocated and altered the native distribution of many species, including marine crustaceans (Galil et al. 2011). While the accurate number of displacements may only be guessed, numerous alien crustaceans have become *invasive*, meaning they have established a self-maintaining population, continuously expanding in range (Falk-Petersen et al. 2006). Among crustaceans, decapods are one of the most successful higher trophic level taxa establishing in numerous freshwater and marine habitats of the world (Galil et al. 2011). The Norwegian biodiversity authority has registered 14 alien crustacean species in 2012, with 5 decapods being put on the black list, considered to pose a high risk for the ecosystem (Gederaas et al. 2012). Alien decapods have led to marked ecological consequences in some of the invaded systems around the world and have caused high economic costs, from repairing damages caused to fisheries and in the environment (Ruiz et al. 2011). Other species, such as the Pacific white shrimp (*Litopenaeus vannamei*) and the Norwegian red king crab (*Paralithodes camtschaticus*) are commercially exploited and contribute to local income (Liao & Chien 2011, Falk-Petersen 2012).

Most invasive species have certain traits which facilitate their establishment and success in their new habitat (Ricciardi et al. 2013). Displacements of crustaceans out of their native range mostly happens in the larval stage, via propagules travelling with human transport or drifting with ocean currents. Large decapods are in addition quite mobile and may walk over long distances across the sea floor, helping to expand their current range (Weis 2010). Some decapods may perform migrations and ontogenetic changes of habitat over their life cycle, thereby affecting a range of different habitats (Boudreau & Worm 2012). Short generation cycles and high fecundity of many decapods aid in their establishment when a suitable habitat is found. Decapods have a broad tolerance for different salinities and water temperatures, possess a generalist feeding strategy and a wide dietary niche. These characteristics, along with their behavioural competiveness, make decapods successful invaders (Weis 2010, Hänfling et al. 2011).

The impacts of invasive decapods are often related to changes in trophic interactions, competition and habitat modification (reviewed by Snyder & Evans 2006, Hänfling et al. 2011). Common direct predation effects of invasive decapods are the reductions in the density of prey, changes in in community structure, composition and biodiversity (e.g. Grosholz et al. 2000, Snyder & Evans 2006). Because of their omnivorous feeding behaviour, invasive decapods often feed on different trophic levels (Commitol & Ambrose 1985), and these consequences may be complex and indirect, potentially affecting food web structure and energy flow throughout the system (Hänfling et al. 2011). Large generalist decapod predators have been shown to play important roles in the food web by linking multiple trophic levels and having widespread effects on the food web (Snyder & Evans 2006). Some introduced decapods may act as *ecosystem engineers* by modifying habitat through sediment disturbance or inducing trophic cascades affecting habitat structuring species (Weis 2010). For example, the Portunid crab (*Charybdis japonica*) in New Zealand, which feeds on bioturbating sea urchins, which are important in nutrient recycling (Townsend et al. 2015). Effects on macroalgae through predation or herbivore suppression, is well documented for a number of (invasive) decapods, like crayfish (e.g. *Procambarus* spp., *Orconectes* spp.), which prey on herbivorous snails and other invertebrates with positive effects for algae. At the same time they may switch to herbivorous feeding and thereby reduce algal biomass substantially (Nyström 1999, Gherardi 2007, Hansen et al. 2013).

The most widely distributed decapod and presumably one of the best studied invasive species, is the European green crab (*Carcinus maenas*). This crab species is native to the Atlantic coast of Europe and North Africa, has been recorded in 3 oceans and has established populations along the coasts of 4 continents (North and South America, South Africa and Australia, see Grosholz & Ruiz 1996, Brockerhoff & McLay 2011). It has been documented to significantly reduce the abundance of native benthic invertebrates such as clams and other crabs, and also alters community composition through indirect effects (Grosholz et al. 2000). It caused a long lasting habitat shift in the native shore crab, *Hemigrapsus oregonensis* (De Rivera et al. 2011), and has become important prey for other invasive crabs and birds (Griffin et al. 2008, Wong & Dowd 2013). The European green crab has been associated with the reduction in commercial shellfish and total economic costs of threatened shellfish fishery are estimated to be substantial if crab abundance increases (Lafferty & Kuris 1996, Grosholz et al. 2010).

Examples of large invasive decapod crabs at high latitude environments are the Atlantic rock crab (*Cancer irroratus*), which has spread rapidly in coastal waters of Iceland since 2006 (Gíslason et al. 2014) and the snow crab (*Chionoecetes opilio*), which is native to the north Pacific and the northwest Atlantic, but is quickly expanding its range in the Barents Sea (Alvsvåg et al. 2008, Sundet & Bakanev 2014). Lithodid crabs have recently been observed to become more numerous at the Antarctic shelf, where warming temperatures have likely helped them to reconquer this cold habitat (Thatje et al. 2005, Aronson et al. 2015). Ecological consequences of these large decapods are generally unknown, though these species may have a high commercial importance. For example, the snow crab has high economic potential in the Barents Sea (Hansen 2016) and a fishery commenced by Russian and Norwegian vessels in 2014.

1.3 The red king crab – invasive history, management and research

The first catch of an adult red king crab in Norwegian waters was registered in 1977 (Nilssen 2003), about 150 km from its place of introduction into the Russian Barents Sea in the 1960s and 1970s by scientists (Orlov & Ivanov 1978). In the 1990s, the crab became a common bycatch and an annoyance for cod fishermen in the Varanger area, who had to deal with crabs entangled in their line- and fishing nets. Since then, the crab has spread westwards along the Finnmark coast, establishing first in Laksefjord, then Porsangerfjord and around Sørøya (Fig. 1). By definition it has become invasive (Falk-Petersen et al. 2006), continuously expanding its range (Windsland et al. 2014). Its current distribution stretches from the southwestern to the southeastern Barents Sea along the Kola Peninsula (Fig. 1). In Norwegian waters it is considered a coastal species, with the highest densities inside fjord systems (Sundet & Hoel 2016). However, it has been recorded in offshore areas around the Tromsø plateau, dominating benthic mega-fauna biomass (Jørgensen et al. 2014). Newest records of juvenile and adult king crabs in the area around Tromsø and in Balsfjord at 69° N (E. Nilssen, UiT, pers. comm.) illustrate the ongoing process of establishment.

Temperature is thought to be the major constraining factor for distribution in lithodid crabs (Hall & Thatje 2009). The red king crab is a boreal species with a temperature optimum of around 4 °C (Hansen 2002, Siikavuopio & James 2013), mostly because of restrictions to larval development, which is significantly delayed at water temperatures below 2°C (Stevens 2014). Recent records of crabs in the White Sea indicates that this cold habitat may become seasonally available for crabs, but due to sub-zero temperatures and low salinities it may not be suitable as a permanent habitat (Starikov et al. 2015). First single catches occurred in Porsangerfjord in 2002, and were followed by an establishment of red king crabs in the outer and middle areas of the fjord, and a commercial fishery began in 2008. Only recently, in 2012, were crabs registered in the inner, cold part of Porsangerfjorden, with mainly small crabs in shallow water but increasingly larger catches of adult crabs in the past few years (E. Nilssen, UiT, pers. comm.).

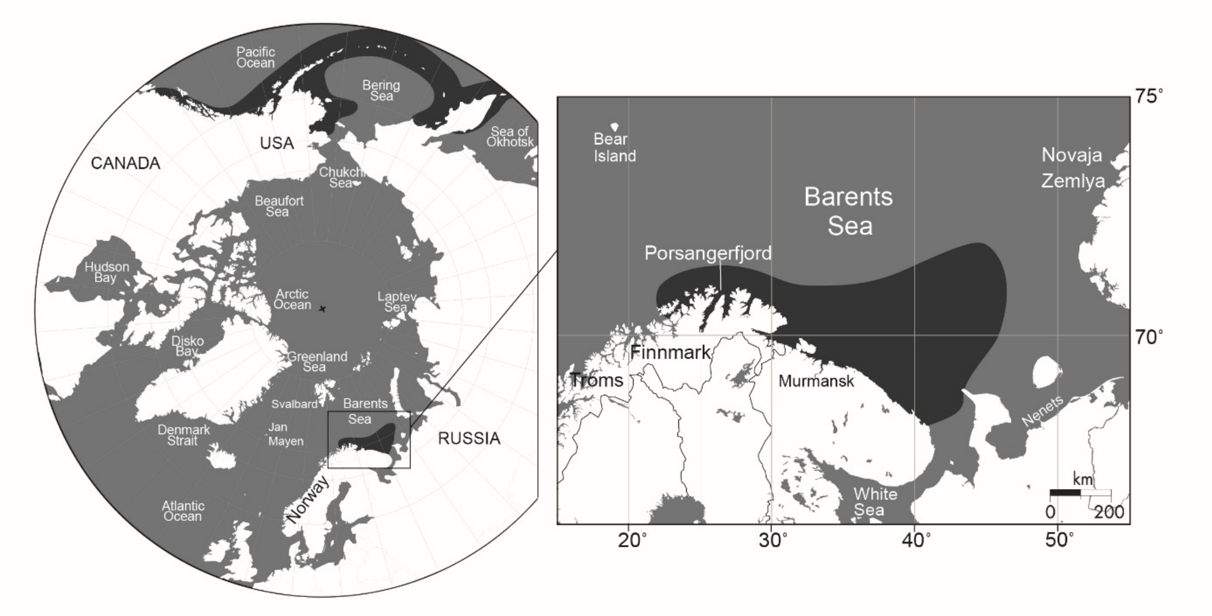


Fig. 1 Distribution area of red king crab in the native area of the Pacific and in the new range of the Barents Sea. Source: IMR 2015.

Following larval settlement, small juvenile crabs remain at shallow waters for 2-3 years, where podding behaviour may occur (Dew 1990). Red king crab mature at a carapace length of approximately 110 mm (Hjelset et al. 2009), and generally remain at habitats > 100 m water depth during summer and autumn. Mature crabs migrate upwards to shallow waters in late winter, followed by mating and breeding in springtime (Stone et al. 1992). Adults are often found aggregated according to size and sexes (Stone et al. 1993, Jørgensen & Nilssen 2011). Whether red king crabs residing in Norwegian fjords follow the same pronounced migration patterns as in native areas, has not been fully established. More restricted movement patterns of king crabs in Norwegian waters are likely due to higher complexity in bottom topography (Jørgensen & Nilssen 2011, Windsland et al. 2014).

Since 2008, the red king crab fishery in Norway is divided into two management regimes, the quota-regulated and the open-access fishery (Sundet & Hoel 2016). The latter is aimed at limiting the spreading of crabs and occurs westwards of 26° E. Quota are mostly allocated to small boats and are initially intended as a compensation to fishermen most affected by the bycatch of crabs in their nets used in the cod-fishery. Up to date, over 500 vessels are involved in the quota-regulated fishery and land annual catches worth 150 million NOK (Sundet & Hoel 2016). The current total stock of crabs with > 70 mm carapace length is estimated to approximately 3.090.000 individuals in Norwegian waters (source: IMR, 2014, available at http://www.miljostatus.no), while there are no good stock estimates for smaller crabs. In recent years the commercial stock has declined in the Russian Barents Sea (Dvoretsky & Dvoretsky 2015), and fishing pressure on large males has altered size composition in the stock (see Hjelset et al. 2012, Dvoretsky & Dvoretsky 2015). First research activities in Norwegian waters were related to problems in bycatch and a Russian/Norwegian research agreement was established in 1994. In the following years the research quota increased steadily and crab dispersal, as well as stock size, became major objects of science.

Significant research effort regarding the impact of the king crab on its environment, did not occur until the late 90s (Sundet et al. 2000, Gudimov et al. 2003, Jørgensen 2005, Jørgensen & Primicerio 2007, Mikkelsen & Pedersen 2012). The red king crab is one of the largest decapods in the world. As a generalist predator, it feeds on numerous benthic invertebrates, including in and- epifaunal molluscs, polychaetes, other crustaceans and echinoderms (reviewed in Falk-Petersen et al. 2011). It feeds by scooping the sediment or using its claws to pick up and crush hard shelled organisms. Diet in adults seems to vary with the location studied, indicating an opportunistic feeding strategy, but little is known about diet of small crabs (Falk-Petersen et al. 2011). A study on the benthic community in the Norwegian Varangerfjorden documented reduced abundance in prey taxa, a shift in community composition and reduced substrate quality due to the removal of bioturbating infauna (Oug et al. 2011). A reduction in density and biomass of prey fauna is also reported from Russian studies (Pavlova 2008, Pavlova 2009), but these impacts were not believed to affect biodiversity and community structure substantially (Britayev et al. 2010). The red king crab is listed in the highest risk category (severe risk) of invasive species in the black list of the Norwegian biodiversity authority (Gederaas et al. 2012). Documented impacts on higher trophic levels and competitive effects have not been studied thoroughly (but see Mikkelsen 2013).

1.4 The challenge of measuring an impact

Proportional to new species introductions and increasing propagule pressure, the field of invasion biology has become its own strand of science, with an exponential increase in articles, books and journals dedicated to this topic (Richardson & Pyšek 2008). Of major interest in this field is the *impact* of alien and invasive species. The impact describes how the alien species affects the chemical and biological environment (Richardson et al. 2011). Definition of an impact strongly depends upon perception, and often it is recognized only in relation to the human value system by the provision of ecosystem services related to an economic value (Lockwood et al. 2013) that fails to capture ecological consequences. Ricciardi et al. (2013) defines impact as "a measurable change to the properties of an ecosystem by a non-native species," with all alien species having some sort of impact, simply due to the fact that they create interactions with native species. This allows impacts to be positive or negative (or value-free) and I will follow their definitions throughout this thesis.

Common to any definition of the impact term is that impact means *change*, induced (for example) in the abundance of a prey population. Changes can be measured over temporal or spatial scales and at the individual (mortality), population (genetic effects, abundances), community (biodiversity) or ecosystem level (Parker et al. 1999, Ricciardi et al. 2013). Ecological indicators such as abundance and biomass can be used to measure and reconstruct past changes (Coll & Lotze 2016). Species traits, such as feeding guilds, size structure (Coll & Lotze 2016), and productivity can reveal changes in an ecosystem context beyond taxonomical composition and relate to community function. Food web models may be used to address more complex changes in ecosystems, with respect to structure and function (Coll & Lotze 2016, see below). Mass-balance models (Ecopath with Ecosim) can and have been be used for quantifying the impact of a trophic species on other groups and the overall food web (see e.g. Coll et al. 2013). Impact is a scaled and gradual concept and quantification in classic impact studies is best achieved by experimental studies (Richardson et al. 2011). Experimental studies may however be logistically difficult, bring certain biases due to the setup and may only be representable of local conditions or habitats. In that case, correlational studies can help to identify impacts, but may be less effective in establishing cause and effect relationships due to natural variation and other factors influencing the study object (see Paper I).

1.5 Food web concepts and tools

“No fish is an island”

(Ecopath quote, adapted from a poem by John Donne from 1624)

…and neither is a crab.

All species in an ecosystem interact with one another, through trophic (predation, parasitism) and non-trophic relationships (competition and facilitation). More recently, impact studies of invasive species have begun to investigate the indirect effects of invaders, the impact on trophic flow, food-webs and ecosystem processes (Vander Zanden et al. 1999, Grosholz 2002, Wong & Dowd 2013). Of essential interest is whether impacts concern prey organisms only, or if there will be changes concerning other species. These may be indirectly linked to the invader through trophic chains or share similar resources. In conjunction with this approach, one needs to approximate and represent (trophic) interactions in the system in question, for example in the form of a food web. As it happens, one of the pioneers in invasion biology, Charles S. Elton, who published the most cited book in this discipline *(The ecology of invasions by animals and plants in 1958*, reviewed by Richardson & Pyšek 2008), also constructed one of the first food webs ever (Bear island, Summerhayes & Elton 1923), laying the foundation for this ecological concept.

In food webs, the trophic position (or trophic level) of a species represents the number of feeding links separating an organism from the primary production, which is set at trophic level 1. In early theory the trophic level concept was applied to simple food chains, producing discrete trophic levels for each consumer. Most food webs are of course much more complex, including taxa that feed at more than one trophic level (so called trophic omnivory), resulting in non-discrete trophic positions (Thompson et al. 2007). In addition, the role of a species and its trophic position in the food web may change during its life cycle, due to a change in diet or its predators. Ontogenetic niche shifts are therefore important to address, but are rarely assessed in food web studies.

In order to establish who eats whom and how much, we need to obtain knowledge about the trophic ecology of each participant in the local food web. Ideally, we want to capture the entire width of its trophic niche, i.e. dietary diversity. Stomach (or gut content) analysis is frequently used to get an overview of a species’ prey and their proportions, since it can give detailed information on prey identity and quantification can be approximated in (larger) species.

However, stomach samples pose certain limitations and biases since their content is merely a snapshot of the full range of a species' diet and often biased towards slow, digestible prey.

Stable isotope ecology has advanced as one of the major methods to study a species trophic niche and interactions in the food web (Hobson & Welch 1992, Newsome et al. 2007, Layman et al. 2007a, Layman & Allgeier 2012). Stable isotope analysis relies on the principle of stepwise enrichment via the food chain of the heavier isotope and the natural variation in the environment. It is now one of the major tools to investigate marine food web structure (Whiteledge et al. 1988, Hobson & Welch 1992, Iken et al. 2001, Iken et al. 2005, Layman et al. 2012), where $\delta^{15}N$ is usually used to assess trophic position and $\delta^{13}C$ to trace carbon source (Fig. 2). The isotopic niche concept has emerged to investigate a species' ecological niche, with regard to resource and habitat use (Newsome et al. 2007). It is usually defined as the area occupied by individual signatures of a population in the two-dimensional isotopic space of $\delta^{13}C$ and $\delta^{15}N$. Isotopic niche width can then be quantified by a number of available metrics measuring dispersion (Bearhop et al. 2004, Jackson et al. 2011, Layman et al. 2012). The isotopic niche concept has been widely applied to detect ontogenetic niche shifts in the same species (Hammerschlag-Peyer et al. 2011, Ramsvatn & Pedersen 2012), habitat use (Cummings et al. 2012, O'Farrell et al. 2014), niche differentiation and trophic niche overlap (Guzzo et al. 2013, Jackson et al. 2014, Le Bourg et al. 2015). However, stable isotopes are only valid in combination with stomachs if the purpose is to investigate prey composition. With diet proportions obtained from mixing models, stable isotope signatures may be used as input to food web models (Ramsvatn 2013) or to validate trophic levels estimated in models (Nilsen et al. 2008).

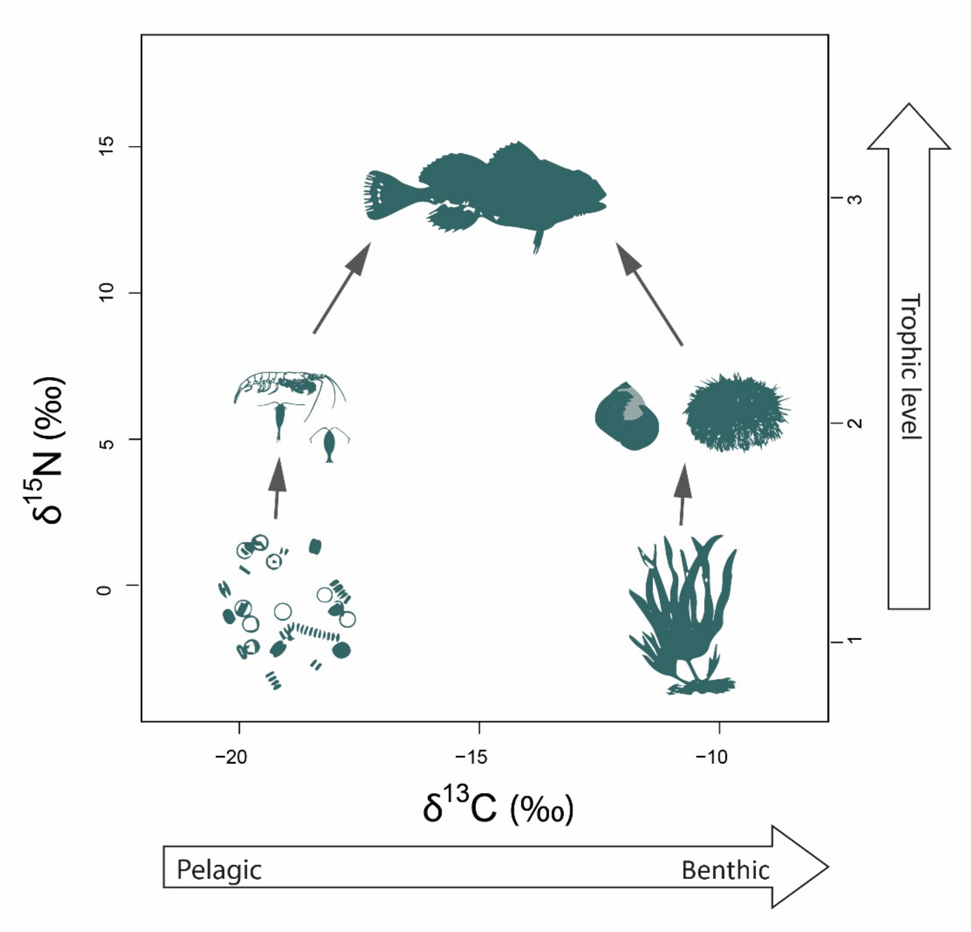


Fig. 2 Schematic drawing of primary producers and consumers isotopic ratios (in‰) in the food web. Stable isotope signatures of carbon ($\delta^{13}C$) can be used to trace pelagic and benthic pathways, while nitrogen isotope ratios ($\delta^{15}N$) can be used to determine trophic levels. Figure modified after Rombouts et al. (2013).

1.6 Food web models

Food web models usually aggregate species into functional groups with similar prey and predators, though food webs in nature are inherently complex and a model will never be a representation of the real world (Pimm 1982). Simple models can however help revealing underlying complexity and assist in generating hypotheses, guide data collection, identify major uncertainties, explain past changes, and make predictions about potential future changes (Epstein 2008). Local data will improve any model and the availability of time series data can create more realistic predictions. The type of research question determines which modelling approach should be used. The applicability of quantitative food web models for management purposes is a clear advantage over qualitative modelling, however extensive input data is often needed.

1.6.1 Ecopath with Ecosim (EwE)

Currently, Ecopath is the most frequent multispecies trophic model applied to aquatic ecosystems and is used mainly for evaluating ecosystem functioning and the effects of different exploitation regimes (Pauly et al. 2000, Colléter et al. 2015). Most models that exist today focus on pelagic interactions, but increasingly incorporate high resolution in, or focus entirely on, the benthic compartments (e.g. Byron et al. 2011, Ortiz et al. 2015, Aydin & Whitehouse 2016). EwE-modelling has been used to investigate ecosystem effects of invasive species (Arias-González et al. 2011, Pinnegar et al. 2014) and address possible management measures (Wong & Dowd 2013). Establishing an Ecopath model requires extensive information on species biomass, productivity, diet and consumption, often linked to elaborate field sampling. Once the baseline model is established, it can be expanded and used for various purposes.

The Ecopath package offers a wide range of simple metrics to more advanced ecological network analysis tools and indicators (Ulanowicz 1986, Christensen & Walters 2004, Christensen et al. 2005), used in the description of food web structure and emergent food web properties relevant to system health, stability and maturity (Vasconcellos et al. 1997). These are among others *trophic level* (TL), *connectance* (number of possible links compared to realized links), the system *omnivory* index (a measure of how feeding interactions are distributed over trophic levels as the mean variance of TLs in each consumers diet (Christensen & Pauly 1993), and biomass residence time, which equals system biomass divided by the total throughput (Biomass/Export + Respiration, Christensen 1995). The impact of individual species groups in the food web may further be evaluated using the *mixed trophic impact* (MTI_i), the *total relative impact* ε_i (Libralato et al. 2006) and *keystoneness* indices (Power et al. 1996, Christensen et al. 2005, Libralato et al. 2006) (see below and section 2.2 for explanation of these indices).

The concept of a keystone species was first introduced by Robert Paine (1969) to explain the changes observed in a community after removing a predatory seastar, which controlled space competitors in a rocky intertidal food web (Paine 1966), which Paine hypothesized was important for maintaining overall structure, diversity and stability. The concept was later refined as a species "whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance" (Power et al. 1996). Impacts by keystone species have since been well documented, and also include a few generalist decapods, like the lobster (*Jasus edwardsii*) (Eddy et al. 2014). Large decapods may play keystone roles by exerting strong top down control on prey, supressing herbivory or space competitors (reviewed in Boudreau & Worm 2012). The *keystoneness* indicators implemented in Ecopath can be used for identifying a keystone species as a function of its total impact ε_i , and its biomass (Power et al. 1996, Libralato et al. 2006).

1.7 Benthic secondary production at high latitudes

Despite seemingly unfavourable environmental conditions, benthic communities of high latitude systems are, often diverse assemblages of high biomass. Increased research in these regions has shown that the common notion of the Arctic benthic communities being poor in biodiversity is no longer applicable (Piepenburg 2005). Benthic macrofaunal organisms perform numerous important functions in marine ecosystems, ranging from non-trophic functions as habitat facilitators, sediment turbators and stabilizers, their involvement in nutrient recycling (Welsh 2003), to their roles as significant links among multiple trophic levels (Commitol & Ambrose 1985, Snelgrove 1998). Ecosystem models from the coastal northeast Atlantic suggest that a significant amount of energy is channelled via the benthos (Bax & Eliassen 1990, Pedersen et al. 2008, Pedersen et al. 2016). Benthic secondary production often comprises a crucial component of the energy flow in ecosystems, particularly at high latitudes (Petersen & Curtis 1980, Nilsen et al. 2006, Blicher et al. 2009) and may support commercial fish species such as cod (*Gadus morhua*) (Kanapathippillai et al. 1994), bottom-feeding fish, mammals, and birds (Grebmeier et al. 2006). Benthos inhabiting soft sediments represent long term integrators of environmental conditions and processes in the overlaying water column, making them an ideal study object. Species such as infaunal polychaetes, are often especially productive due to small body masses and high production/biomass (P/B) ratios (e.g. Nilsen et al. 2006). Infaunal organisms provide food for numerous organisms within and outside the benthos, such as crabs, fish (e.g. haddock) and birds. Among those, the commercially targeted snow and red king crab in the Barents Sea.

Benthic species and communities are often quantified in terms of abundances and biomass. These are static measures at a certain time, usually given per unit area. Secondary production can be defined as the formation of heterotrophic biomass through time (Allen 1971, Benke 1996), and is a process which results from the growth of an organism, creating biomass with losses to excretion, respiration and reproduction, which then is transferred to the next trophic level by predation. Secondary production therefore integrates static measures (density, biomass), dynamic population measures such as growth, recruitment and mortality, as well as biotic and abiotic interactions in a population (e.g., Valentine-Rose et al. 2011, Dolbeth et al. 2012), into an overall functional measure of energy flow through the system. Most importantly, somatic secondary production largely determines the carrying capacity for predators. Production is usually expressed in terms of energy (Joule m^{-2} y^{-1}) or mass (carbon m^{-2} y^{-1}), using conversion from wet or dry masses. The application of secondary production in ecological studies includes: the quantification of energy flow in food webs, finding limits and drivers of production, addressing the ecological performance of populations, and the use of production as a response variable to environmental change (Benke 1996). For example, Dolbeth et al. (2012) showed that density and biomass may contradict trends of benthic production following disturbance events, stressing the additional value in providing production estimates along with these static measurements.

With research increasing in high latitudes, we are slowly beginning to understand more about patterns and drivers of benthic production in these areas (Brey & Gerdes 1998, Kędra et al. 2013, Fuhrmann et al. 2015, Degen et al. 2016, Lin et al. 2016). Common to these studies is the high variability in benthic production on local and regional scales. However, the ways in which environmental factors influence benthic production is debated in the literature (Cusson & Bourget 2005). Among the environmental factors, temperature, depth, food quality and food supply due to tight bentho-pelagic coupling seems to be of major importance (Grebmeier & McRoy 1989, Piepenburg 2005, Bolam & Eggleton 2014, Degen et al. 2015, Degen et al. 2016). Additionally, sediment characteristics (Bolam et al. 2010, Lin et al. 2016) and disturbances like trawling (Jennings et al. 2001) strongly affect inherent biological traits (abundance, size structure, composition, diversity) of the community present and may result in different production and P/B patterns. Trophic interactions, such as predation, is known to structure benthic communities (e.g. Virnstein 1977, Gilinsky 1984, Quijon & Snelgrove 2005). A few direct attempts have been made to link benthic predation and secondary production (Evans 1983, 1984, De Lange et al. 2004), but our understanding of how exploitation can affect production processes in a benthic community is generally poor.

1.8 Main objectives

The goal for the Barents Sea management plan is to “maintain ecosystem structure, function and productivity” (Anonym 2006, Falk-Petersen 2012), which calls for a close investigation of participating species and their contribution to these properties. Yet, we are missing a comprehensive approach investigating the role of the red king crab in the food web and how these metrics of function and productivity could be affected by this new and abundant benthic predator. At the same time, in order to assess future changes, we need data which describe the *status quo*. Therefore, the overall objective of this thesis was to evaluate the role of the red king crab in the food web and its impact on other species in the ecosystem. With respect to future monitoring, we also aimed at quantifying energy flow and provided a baseline of soft bottom macrofauna in Porsangerfjord. More specific, our objectives were to:

1. Estimate macrobenthic biomass, production and community characteristics along the fjord with respect to environmental gradients and different red king crab densities (Papers I).

2. Characterize crab diet and feeding strategy related to body size and foraging location (Paper II)

3. Investigate the king crab’s trophic position and niche overlap with potential native competitors (Papers II and III).

4. Use the obtained production and diet data from Papers I and II as input to Ecopath models constructed for Porsangerfjord, looking at energy flow and food web properties along the fjord, specifically addressing trophic control and impact by the red king crab with help of models and Ecosim simulations (Paper III).

2 Approach

2.1 Porsangerfjord – an ecological laboratory

Fjords are a major feature of the Norwegian coast, constantly subjected to human activity in the form of fisheries, aquaculture, transportation, and increasing recreational use. Fjords experience some of the same biological and oceanographic conditions as the open ocean, with additional properties of enclosed systems, posing some advantages when studying ecological processes. The Porsangerfjord (Fig. 3) is one of Norway's largest fjord systems, covering an area of ca. 1800 km^2 along 70.1° to 70.9°N and 25° to 26.5°E. It is considered an open fjord, with depths of over 300 m at the entrance, facing the Barents Sea towards the north. Water exchange with the open sea is considerable and the middle and outer fjord are largely influenced by Atlantic water. Because of its high latitude, water temperatures are generally low in Porsangerfjord, often displaying a well-mixed water column (Mankettikkara 2013). The inner part of Porsangerfjord is rather isolated, with a shallow sill and a narrowing separating it from the rest of the fjord. This inner area comprises two deep basins at around 100 m depth, Austerbotn and Roddenes (Fig. 3). Arctic water is locally formed in the inner area and lingers in the deep basins during summer, causing bottom temperatures to remain around 0 °C throughout the year (Mankettikkara 2013). The inner part also receives a considerable input of freshwater due to river runoffs, resulting in a decreasing salinity gradient from the outer to the inner part, with mean annual bottom salinities of approximately 34.7 ‰ and 33.8 ‰, respectively. The distribution of bottom sediments in Porsangerfjord is not well studied but is currently being mapped by the Norwegian Geological Survey. Mud and sandy-mud sediments are common at larger depths along the east and west side of the fjord and the inner fjord basins. Sandy, mixed, and hard bottoms are present at shallow depths, mainly in the middle of the fjord and along islands and skerries.

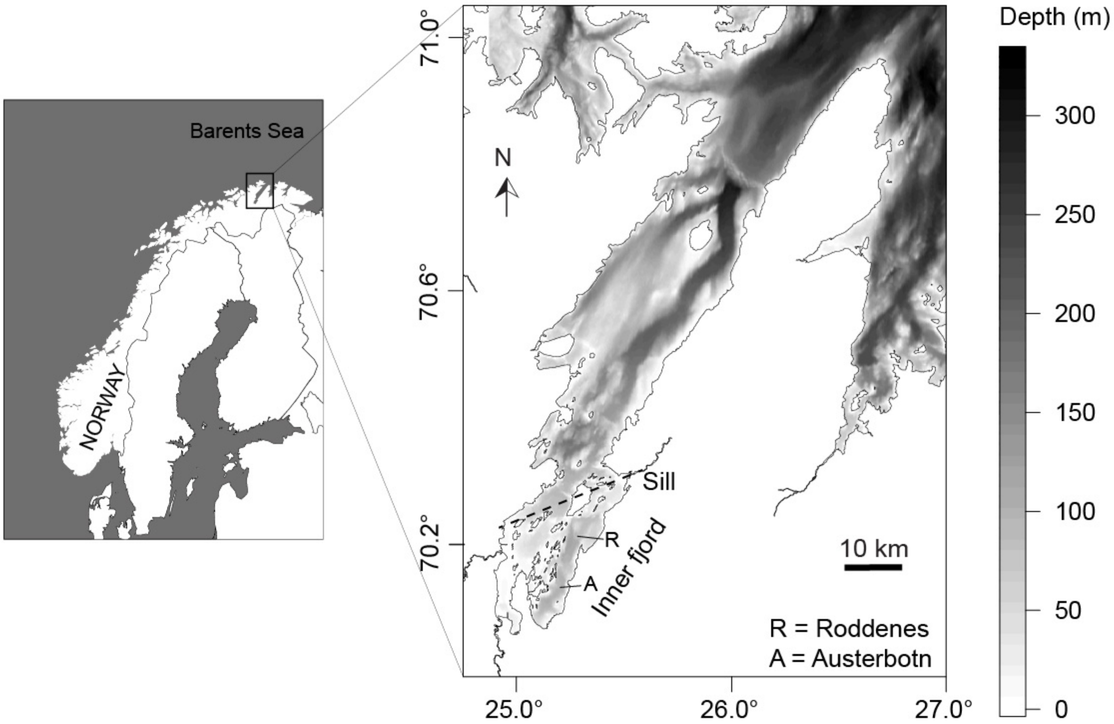


Fig. 3 Map of the study area, Porsangerfjord in Northern Norway. The sill towards the inner fjord is marked by the dotted line, the deeper basins towards the east are denoted by R (Roddenessjøen) and A (Austerbotn).

Macroalgae comprise large and unique intertidal kelp formations in the inner part, mostly at the west side (Sivertsen & Bjørge 2015). Sublittoral macroalgae in the middle and outer part of the fjord have been subject to intensive downgrazing by sea urchins (*Strongylocentrotus droebachiensis*), which has affected the north-Norwegian coast since the 1970s (Norderhaug & Christie 2009). In Porsangerfjord, previous macroalgae beds have not entirely recovered (Sivertsen & Bjørge 2015) and some areas remain barren grounds. Recent studies have given rise to the hope that red king crabs can help in reestablishment of kelp beds, important for a number of invertebrates and fish (Bodkin 1988, Norderhaug et al. 2005, Christie et al. 2009), by predating on sea urchins (Falk-Petersen et al. 2011). Historically, cod was the target of the major fishery, but the coastal cod population in Porsangerfjord has declined dramatically since the 1990, likely due to a combination of fishery and loss of nursery grounds and/or a harp seal invasion in the 1980s (Nilssen et al. 1992). Today, cod is mostly distributed in the outer and middle fjord, while large cod remains absent from the inner area.

The heterogenic environmental conditions and past and present ecological changes in Porsangerfjord provide a field laboratory to investigate factors governing these processes. The inner fjord, now also part of the quota-regulated fishery for red king crab, has been suggested to be declared as a marine protected area (Miljødirektoratet 2004) but so far the initiative has yet to overcome the planning phase. Since crabs had not invaded this part by the time of this study in 2010, it presented us with the opportunity to study an "undisturbed" benthic community. A few species, with mainly Arctic distribution, such as *Clinocardium ciliatum*, *Pectinaria hyperborea* (Oug & Fuhrmann 2013), *Sclerograngon boreas* and the polar cod, *Boreogadus saida* (Christiansen & Fevolden 2000) occupy the inner fjord. The cold temperatures and ice coverage during the winter make Porsangerfjord suitable to study ecological processes in high-latitude habitats and may give insights into the impact of the invasion by decapods into these habitats.

2.2 EwE modelling

The open access software Ecopath (http://ecopath.org) was originally developed by Polovina (1984) and has since advanced to dynamic modelling over time (Ecopath with Ecosim - EwE) and space (Ecospace) (Christensen & Pauly 1992, Pauly et al. 2000, reviewed in Villasante et al. 2016). Ecopath creates a model of resources and their trophic interactions over a limited amount of time. It assumes mass-balance, with the option to allow for migration, biomass accumulation or reduction, emigration, or immigration. Ecopath is based on two master equations, describing (1) the production term, and (2) ensuring energy balance for each model group.

(1) Production = catch + predation + net migration + biomass accumulation + other mortality
(2) Consumption = production + respiration + unassimilated food

The main input parameters for groups are biomass (B), production per biomass (P/B), consumption per biomass (Q/B), diet proportions, fishery catches and ecotrophic efficiency (EE), which describes how much of the production is used in the system and equals 1 – other mortality. Values are usually averaged over the time period of 1 year. Unit of material flow is carbon and rates are expressed as carbon flow per year.

In Ecopath, species may be grouped into functional ecological guilds, based on similarity in diet, growth and consumption rates, habitats, and predators. Models developed for Porsangerfjord (Paper III) comprised 63 groups, including multi-stanzas for red king crabs and three fish species. In contrast to most other published models, we aimed at high resolution in the benthic compartments, allowing the capture and evaluation of trophic interactions with the red king crab. Ideally, an Ecopath model needs to include the full habitat range of the included species. Based on different environmental conditions and species distributions, sampling was designed to establish 5 models, one for each subarea, developed for the core period of 2009 to 2011.

The impact of the red king crab was investigated by looking at mixed trophic impact, MTI_i, which is a measure of how change in biomass of group *i* will affect other groups in the system, and the total relative impact ε_i which is based on MTI_i (Libralato et al. 2006), niche overlap and Ecosim simulations. The *keystoneness* index implemented in EwE has been criticized for not compensating sufficiently for high biomass in high impact species (Valls et al. 2015), for example resulting in phytoplankton ranking high in keystoneness. This conflicts with the original definition of a keystone species, where a species impact should be disproportional to its biomass (Power et al. 1996, see above). Based on the good performance in a meta-analysis by Valls et al. (2015) I instead calculated the therein suggested *keystoneness* (KS_3) given as

$$KS_3 = IC_L \times BC_0 \qquad \text{(Valls et al. 2015)}$$

with IC_L being the impact component (equals the relative total impact ε_i in Ecopath) and BC_0 being the biomass component (equals in this case descending rank of the biomass of i).

Ecosim (Walters et al. 1997, Christensen & Walters 2004) is a dynamic model developed for testing food web disturbances such as fishing and changes in primary production. Trophic flows will vary with changing biomass of predator and prey. In nature, species display a range of behaviours (such as seeking refugees, spatial displacements); Ecosim relies on principles inherent to the foraging arena theory, where exchange rates between predator-prey are restricted by spatial arenas (Walters et al. 1997, Christensen et al. 2005). A vulnerability parameter (which can be set by the user) partitions prey populations to vulnerable and non-vulnerable components, where foraging takes place in limited volumes. This represents a more realistic picture and helps improving predictions of aquatic ecosystem responses (Ahrens et al. 2012). Simulations with varying crab densities in EwE allowed us to investigate and quantify the predation impact (in this case the change of biomass in other species groups) over time (Paper

III). Crab removal was implemented by increasing fishing mortality at the beginning, followed by applying a forcing function to increase biomass. Initiating biomass at low levels and forcing biomass with the help of a time series has been shown to perform well in modelling invasive species impacts in EwE (Langseth et al. 2012). Despite looking at the effect on individual groups, we “sampled” the ecosystem at certain points in time and were able to compare how system properties (*omnivory*, *connectance*, and biomass residence time) would be affected by changing crab abundances.

2.3 Data collection

The assessment of macrobenthic biomass and production served three principle purposes: identification of patterns along environmental and predation gradients, obtaining input data for Ecopath models and establishing a status quo for future impact studies (with focus on the inner fjord where crabs had not yet established by 2010).

Benthic macrofauna on soft bottom substrates (Paper I) were sampled by grabs in 2010, following a random stratified design per area, with the aim of obtaining a large areal coverage instead of increasing precision at a single station. Input parameters for the Ecopath models of Porsangerfjord (Paper III) were based on a combination of field work between 2008 and 2012, regional literature data and estimates that could be obtained from catch statistics (mortality rates). The cooperative work within the EPIGRAPH project made it possible to obtain comprehensive biomass and diet data needed for the several species groups (details of sampling methods are described in the appendix of Paper III). Biomasses and P/B values estimated in Paper I were used as an input for most soft bottom taxa (infauna); sparsely distributed epifaunal organisms (e.g. suspension feeders) were sampled by an epibenthic sledge standardized to towing time. The estimated biomass of large infaunal and epifaunal bivalves such as *Chlamys islandica* and *Mytilus edulis* was not high enough to meet predator demand in the Ecopath models, mostly because sampling did not cover shallow habitats and sparsely distributed “beds”, which is why biomass of this group was estimated in the model.

During the course of this study it became clear that benthic community structure was different in the outer, middle, and inner fjord, but also showed quite a pronounced east-west disparity, not entirely corresponding to strata (sub areas) chosen *a priori* in Paper I and III. Averages given for defined areas (Paper I and III) therefore do not represent spatial heterogeneity within these subareas. Since we were constrained by effort and cost, grab samples were only taken during one year, and our estimates represent somewhat of a snapshot. However, some stations from the inner area were resampled during similar seasons in 2006 and 2011. Resampling showed that estimates for 2010 were representative for 2011 in this area (see section 3: supplementary results to Paper III). Data treatment in Paper I and III involved the aggregation of species into taxonomical (Paper I) and ecologically meaningful entities (Paper III), resulting in the loss of information concerning biodiversity estimates, but giving a reasonable representation of community structure and energy flow. Conversion into a relevant unit for energy flow (carbon or kJ) assured comparability to other studies and was performed for all invertebrates and groups in the Ecopath model by established conversion factors from literature.

2.3.1 Red king crab distribution

One of the major challenges in this study was to capture red king crab distribution in the fjord, with unknown effects of environment and substrate, crab behaviour (aggregations of size classes and sexes) and catchability of small size classes. Commercial stock estimates did not aim at predicting distribution patterns, and omit juvenile crabs < 70 mm carapace length, which left us little information on crab densities at macrofaunal sampling locations. For Paper I, we were interested in relative abundances of crabs at grab stations, representing an “average relative impact” of predation at these localities. Kriging was thus applied on swept area based catches from trawls, providing uncertainty estimates around predicted densities. Trawl catches were verified using relative abundances from traps. Red king crab biomasses used in Ecopath (Paper III) were calculated from back-calculation procedures, using abundances of large crabs estimated by crab trawls and represent averages for the subareas.

2.3.2 *Diet analysis*

In order to describe the diet and foraging patterns of red king crab (Paper II) and obtain input for the Ecopath models (Paper III) in Porsangerfjord, we combined stomach and stable isotope analysis. Since the crab is known to have a large variation in prey (Falk-Petersen et al. 2011) and little was known for small size classes foraging in shallow water, local diet information was needed. Stomachs were taken from crabs and various species, and diet data was included in the Ecopath models, where quantitative information was needed as an input. Estimating diet proportions is challenging in crabs, since stomach teeth grind content to small pieces, making identification and quantification especially difficult. Prey proportions for Ecopath were therefore based on frequency of occurrence, and adjusted during the balancing process.

Stable isotopes were used to obtain a less invasive, time-integrated estimate for diet differences in different size classes and sex of crabs. Together with stomach information, we applied the isotopic niche concept (Newsome et al. 2007) (see section 1.5) and used metrics defined in Jackson et al. (2012) in order to approximate trophic niche width and trophic overlap between size classes and with other native predators in the system (see Paper II). Trophic levels (TL) and diet obtained from stable isotopes were used to validate input and structure of the Ecopath models (Paper III). Isotopic ecology is prone to a number of caveats and limitations regarding sample treatments, tissues sampled (Post 2002, Post et al. 2007), fractionation factors, and variability in baselines used in TL estimation (Solomon et al. 2008, Middelburg 2014, Jennings & van der Molen 2015), often providing the researcher with local knowledge only. Intensive baseline sampling and experimental work addressing fractionation factors in crab tissues would likely improve data interpretation in this study.

2.3.3 Environmental data

Gradients in environmental data corresponded to decreasing temperature, depth, and salinity from the outer towards the inner fjord. An extensive monitoring program by the University of Tromsø provided data on temperature and salinity from fixed stations (see Paper I), which were sampled at all depths, over several years and throughout seasons. Temperature was used to estimate benthic production to biomass ratios (P/B) and adjust literature Q/B ratios for shrimps, since the latter were expected to be smaller at low bottom temperatures of the inner eastern basins (4E, Paper III). Substrate type likely influences benthic community structure and may account for differences in biomass and production. A detailed investigation of drivers of benthic production should therefore include substrate samples, but was outside the scope of this study.

2.4 Estimation of benthic production and P/B

Direct measurements of benthic production are usually based on cohort methods (see Allen 1971), growth rates or size frequency methods (see Benke 1996). The annual production to biomass (P/B) ratio of a population is the weighted average of biomass growth rates of the all individuals in that population over the course of a year (Benke 1996). The major determinant of a species P/B ratio is lifespan (Robertson 1979) and more recently, indirect methods use the empirical relationships between production and an organism’s lifespan or body mass (Banse & Mosher 1980, Tumbiolo & Downing 1994), with particular attention to the role of temperature affecting a species metabolism (Brey 1999a, Brey 2001, Tagliapietra et al. 2007). Brey

(1999a,b) showed that natural mortality and P/B are linearly related in unexploited benthic invertebrate populations. In order to estimate benthic P/B values in Porsangerfjord (given in Paper I and as input to Paper III), we adopted the annual neural network by Brey (2012) with individual body mass as the major input. In addition to environmental variables (mean temperature, depth and tidal elevation), it uses also taxonomic identity and habit (motility, habitat, feeding), which improves estimates of benthic secondary production (Cartes et al. 2002, Cusson & Bourget 2005), and perform better than common regression models (Brey et al. 1996, Brey 2012). Production can then be calculated from P/B*Biomass.

3 Summary of results

Paper I

Fuhrmann MM, Pedersen T, Ramasco V, Nilssen EM

Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab

Journal of Sea Research 106:1-13 (2015)

We found soft bottom community biomass and production to vary in the Porsangerfjord, attributable to differences in community composition along environmental gradients and possibly due to predation by the red king crab. Despite cold bottom temperatures and lower P/B ratios, benthic biomass and production were larger in the inner fjord, due to a community differing in terms of taxonomic composition and constituting larger taxa. Macrobenthic communities were characterized by high productivity of tube-building Polychaeta, also dominating biomass and abundance. Scarcity of larger and long-lived species (such as large bivalves and echinoderms) in areas with high king crab densities, are hypothesized to be first indications of predation (see also Paper III). Consumption by the red king crab may have altered the community resulting in high community P/B, but lowered standing stock biomass and production. While benthic production in the outer and middle fjord was mostly below estimates from fjord locations in the Barents Sea, the inner subarea exceeded values given for similar latitudes and hot spots of production in Arctic seas. The study presents an important contribution to monitor future development of macrobenthic communities in the inner Porsangerfjord.

Paper II

Fuhrmann MM, Pedersen T, Nilssen EM.

Trophic niche of the invasive red king crab (*Paralithodes camtschaticus*) in a native benthic food web

Under review in Marine Ecology Progress Series (2016)

Combining stomach analysis with $\delta^{15}N$ and $\delta^{13}C$ stable isotopes supported the hypothesis of a generalist, opportunistic feeding strategy of red king crab, consuming prey resources at multiple trophic levels. Common soft bottom taxa in Porsangerfjord, such as small bivalves and polychaetes, dominated gut contents. Larger filtrating bivalves were likely also part of crab diet, but were not detected by stomach analysis. We found variation in diet across size classes, related to different foraging habitats and crab aggregation at certain depths. However, we did not find indications for a distinct ontogenetic niche shift. Isotopic niches were similar among size classes, with spatial variability possibly concealing size effects. Sea urchins were an important diet item especially for small crabs residing in shallow water and feeding on more littoral species. Stable isotopes signatures indicated site fidelity in some individuals, with stable isotope signatures being similar among stations close to each other and $\delta^{13}C$ reflecting diet items found in stomachs. Considering the variance in baseline isotopic value, red king crab fed on average at trophic level 3.1, which is lower than all the fish species investigated, which also used more pelagic pathways. Isotopic niche overlap with other decapods, predatory sea stars, and gastropods indicated possible competition with the red king crab for similar food resources.

Paper III

Pedersen T, Fuhrmann MM, Lindstrøm U, Nilssen EM, Ivarjord T, Ramasco V, Jørgensen LL, Sundet JH, Sivertsen K, Källgren E, Hjelseth A-M, Michaelsen C, Systad G, Norrbin F, Svenning MA, Bjørge A, Steen H, Nilssen KT (2016).

Modelling ecosystem structure and trophic control by the invasive red king crab in Porsangerfjord, northern Norway

Manuscript

Ecopath baseline models revealed differences in food web structure and properties along the fjord, owing to differences in species distributions and trophic interactions. The inner cold subareas were characterized by high benthic biomass and production by detritivores, accompanied by lower benthic P/B values and biomass residence times. High benthic biomass here was likely a combination of food supply, larger body masses at low temperatures and low predation pressure. Red king crabs fed at trophic level 3 and were important predators of herbivorous echinoids, predatory gastropods and asteroids, large suspension feeders and the mud star *Ctenodiscus crispatus,* in which they caused high relative mortality rates. Feeding on several trophic levels, king crabs raised the system *omnivory* index. Other than for human consumption, crabs were not of major importance as prey themselves. Trophic niche overlap with red king crab was detected in predatory benthic invertebrate -and fish groups (such as flatfish and large haddock) and invertebrate feeding birds in the outer areas. Next to important demersal fish such as cod, medium red king crab had a high impact (mixed trophic impact, relative total impact), mostly in the middle fjord where crabs were most abundant. Simulated removal followed by a forced increase in biomass in EwE, suggested a strong top down control on long lived prey groups (see above) as well as competitive effects in some of the same groups and also in sea birds. Changes in biomasses in red king crab prey did not affect pelagic compartments, due to little niche overlap with fish. Simulations indicated that red king crab replaced major predators of large bivalves, resulting in little effect on this group. King crabs had a positive impact on recruiting macroalgae through predation on sea urchins, the effect this could have on macroalgae regrowth could not be realistically modelled. Part of the crab predation was buffered by high benthic production, mostly in the inner area. Simulations suggest that high red king crab densities affect P/B of the benthic invertebrate community, leading to low maturity and high turnover systems.

3.1.1 Supplementary results to Paper III: Keystoneness of red king crab

Keystoneness was calculated similar to the method defined in Valls et al. (2015) for all functional groups (excluding detritus). In subarea 3 (middle fjord), where king crabs had high biomass, KS_3 for medium red king crabs was around 12, similar to subarea 4E (inner eastern fjord) (Fig. 4). The red king crab ranked 6 and 7 (8 for large red king crab) in these areas respectively. In the outer areas (1 and 2) and the inner western fjord (4 W), KS_3 was higher at values around 20, but with similar ranks.

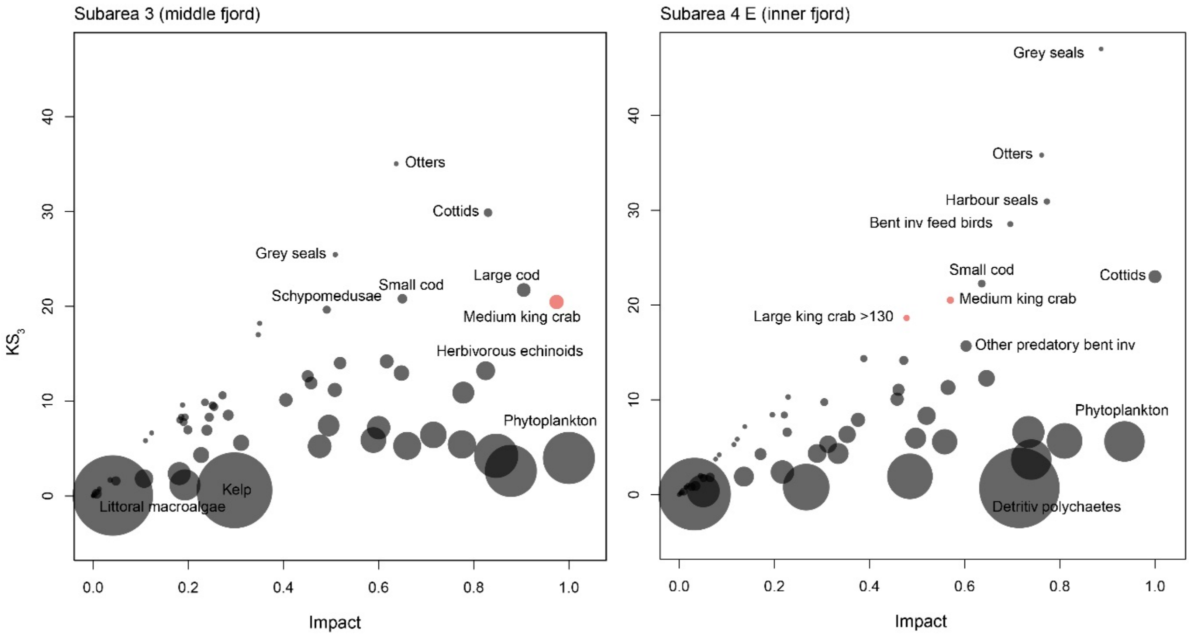


Fig. 4 *Keystoneness* (KS$_3$) versus relative total impact for the Ecopath model of subarea 3 and 4E in Porsangerfjord. Circles are scaled to biomass of groups.

4 Discussion

In this thesis, I combined different approaches to investigate the role of the invasive red king crab in the food web of Porsangerfjord. Through empirical and modelling work I provide evidence that the red king crab serves an important role in the food web, and despite a wide range of diet, controls biomass of some large invertebrates and with that, may impact biomass and productivity of the benthic compartment in the food web.

4.1 Eating and being eaten– feeding strategy and predation pressure

Common to most alien species is the ability to use a wide range of prey organisms (Hänfling et al. 2011, Griffen et al. 2012), which is likely also one of the reasons for the successful establishment of the red king crab in the Barents Sea. Diet analysis (Paper II) showed a high diversity of prey, similar to results from previous diet studies (Rafter et al. 1996, Sundet et al. 2000, Falk-Petersen et al. 2011). We also found that the red king crab had one of the highest *omnivory* indices of all species groups in the system (Paper III). The red king crab has been documented to show high feeding plasticity with regard to handling and type of prey, in laboratory experiments it was able to quickly adapt to offered prey items and showed individual feeding techniques (Jørgensen 2005, Jørgensen & Primicerio 2007, Michelsen 2011). It is also able to make use of seasonally available prey, such as post-spawning capelin (Mikkelsen 2013). Prey size is constrained by the ability of crabs to handle it with their claws (Jørgensen & Primicerio 2007). Adult red king crabs have been hypothesized to be size selective feeders (Falk-Petersen et al. 2011), targeting large animals first, with a high yield compromising for longer handling times. Similar size targeting has been shown for other crabs, such as the Portunid crab, *Charybdis japonica* (Townsend et al. 2015). However, results from Paper II showed that crabs frequently prey on small infaunal species or those that were most abundant in grab samples (Paper I). This may be a result of feeding in an already “impacted” environment, with fewer large organisms available or the fact that crabs did not ingest hard parts and these were missed in stomach content analysis (such as bivalves, which were likely underestimated in our diet study) (Jørgensen 2005). Feeding on what is most abundant supports a true opportunistic foraging strategy. Concomitant with the ability to switch between resources, the red king crab likely has an advantage over other native predators in our study system. Selective feeding was not observed in Paper II, but may need closer investigation using field and stomach data from the same location. Additionally, size selective feeding, such as crab juveniles feeding on small sea urchins, may locally shift size distribution. Results from our stable isotope analysis (Paper II) indicated a certain side fidelity in crabs, which is likely due to the generalist feeding strategy enabling crabs to stay within a foraging area for some time, instead of investing energy to search for suitable prey. However, there may be considerable individual differences in how much crabs move over time (Jørgensen et al. 2007, Windsland et al. 2014) as movements have been linked to other causes such as mating migrations (Jørgensen & Nilssen 2011). Different diets at different habitats were reflected in stomach contents and stable isotopes. Adults and small size classes share similar resources in shallow waters at least part of the year. However, larger crabs are mostly found at greater depths, and separate habitats likely contributing to less intraspecific competition. We did not find a distinct ontogenetic niche shift linked to an increase in trophic level with crab size. Such niche shift may be expected due to large crabs being able to utilize a wider size range of organisms or different nutritional requirements for growth, as this has been documented in other large decapods (Sainte-Marie & Chabot 2002, Griffen et al. 2012). Stable nitrogen isotope sigantures for prey organisms spanned over multiple trophic levels (Paper II), and did not neccecarily reflect size composition of species (see also Jennings et al. 2002). This is likely why most studies on decapod crabs fail to detect clear increases in TL with size, but instead emphasize the importance of foraging area for differences in diet (Bodin et al. 2007, Divine et al. 2015). Trophic levels estimated for red king crab size classes from $\delta^{15}N$ (3.0–3.1) was similar to Ecopath model results (around 2.8–2.9); small discrepancies could be due to baselines used in TL estimation (Paper II).

While invasive crustaceans may become a prey source for native fauna (De Rivera et al. 2005, Wong & Dowd 2013), mega-decapods often have a low significance as prey for any organisms other than humans (Boudreau & Worm 2012). Predation mortality for red king crabs estimated from Ecopath models was relatively low (Paper III), and confirms the assumption that red king crabs experience low predation pressure from natural predators. This is most likely due to their size and spiny armour, and may be one of the major reason for its success in colonizing new areas (see Lockwood et al. 2013). Predators on king crabs in its native areas are mostly pacific cod and large groundfish (reviewed in Falk-Petersen et al. 2011), feeding on crabs during or shortly after moulting. Predation by mammals may also occur on adults in the Pacific Ocean (Aydin et al. 2002). Some uncertainty around predators was given in our Ecopath models and more stomach samples from potential predators are necessary to improve diet input. Falk-Petersen et al. (2011) list salmon, saithe, a number of flatfish, skates and sculpins (*Cottidae*) as probable predators on crab larval stages and post-recruits in the Barents Sea . Ecopath models indicated that a small change in proportion of abundant predators, such as cod, may have a large impact on the crab population, despite the low proportions of crab in predator diets. Predation on juvenile crabs by sculpins (Aydin et al. 2007) has been observed in Porsangerfjord (H. K. Strand, IMR, pers. comm.) and may be significant in the inner area where sculpins are abundant (Paper III).

Cannibalism on small size classes was not documented in Porsangerfjord and is not seen as a major source of mortality in our study area. Cannibalism for red king crab has been documented from laboratory experiments (Borisov et al. 2007, Long et al. 2012) and Varangerfjord (Haugan 2004, own observations). It has to be noted that cannibalism may be difficult to distinguish from consumption of own moults, common in crustaceans, leading to misconceptions about the importance of cannibalism in the field.

4.2 Predation impact

Differences in the distribution and diet of small and large crabs leads to the assumption that these factors may affect different habitats, with juvenile crabs impacting the sublittoral zone and adults affecting deeper, soft bottom habitats. Small crabs have a higher consumption to biomass ratio and are often aggregated, potentially causing a more concentrated effect on local native fauna inhabiting the more shallow water. The most pronounced effect was caused through predation by medium and large red king crabs, which affected mostly larger, epibenthic invertebrates (Paper III) with often relatively low P/B ratios (Paper I). In model simulations, crab consumption exceeded production in these groups and resulted in a decline in biomass with increasing red king crab abundance.

4.2.1 Direct predation impact on large, long-lived invertebrates

Slow moving, and long-lived benthic organisms take over important roles in ecosystem functioning, such as bioturbation. However, large size and longevity are traits that often make species vulnerable to disturbances (Tumbiolo & Downing 1994, Solan et al. 2004, Norkko et al. 2013a).

One of the species heavily impacted by predation was the mud star, *Ctenodsicus crispatus*, a species which is targeted mostly by large- and medium-sized red king crabs (Paper II), likely due to their occurrences in deeper waters on muddy sediments (Paper I). This is one of the species which has shown to nearly disappear in heavy invaded areas of Varangerfjord (Oug et al. 2011) and may be a good indicator species of predation effects by larger crabs. Similar to that study, the soft bottom sediments of outer and middle Porsangerfjord were characterized by small maldanid and oweniid polychaetes, suggested that these may not be affected by predation (Oug et al. 2011). In contrast, there was a low abundance and biomass of large bivalves (such as *Cardiidae*) and large echinoderms, the latter consisting mostly of small, juvenile brittle stars. Large infaunal bivalves were suggested to decrease as a result of predation in Russian areas of crab invasion (Britayev et al. 2010). In EwE simulations (Paper III), large bivalves did not seem to be affected by crab predation, because the crab substituted predation by other predators. Large infaunal bivalves constituted only a small proportion of the crab diet, which may be due to either low abundance in the outer part and consequently not represented in the diet, or misidentification since hard parts were not found in stomachs. Other diet studies have shown large bivalves and other mollusks to be a major prey source when encountered (see reviews by Britayev et al. 2010, Falk-Petersen et al. 2011), and consider these species especially vulnerable to predation (Jørgensen 2005, Jørgensen & Primicerio 2007). In our study, very few stomach samples from large crabs were obtained from the inner fjord soft bottom habitats (Paper II), where crabs may forage in the future for abundant large bivalves (such as *Yoldia hyperborea*). A study in the northern Norwegian Sørfjord, where crabs have not invaded, showed that large bivalves contributed substantially to benthic biomass (Nilsen et al. 2006). Predatory snails (*Buccinum undatum, Neptunea spp.*, *Naticidae*) and large sea stars (e.g. *Asterias rubens, Henricia spp.*) were affected by increasing king crab abundances in simulations (Paper III) and had low biomasses in the outer areas, supporting results from Oug et al. (2011) and epifaunal surveys in Porsangerfjord, who had observed a decline in these species in areas with high crab densities (E. Nilssen, UiT, pers. comm.). While these species often only contribute little to total benthic production (Paper III), a reduction in these large species has consequences for benthic community composition and size structure.

4.2.2 Benthic production and P/B

It is well established that benthic community attributes such as species composition, biomass and production change along environmental gradients (e.g. Rosenberg 1995, Cusson & Bourget 2005, Blanchard et al. 2013) . We show in Paper I that different spatial variability in production to biomass ratios (P/B) and production was mainly driven by community structure, which differed under heterogenic environmental conditions in the fjord (cold bottom temperatures in the inner fjord). Biotic interactions, such as predation, have great potential to structure ecological communities (e.g. Paine 1974, Virnstein 1977, Gilinsky 1984, Quijon & Snelgrove

2005). Predation may affect benthic production processes (De Lange et al. 2004) and size structure of benthic communities by removing large sized individuals or species (Blumenshine et al. 2000), with unknown consequences for ecosystem functioning.

Soft sediments in the outer and middle Porsangerfjord were dominated by small sized species, such as small bivalves (*Yoldiella* spp.) and polychaetes (*Maldane sarsii* and *Oweniidae*), raising benthic community P/B. EwE simulations from Paper III lend support to the hypothesis that observed patterns in Paper I can partly be explained by red king crab predation. Predation caused high mortality rates in some large, long-lived invertebrates, leading to an increase in community P/B (as a combination of a change in group P/B and community composition) and a reduction in benthic biomass. This was also reflected in lower system biomass residence times (Paper III). High production by detritivorous polychaetes buffered predation by the red king crab, especially in the inner fjord. However, reduction of benthic biomass due to the removal of some larger species, lead to a decrease in total benthic production, which was not entirely compensated by elevated P/Bs. The northern Norwegian Ullsfjord-Sørfjord system has a similar trend in the distribution of smaller species with lower P/B dominating the outer and warmer Ullsfjord, attributable to higher temperatures and predation mortalities (Pedersen et al. 2016). Estimated P/Bs are lower in Ullsfjord (0.51) than in outer Porsangerfjord, however benthic production is similar due to higher benthic biomass in Ullsfjord.

Bottom trawling has been documented to shift soft bottom habitats towards high turnover and lower biomass systems (Jennings et al. 2001), ultimately with consequences for energy flow (Dannheim et al. 2014). An increased production of opportunistic species or young individuals may be seen in systems experiencing environmental pollution or weather extremes (Dolbeth et al. 2011). Communities dominated by taxa exhibiting high renewal rates may be more resilient towards perturbations because of fast recovery (Tumbiolo & Downing 1994). In contrast, fish populations altered by fishing experience a high turn-over rates of species and a dominance of younger age-classes and are proposed to make stocks more sensitive to environmental changes with less capacity to buffer disturbances (Planque et al. 2010).

Overall, body size is a proxy for a number of species' traits affecting food web structure and dynamics (Woodward et al. 2005). Large organisms may contribute considerably to benthic biomass, as we show in Paper I and III, and may also play important roles in other ecosystem functions. For example, the removal of large individuals in bivalve populations from soft sediments has been documented to affect oxygen and nutrient fluxes (Norkko et al. 2013b). The significance of size structure and resultant differences in P/B ratios for resilience and its ability to absorb perturbations needs more investigation.

4.2.3 Predation on herbivorous echinoids

Herbivorous echinoids (*Strongylocentrotus droebachiensis*) were prey for both large and small crabs foraging in shallow locations (Paper II), and the mixed trophic impact, and model simulations indicated that crabs had a substantial effect on sea urchin biomass (Paper III). This supports results from Russian studies, which reported substantial impact by juveniles on the sea urchin population in Kola and Dal'nezelenetskaya Bay, potentially leading to a reduction of 10-30 % of the sea urchin standing stock (Gudimov et al. 2003, Pavlova 2008, Pavlova 2009) and a change in size structure (with a relative increase of large sea urchins (Britayev et al. 2010). However, no production estimates were integrated in these studies. Predation on sea urchins resulted in indirect positive effects on the recruitment of micro- and macroalgae (Paper III). Whether this would also affect the regrowth of kelp could not be realistically modelled in EwE, due to the lack of a multi-stanza option for primary producers.

Macroalgae function as facilitating species, and dense macroalgae vegetation is often associated with a rich benthic fauna (Christie et al. 2009), where kelp beds function as nursery areas for fish, including cod (Keats et al. 1987). The artificial reduction of green sea-urchin abundance in over-grazed areas has resulted in rapid regrowth of kelp in northern Norway (Leinaas & Christie 1996). Support for successful regulation of juvenile sea urchin recruitment due to predation by decapods, comes from the northwest Atlantic Ocean in the Gulf of Maine, where large crabs (*Cancer* spp.) function as a new apex predator after a decline in local fish predators, keeping sea urchins in check (Steneck et al. 2002). While more severe perturbations may be needed to switch systems from barren grounds to vegetated states (Norderhaug & Christie 2009), decapod predators have been shown to substantially supress herbivory and thereby play keystone roles in ecosystems (Snyder & Evans 2006, Boudreau & Worm 2012). There is no empirical evidence of the hypothesis that predation by the red king crab will aid regrowth of macro-algae along the northern Norwegian coast.

4.2.4 Keystoneness

Red king crab had an intermediate trophic level (approximately 3) and large and medium crabs had relatively high *keystoneness* index, indicating a top-down role in the ecosystem (Papers II and III, supplementary results). A high impact on other groups was coupled to high abundances in the middle subareas of the fjord, pointing to the red king crab being a high impact-high biomass species rather than a true keystone predator (compare Valls et al. 2015). This was supported by typical higher trophic level species (sea otters and seals) being ranked higher than other species in Porsangerfjord. The indirect positive impact on macroalgae recruitment may support the perception of the red king crab as a keystone species, considering the importance for macroalgae as a habitat. Depending on which keystone index is used (from EwE or Valls et al. 2014), results of *keystoneness* differ substantially and the concept seems somewhat arbitrary. Considering this, relative total impact (ε_i) may be a better indicator for ecosystem impact.

4.2.5 *Omnivory*

The red king crab fed on different trophic levels including algae (Papers II and III) and increased system *omnivory* (SOI) in the EwE simulations. The prevalence of trophic omnivory usually increases connectivity of a food web, and with the introduction of multiple links in the food web, can be seen as measure of complexity. *Connectance* was not affected in EwE models, due to the inherent structure of models not being changed throughout simulations, which makes the omnivory index a better indicator for food web connectivity (Christensen et al. 2005). Species' feeding strategy and niche width strongly influence food web structure (Beckerman et al. 2006, Ingram et al. 2009) and it has been shown in qualitative food web models that boreal generalist fish such as cod alter food web structure and possibly function (Kortsch et al. 2015). The importance of trophic omnivory for food web dynamics (especially in marine systems) is not quite clear from ecological literature, but has been found to correlate with ecosystem stability (Morissette 2007). Recent theoretical models suggests that weak omnivory stabilizes food webs (Gellner & McCann 2012) through reducing the probability for strong top-down control, weakening trophic cascades (Bascompte et al. 2005); whereas in general, the relationship between omnivory and stability largely depends on the feeding behaviour and structure of the studied food web (Vandermeer 2006). We show that despite being a highly omnivorous predator, the red king crab has the potential to exert strong top down control on a few prey species, and may lead to indirect effects on other species. Vasconcellos et al. (1997) did not find a correlation in the SOI and stability (recovery time) in marine ecosystems after simulated perturbation and it seems that the relationship between omnivory and stability in food webs needs further investigation.

4.3 Niche overlap and competitive effects

Low competition in a system may facilitate the establishment of an alien species, based on the theory that increased occupancy of available niches decrease invasiveness of a community (Elton 1958). Trophic niche overlap is one of the reasons why competition could arise in the first place, with consequences either for the invader or native species. In practice, competition will only affect the native biota if either resources are limited or the invader acts superior and/or is more efficient in using limited resources.

The king crab is an effective feeder on infaunal organisms, such as detritivorous polychaetes, which are not utilised by many other species (Paper III), and at the same time had high production in Porsangerfjord (Paper I). Results from stable isotopes (Paper II) and Ecopath niche overlap (Paper III) show that the red king crab has a large overlap in trophic niche with some predatory invertebrates, mainly native large crustaceans (*Lithodes maja*, *Pagurus* spp., *Hyas* spp.), predatory snails (*Neptunea* sp., *Buccinum undatum*) and sea stars (*Henricia* sp., *Asterias rubens*), with some of these also serving as prey. Ecopath models also indicated niche overlap with crangonid shrimps (*Sclerocrangon boreas* and *Sabinea septemcarinata*) and predatory polychaetes, not strongly overlapping in isotopic niches (Paper II). For the two named shrimps, stable isotopes is likely a better indicator because samples were taken locally, while diet input to Ecopath models was taken from literature for these species. Among other things, the little effect on these groups is owed to the high productivity in polychaetes, a major food source. The large impact on some of the benthic predators (sea stars and predatory gastropods) was mainly a result of predation, but competitive effects contributed to this.

Due to its size and claw strength, the king crab is assumed to be superior to most of these predators with regard to competitive behaviour. Niche displacements by invasive crustaceans have been documented in a number of freshwater habitats (Snyder & Evans 2006, Gherardi 2007), but are less documented for marine decapods and mainly inferred from experimental behavioural studies (MacDonald et al. 2007, Weis 2010). The impact by the red king crab on other benthic predators also depends on their ability to switch prey items, which may be limited in certain species, for example predatory sea stars.

The further northwards expanding edible crab (*Cancer pagurus*) may become a new competitor along the coast. So far, low habitat overlap between the red king crab and the snow crab (*Chionoecetes opilio*) suggests little competition, despite large overlap in food sources (Sundet & Bakanev 2014, Divine et al. 2015)

The king crab niche overlap with fish species such as haddock, cod and flatfish was considerably low (Paper II and III), and these species were not affected by increasing abundances of crabs. Most fish fed on pelagic pathways, while the crab utilised mostly detritus pathways (Paper III) and fed at higher trophic levels (Paper II and III), primarily due to the facts that these crabs can utilize large and mobile (and mostly more predatory) prey species. Cottids and haddock share similar prey resources with red king crabs (Paper III), which is not indicated by isotopic niches (Paper II and Källgren et al. 2014). Our results demonstrated little effect on these fish species in model simulations and this was likely due to the actual high production in prey, such as polychaetes. A low negative impact on fish species would support the claim by Dvoretsky and Dvoretsky (2015), who compared fluctuations in major commercial fish stocks in the Barents sea (haddock, cod, saithe and capelin) to red king crab abundances (since its introduction) and concluded that there was no effect by the crab. However, there is evidence for an impact on lumpsucker (*Cyclopterus lumpus*) recruitment, due to predation on eggs (Mikkelsen & Pedersen 2012). A few fish eggs were found in crab stomachs in this study (Paper II) but were not further identified to species. Fish eggs predation was not implemented in Ecopath models. Thus, effects by egg predation could not be evaluated and competition with fish at other localities cannot be excluded.

Ecopath models and simulations indicated a competitive effect on benthic invertebrate feeding sea birds in the outer areas (Paper III). A negative impact on bird populations due to an introduction of a decapods has, to our knowledge, not been documented, mostly because other crabs may act as substitute prey species (Grosholz et al. 2000, Wong & Dowd 2013). Common eider ducks (*Somateria molissima*), one of the dominating species in this group (Paper III), are unlikely to be able to use king crabs as major prey, while gulls have been observed to feed on red king crabs (my observations), but it is very uncertain to what extent. Decline or behavioural responses such as the switch of foraging areas may be a consequence of king crab invasion in Porsangerfjord.

4.4 Applicability and limitations of this work

The present study built on extensive local field sampling which improved data quality and accuracy of measures. Despite only looking at one fjord ecosystem, there is no reason why the approach used in this study is not applicable to other high-latitude systems, and the role of the red king crab in the food web and its impact are likely to be similar in other invaded areas.

As with many other ecological studies, the present study was restrained by cost and effort and has a number of flaws and limitations, due to common fluctuations and imprecisions regarding sampling and sample treatment.

One of the major restrictions is that we lack quality time series and pre-invasion data, which would largely help in evaluating proposed impacts and separate environmental impacts from predation impacts (see Paper I). Such data exists for the inner-eastern section of Porsangerfjord, and this data illustrates that benthic inter-annual variation in biomass was considerably low from 2006 to 2011, validating estimates given in Paper I (Fig. 5). Additionally, information on sediment characteristics would likely help in explaining observed patterns of benthic production (e.g. Lin et al. 2016).

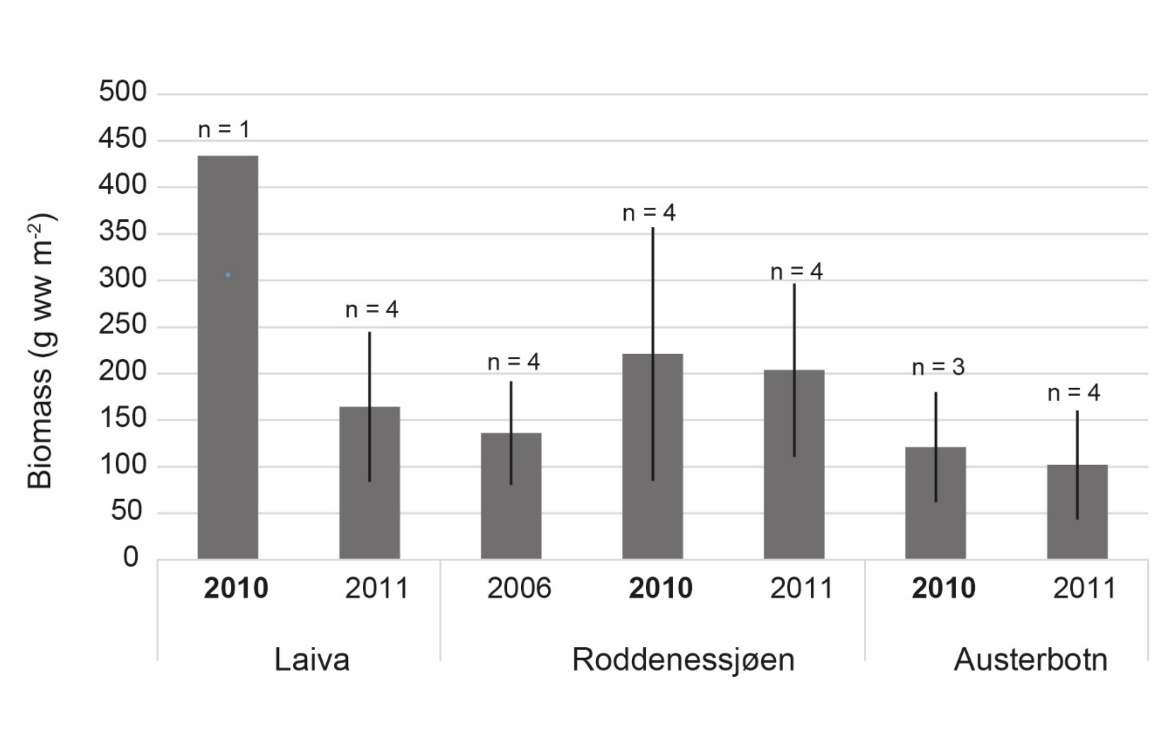


Fig. 5 Macrobenthic biomass (g wet weight m^{-2}) at sampled locations in inner Porsangerfjord in the years 2006 (Oug & Fuhrmann 2013), 2010 (data from Paper I) and 2011 (Oug & Fuhrmann 2013). A high biomass in Laiva (shallow station located between Austerbotn and Roddenessjøen, see Fig. 2) in 2010 was due to one large bivalve in the single replicate. Error bars denote standard deviations.

We omitted how predation may affect benthic biodiversity. Biodiversity is considered important for ecosystem function (McCann 2000, Hooper et al. 2005) and invasive species are seen as a major threat causing species extinctions on a local and global scale (Bax et al. 2003, Molnar et al. 2008), with the latter scale being likely more uncertain (Gurevitch & Padilla 2004). There does not seem to be evidence for biodiversity *per se* as a major driver of benthic production and looking at functional biodiversity or trait composition (including body sizes) may be more relevant in this aspect (Bolam & Eggleton 2014 and Paper I). However, biodiversity may have implications for energy flow, productivity and stability in food webs, and may be worth addressing (Worm & Duffy 2003, Pedersen et al. 2016).

One should keep in mind that non-trophic interactions such as habitat facilitation and modification also play an important role in ecological communities (Stachowicz 2001). We have exclusively looked at trophic interactions, while the red king crab may affect habitats and, as we show in paper III, structuring species (such as macroalgae). For instance, red king crabs have been shown to effect sediment quality by removing bioturbating species (Oug et al. 2011). More recently, mediating functions have been incorporated into EwE (Christensen et al. 2008), allowing for a better representation of habitat provisions by certain species. These functions may be applied in the future to our EwE model for a closer investigation of the importance of macroalgae as a habitat for benthic fauna and juvenile fish in areas where red king crab prey on grazing sea urchins.

The grouping of species in Ecopath models may blur effects on species levels. Uncertainty in Ecopath usually reflects the quality of the input data and could be reduced by more field data. Diet input for red king crabs to Ecopath (Paper III) was based on the frequency of occurrence of prey in stomachs (Paper II), which is not ideal for accurate estimation of diet proportions. Stable isotopes can be used as an input to food web models (Ramsvatn 2013), but mixing models tend to have difficulties dealing with multiple possible prey resources as is common in generalists (Newsome et al. 2012). Grouping prey items usually introduces additional uncertainty (Ward et al. 2011). Although Bayesian models can deal with numerous potential resources, they are sensitive towards accurate discrimination factors $\Delta\delta^{13}C$ and $\Delta\delta^{15}N$ (Bond & Diamond 2011) in which these models are no longer applicable. The spread in benthic stable isotope signatures was considerable between species groupings used in Ecopath models, indicating different diets. In this way, Ecopath groupings present generalizations, and are a consequence of trade-offs between minimizing complexity and obtaining sufficient resolution in order to describe major energy flows.

4.5 Conclusions and future perspectives

This thesis provides new knowledge on how predation by the red king crab may effect benthic community productivity and pertubate the food web. Simultaneously, this thesis lays the foundation for future monitoring in the Porsangerfjord and identifies important species (e.g. long-lived benthic invertebrates and macroalgae) as indicators of predation effects.

Benthic communities in Porsangerfjord followed environmental and predation gradients, which affected community traits, such as composition and size structure, resulting in different production and P/B patterns. The red king crab is a generalist, opportunistic predator, feeding on multiple trophic levels. Small and large crabs are likely to affect different habitats and prey species, but took a similar trophic position in the food web. The red king crab played an important role in the Porsangerfjord food web though top-down effects on large, long-lived benthic invertebrate groups by medium and large sized crabs, but had little significance as prey for higher trophic levels and effected mostly the benthic compartment of the food web. Niche overlap and competitive effects with fish species was comparably low, but may be of significance for benthic invertebrate feeding birds and large predatory invertebrates, the latter also being prey for red king crabs. In the future, king crabs may partly replace these invertebrates as major predators in the benthos. Figure 6 summarizes the role of the red king crab, its trophic links and hypothetical impacts in the food web of Porsangerfjord. Predation pressure by the red king crab may be buffered by high production in some prey, such as polychaetes, but may lead benthic communities to an overall lower biomass and higher turnover system, with unknown consequences for ecosystem stability and resilience. King crabs could however help in the regrowth of macroalgae through predation on herbivorous sea urchins, but this needs further empirical evidence and implementation in future models. The total impact of the red king crab will largely depend on the abundance and the distribution of red king crabs. Knowledge on local and regional distribution of different size classes and seasonal patterns in red king crab migration would largely benefit future impact studies.

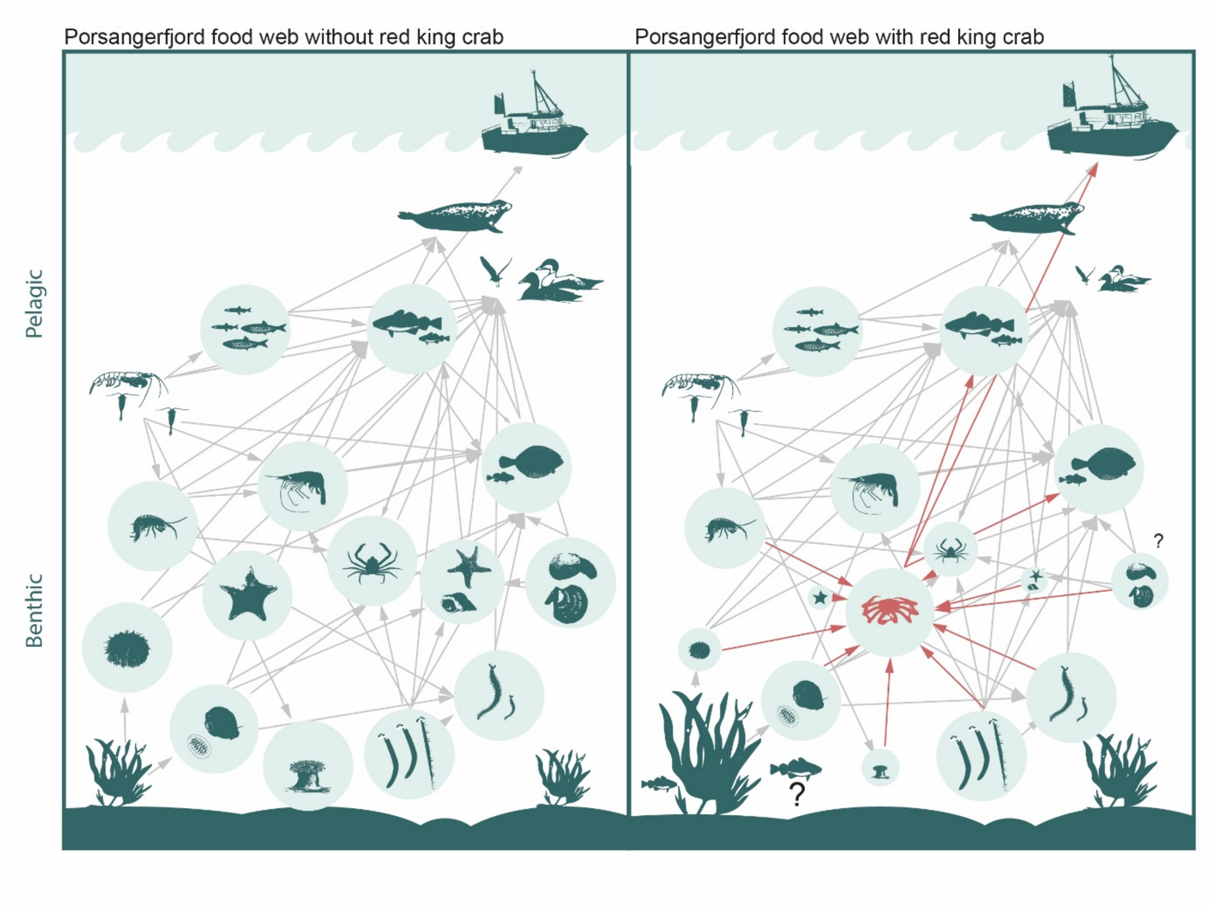


Fig. 6 Conceptual model of a simplified food web in Porsangerfjord, illustrating the role and hypothetical effect of invasion by the red king crab (in red). Excluded are pelagic primary producers and detritus sources. Circle size is scaled to change in biomass due to an increase in red king crab abundances obtained from the EwE scenario for subarea 3 (Paper III).

EwE modelling can help to uncover indirect consequences, but time series data are needed to validate possible mechanisms. Experimental studies are important for model parameterization and uncertainty in consumption estimates could be overcome by future experiments imitating local conditions of the system in question.

The dispersal of the red king crab is an ongoing process (Windsland et al. 2014) along with the dispersal of snow crabs into the Arctic (Alvsvåg et al. 2008, Sundet & Bakanev 2014). As red king crabs become more abundant in the inner area of Porsangerfjord, results from this study provide valuable pre-invasion data on benthic biomass and production. Because of the Arctic nature of this inner fjord area, we hope that this time-series study can continue, as it will provide valuable information on how Arctic benthic communities will respond to invasive species.

In Varangerfjord, where red king crabs had reached high initial densities and caused a reduction in benthic biomass (Oug et al. 2011), there were indications that crabs have exceeded the limits of the natural carrying capacity (i.e. benthic production), which was reflected in lower individual fecundity and a recent reduction in stock (Hjelset et al. 2012, Windsland 2014). However, it remains difficult to distinguish the effects caused by high fishing pressure from the crab's invasion history. In Norway, red king crab management aims at sustaining a viable stock, while further reducing the spread of the current population. In general, king crab management in the Barents Sea still largely depends on the socio-economic benefits of the fishery (Falk-Petersen 2012). With the results of this study in mind, it is crucial to continue the effort of limiting the further expansion of this stock if the overall goal is to maintain ecosystem structure and functionality.

5 References

Ahrens RNM, Walters CJ, Christensen V (2012) Foraging arena theory. Fish and Fisheries 13:41-59. doi: 10.1111/j.1467-2979.2011.00432.x

Allen KR (1971) Relation between production and biomass. Journal of the Fisheries Board of Canada 28:1573-1581. doi: 10.1139/f71-236

Alvsvåg J, Agnalt A-L, Jørstad KE (2008) Evidence for a permanent establishment of the snow crab (*Chionoecetes opilio*) in the Barents Sea. Biol Invasions 11:587-595. doi: 10.1007/s10530-008-9273-7

Anonym (2006) St.meld.nr. 8 (2005 –2006). Helhetlig forvaltning av det marine miljø i Barentshavet og havområdene utenfor Lofoten (forvaltningsplan). Ministry of Environment, Oslo (available in English from the Norwegian Ministry of Environment). https://www.regjeringen.no/contentassets/f0f38e6b95224570ba44da87b1093d03/no/pdfs/stm200520060008000dddpdfs.pdf

Arias-González JE, González-Gándara C, Luis Cabrera J, Christensen V (2011) Predicted impact of the invasive lionfish *Pterois volitans* on the food web of a Caribbean coral reef. Environ Res 111:917-925. doi: 10.1016/j.envres.2011.07.008

Aronson RB, Smith KE, Vos SC, McClintock JB, Amsler MO, Moksnes P-O, Ellis DS, Kaeli J, Singh H, Bailey JW (2015) No barrier to emergence of bathyal king crabs on the Antarctic shelf. PNAS 112:12997-13002. doi: 10.1073/pnas.1513962112

Aydin KY, Gaichas S, Ortiz I, Kinzey D, Friday N (2007) A comparison of the Bering Sea, Gulf of Alaska, and Aleutian Islands large marine ecosystems through food web modeling. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-178, 298 p. http://www.afsc.noaa.gov/Publications/AFSC-TM/NOAA-TM-AFSC-178.pdf.

Aydin KY, Lapko V, Radchenko V, Livingston P (2002) A comparison of the eastern Bering and western Bering Sea shelf and slope ecosystems through the use of mass-balance food web models. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-130, 78 p. https://www.pices.int/meetings/workshops/2006_workshops/ESSAS/Aydin_NOAA-TM-AFSC-130.pdf.

Aydin KY, Whitehouse GA (2016) Trophic Structure of the Eastern Chukchi Sea: An Updated Mass Balance Food Web Model. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-318, 175 p. doi: 10.7289/V5/TM-AFSC-318

Banse K, Mosher S (1980) Adult body mass and annual production/biomass relationships of field populations. Ecol Monogr 50:355-379. doi: 10.2307/2937256

Bascompte J, Melian CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. PNAS 102:5443-5447. doi: 10.1073/pnas.0501562102

Bax N, Eliassen J-E (1990) Multispecies analysis in Balsfjord, northern Norway: solution and sensitivity analysis of a simple ecosystem model. ICES J Mar Sci 47:175-204. doi: 10.1093/icesjms/47.2.175

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. Marine Policy 27:313-323. doi: 10.1016/s0308-597x(03)00041-1

Bearhop S, Adams CE, Waldron S, Fuller RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. J Anim Ecol 73:1007-1012. doi: 10.1111/j.0021-8790.2004.00861.x

Beckerman AP, Petchey OL, Warren PH (2006) Foraging biology predicts food web complexity. PNAS 103:13745-13749. doi: 10.1073/pnas.0603039103

Benke AC (1996) Secondary production of macroinvertebrates. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology. Academic Press, San Diego, USA.

Blanchard AL, Parris CL, Knowlton AL, Wade NR (2013) Benthic ecology of the northeastern Chukchi Sea. Part I. Environmental characteristics and macrofaunal community structure, 2008–2010. Cont Shelf Res 67:52-66. doi: 10.1016/j.csr.2013.04.021

Blicher ME, Sejr MK, Rysgaard S (2009) High carbon demand of dominant macrozoobenthic species indicates their central role in ecosystem carbon flow in a sub-Arctic fjord. Mar Ecol Prog Ser 383:127-140. doi: 10.3354/meps07978

Blumenshine SC, Lodge DM, Hodgson JR (2000) Gradient of fish predation alters body size distributions of lake benthos. Ecology 81:374-386. doi: 10.1890/0012-9658(2000)081[0374:gofpab]2.0.co;2

Bodin N, Le Loc'h F, Hily C, Caisey X, Latrouite D, Le Guellec AM (2007) Variablility of stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) in two spider crab populations (*Maja brachydactyla*) in Western Europe. J Exp Mar Biol Ecol 343:149-157. doi: 10.1016/j.jembe.2006.09.024

Bodkin JL (1988) Effects of kelp forest removal on associated fish assemblages in central California. J Exp Mar Biol Ecol 117:227-238. doi: http://dx.doi.org/10.1016/0022-0981(88)90059-7

Bolam S, Eggleton J (2014) Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. J Sea Res 88:47-58. doi: 10.1016/j.seares.2014.01.001

Bolam SG, Barrio-Frojan CRS, Eggleton JD (2010) Macrofaunal production along the UK continental shelf. J Sea Res 64:166-179. doi: 10.1016/j.seares.2010.02.003

Bond AL, Diamond AW (2011) Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. Ecol Appl 21:1017-1023. doi: 10.1890/09-2409.1

Borisov RR, Epelbaum AB, Kryakhova NV, Tertitskaya AG, Kovatcheva NP (2007) Cannibalistic behavior in red king crabs reared under artificial conditions. Russ J Mar Biol 33:227-231. doi: 10.1134/s1063074007040049

Boudreau SA, Worm B (2012) Ecological role of large benthic decapods in marine ecosystems: a review. Mar Ecol Prog Ser 469:195-213. doi: 10.3354/meps09862

Brey T (1999a) A collection of empirical relations for use in ecological modelling. Naga, ICLARM Q 22:24-28. http://epic.awi.de/471/1/Brey99_Naga22.pdf

Brey T (1999b) Growth performance and mortality in aquatic macrobenthic invertebrates. Adv Mar Biol 35:153-223. doi: 10.1016/S0065-2881(08)60005-X

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. http://www.thomas-brey.de/science/virtualhandbook/. Accessed 01 Aug 2013.

Brey T (2012) A multi-parameter artificial neural network model to estimate macrobenthic invertebrate productivity and production. Limnol Oceanogr: Methods 10:581-589. doi: 10.4319/lom.2012.10.581

Brey T, Gerdes D (1998) High Antarctic macrobenthic community production. J Exp Mar Biol Ecol 231:191-200. doi: 10.1016/s0022-0981(98)00060-4

Brey T, Jarre Teichmann A, Borlich O (1996) Artificial neural network versus multiple linear regression: Predicting P/B ratios from empirical data. Mar Ecol Prog Ser 140:251-256. doi: 10.3354/meps140251

Britayev TA, Rzhavsky AV, Pavlova LV, Dvoretskij AG (2010) Studies on impact of the alien red king crab (*Paralithodes camtschaticus*) on the shallow water benthic communities of the Barents Sea. J Appl Ichthyol 26:66-73. doi: 10.1111/j.1439-0426.2010.01494.x

Brockerhoff A, McLay C (2011) Human-mediated spread of alien crabs. In: Galil BS, Clark PF, Carlton JT (eds) In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. Springer Science + Business Media B.V., Netherlands. doi: 10.1007/978-94-007-0591-3_2

Byron C, Link J, Costa-Pierce B, Bengtson D (2011) Modeling ecological carrying capacity of shellfish aquaculture in highly flushed temperate lagoons. Aquaculture 314:87-99. doi: 10.1016/j.aquaculture.2011.02.019

Cartes J, Brey T, Sorbe J, Maynou F (2002) Comparing production biomass ratios of benthos and suprabenthos in macrofaunal marine crustaceans. Can J Fish Aquat Sci 59:1616-1625. doi: 10.1139/F02-130

Christensen V (1995) Ecosystem maturity — towards quantification. Ecol Model 77:3-32. doi: 10.1016/0304-3800(93)E0073-C

Christensen V, Pauly D (1992) ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol Model 61:169-185. doi: 10.1016/0304-3800(92)90016-8

Christensen V, Pauly D (1993) Trophic models of aquatic ecosystems, Vol 26. ICLARM Conference Proceedings 26. 1 ed. , Manila, Philippines

Christensen V, Walters C, Pauly D, Forrest R (2008) Ecopath with Ecosim version 6 user guide. Lenfest Ocean Futures Project. ftp://download.ecopath.org/Help/Ewe%20User%20Guide%206.pdf

Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecol Model 172:109-139. doi: 10.1016/j.ecolmodel.2003.09.003

Christensen V, Walters CJ, Pauly D (2005) Ecopath with Ecosim: a user’s guide. Fisheries Centre, University of British Columbia, Vancouver:154. ftp://142.103.47.93/Help/Ewe%20User%20Guide%205_1.pdf

Christiansen JS, Fevolden S-E (2000) The polar cod of Porsangerfjorden, Norway; revisited. Sarsia 85:189-193. doi: 10.1080/00364827.2000.10414571

Christie H, Norderhaug KM, Fredriksen S (2009) Macrophytes as habitat for fauna. Mar Ecol Prog Ser 396:221-233. doi: 10.3354/meps08351

Coll M, Lotze HK (2016) Ecological indicators and food-web models as tools to study historical changes in marine ecosystems. In: Máñez KS, Poulsen B (eds) Perspectives on Oceans Past. Springer Netherlands. doi: 10.1007/978-94-017-7496-3_7

Coll M, Navarro J, Olson RJ, Christensen V (2013) Assessing the trophic position and ecological role of squids in marine ecosystems by means of food-web models. Deep-Sea Res Pt II 95:21-36. doi: 10.1016/j.dsr2.2012.08.020

Colléter M, Valls A, Guitton J, Gascuel D, Pauly D, Christensen V (2015) Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. Ecol Model 302:42-53. doi: 10.1016/j.ecolmodel.2015.01.025

Commitol JA, Ambrose WGJ (1985) Multiple trophic levels in soft-bottom communities. Mar Ecol Prog Ser 26:289-293. doi: 10.3354/meps026289

Cummings DO, Buhl J, Lee RW, Simpson SJ, Holmes SP (2012) Estimating niche width using stable isotopes in the face of habitat variability: a modelling case study in the marine environment. PLoS ONE 7:e40539. doi: 10.1371/journal.pone.0040539

Cusson M, Bourget E (2005) Global patterns of macroinvertebrate production in marine benthic habitats. Mar Ecol Prog Ser 297:1-14. doi: 10.3354/meps297001

Dannheim J, Brey T, Schröder A, Mintenbeck K, Knust R, Arntz WE (2014) Trophic look at soft-bottom communities—Short-term effects of trawling cessation on benthos. J Sea Res 85:18-28. doi: 10.1016/j.seares.2013.09.005

De Lange HJ, Jonge JD, Besten PJD, Oosterbaan J, Peeters ETHM (2004) Sediment pollution and predation affect structure and production of benthic macroinvertebrate communities in the Rhine–Meuse delta, The Netherlands. J North Am Benthol Soc 23:557-579. doi: 10.1899/0887-3593(2004)023<0557:spapas>2.0.co;2

De Rivera C, Grosholz E, Ruiz G (2011) Multiple and long-term effects of an introduced predatory crab. Mar Ecol Prog Ser 429:145-155. doi: 10.3354/meps09101

De Rivera CE, Ruiz GM, Hines AH, Jivoff P (2005) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. Ecology 86:3364-3376. doi: 10.1890/05-0479

Degen R, Jørgensen LL, Ljubin P, Ellingsen IH, Pehlke H, Brey T (2016) Patterns and drivers of megabenthic secondary production on the Barents Sea shelf. Mar Ecol Prog Ser 546:1-16. doi: 10.3354/meps11662

Degen R, Vedenin A, Gusky M, Boetius A, Brey T (2015) Patterns and trends of macrobenthic abundance, biomass and production in the deep Arctic Ocean. Polar Res 34. doi: 10.3402/polar.v34.24008

Dew CB (1990) Behavioral ecology of podding red king crab, *Paralithodes camtschatica*. Can J Fish Aquat Sci 47:1944-1958. doi: 10.1139/f90-219

Divine LM, Bluhm BA, Mueter FJ, Iken K (2015) Diet analysis of Alaska Arctic snow crabs (*Chionoecetes opilio*) using stomach contents and δ^{13}C and δ^{15}N stable isotopes. Deep-Sea Res Pt II: In press. doi: 10.1016/j.dsr2.2015.11.009

Dolbeth M, Cardoso PG, Grilo TF, Bordalo MD, Raffaelli D, Pardal MA (2011) Long-term changes in the production by estuarine macrobenthos affected by multiple stressors. Estuar Coast Shelf Sci 92:10-18. doi: 10.1016/j.ecss.2010.12.006

Dolbeth M, Cusson M, Sousa R, Pardal MA (2012) Secondary production as a tool for better understanding of aquatic ecosystems. Can J Fish Aquat Sci 69:1230-1253. doi: 10.1139/f2012-050

Dvoretsky A, Dvoretsky V (2015) Commercial fish and shellfish in the Barents Sea: Have introduced crab species affected the population trajectories of commercial fish? Rev Fish Biol Fish 25:297-322. doi: 10.1007/s11160-015-9382-1

Eddy TD, Pitcher TJ, MacDiarmid AB, Byfield TT, Tam JC, Jones TT, Bell JJ, Gardner JPA (2014) Lobsters as keystone: Only in unfished ecosystems? Ecol Model 275:48-72. doi: 10.1016/j.ecolmodel.2013.12.006

Elton CS (1958) The ecology of invasions by animals and plants. Chapman and Hall, London, UK

Epstein JM (2008) Why model? J Artif Soc Soc Simul 11:12. http://jasss.soc.surrey.ac.uk/11/4/12.html

Evans S (1983) Production, predation and food niche segregation in a marine shallow soft-bottom community. Mar Ecol Prog Ser 10:147-157.

Evans S (1984) Energy budgets and predation impact of dominant epibenthic carnivores on a shallow soft bottom community at the Swedish west coast. Estuar Coast Shelf Sci 18:651-672. doi: 10.1016/0272-7714(84)90037-4

Falk-Petersen J (2012) Management of the alien invasive red king crab Integrating natural and social science perspectives. Doctoral thesis, University of Tromsø, Norway. http://hdl.handle.net/10037/4236.

Falk-Petersen J, Bøhn T, Sandlund O (2006) On the numerous concepts in invasion biology. Biol Invasions 8:1409-1424. doi: 10.1007/s10530-005-0710-6

Falk-Petersen J, Renaud P, Anisimova N (2011) Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea–a review. ICES J Mar Sci 68:479-488. doi: 10.1093/icesjms/fsq192

Fuhrmann MM, Pedersen T, Ramasco V, Nilssen EM (2015) Macrobenthic biomass and production in a heterogenic subarctic fjord after invasion by the red king crab. J Sea Res 106:1-13. doi: 10.1016/j.seares.2015.09.003

Galil BS, Clark PF, Carlton JT (2011) In the wrong place-alien marine crustaceans: distribution, biology and impacts, Vol 6. Springer Science & Business Media B.V., Netherlands

Gederaas L, Moen TL, Skjelseth S, Larsen L-Ke (2012) Alien species in Norway – with the Norwegian black list 2012. http://www.artsdatabanken.no/file/689/alien%20species.

Gellner G, McCann K (2012) Reconciling the omnivory-stability debate. The American Naturalist 179:22-37. doi: 10.1086/663191

Gherardi F (2007) Understanding the impact of invasive crayfish. In: Gherardi F (ed) Biological invaders in inland waters: Profiles, distribution, and threats. Springer. Dordrecht, Netherlands. doi: 10.1007/978-1-4020-6029-8_28

Gilinsky E (1984) The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology:455-468. doi: 10.2307/1941408

Gíslason ÓS, Halldórsson HP, Pálsson MF, Pálsson S, Davíðsdóttir B, Svavarsson J (2014) Invasion of the Atlantic rock crab (Cancer irroratus) at high latitudes. Biol Invasions 16:1865-1877. doi: 10.1007/s10530-013-0632-7

Grebmeier JM, Cooper LW, Feder HM, Sirenko BI (2006) Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi Seas in the Amerasian Arctic. Prog Oceanogr 71:331-361. doi: 10.1016/j.pocean.2006.10.001

Grebmeier JM, McRoy CP (1989) Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. Mar Ecol Prog Ser 53:79-91.

Griffen BD, Altman I, Bess BM, Hurley J, Penfield A (2012) The role of foraging in the success of invasive Asian shore crabs in New England. Biol Invasions 14:2545-2558. doi: 10.1007/s10530-012-0251-8

Griffin JN, De La Haye KL, Hawkins SJ, Thompson RC, Jenkins SR (2008) Predator diversity and ecosystem functioning: density modifies the effect of resource partitioning. Ecology 89:298-305.

Grosholz E (2002) Ecological and evolutionary consequences of coastal invasions. Trends Ecol Evol 17:22-27. doi: 10.1016/s0169-5347(01)02358-8

Grosholz E, Lovell S, Besedin E, Katz M (2010) Modeling the impacts of the European green crab on commercial shellfisheries. Ecol Appl 21:915-924. doi: 10.1890/09-1657.1

Grosholz ED, Ruiz GM (1996) Predicting the impact of introduced marine species: Lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biol Conserv 78:59-66. doi: 10.1016/0006-3207(94)00018-2

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG (2000) The impacts of a nonindigenous marine predator in a California bay. Ecology 81:1206-1224. doi: 10.1890/0012-9658(2000)081[1206:tioanm]2.0.co;2

Gudimov AV, Gudimova EN, Pavlova LV (2003) Effect of the red king crab *Paralithodes camtschaticus* on the Murmansk coastal macrobenthos: The first estimates using sea urchins of the genus *Strongylocentrotus* as an example. General Biology 393:539-541.

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? Trends Ecol Evol 19:470-474. doi: 10.1016/j.tree.2004.07.005

Guzzo M, Haffner GD, Legler N, Rush S, Fisk A (2013) Fifty years later: trophic ecology and niche overlap of a native and non-indigenous fish species in the western basin of Lake Erie. Biol Invasions 15:1695-1711. doi: 10.1007/s10530-012-0401-z

Hall S, Thatje S (2009) Global bottlenecks in the distribution of marine Crustacea: temperature constraints in the family Lithodidae. J Biogeogr 36:2125-2135. doi: 10.1111/j.1365-2699.2009.02153.x

Hammerschlag-Peyer CM, Yeager LA, Araújo MS, Layman CA (2011) A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. PLoS ONE 6:e27104. doi: 10.1371/journal.pone.0027104

Hansen GJA, Hein CL, Roth BM, Vander Zanden MJ, Gaeta JW, Latzka AW, Carpenter SR (2013) Food web consequences of long-term invasive crayfish control. Can J Fish Aquat Sci 70:1109-1122. doi: 10.1139/cjfas-2012-0460

Hansen HSB (2016) Three major challenges in managing non-native sedentary Barents Sea snow crab (*Chionoecetes opilio*). Marine Policy 71:38-43. doi: 10.1016/j.marpol.2016.05.013

Hansen T (2002) Temperaturpreferanser hos kongekrabbe. In Norwegian. Master thesis, University of Tromsø, Norway. http://www.angelfire.com/on/2mash/Filer/hovedfaget.pdf.

Haugan TA (2004) Bunnsamfunn of naæringsvalg hos kongekrabbe, paralithodes camtschaticus (Tilesius, 1815), på noen lokaliteter i Finnmark. In Norwegian. Master, University of Tromsø, Norway.

Hjelset AM, Nilssen EM, Sundet JH (2012) Reduced size composition and fecundity related to fishery and invasion history in the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters. Fisheries Research 121:73-80. doi: 10.1016/j.fishres.2012.01.010

Hjelset AM, Sundet JH, Nilssen EM (2009) Size at sexual maturity in the female red king crab (*Paralithodes camtschaticus*) in a newly settled population in the Barents Sea, Norway. J Northwest Atl Fish Sci 41:173-182. doi: 10.2960/J.v41.m633

Hobson K, Welch H (1992) Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar Ecol Prog Ser 84:9-18. doi: 10.3354/meps084009

Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol Monogr 75:3-35. doi: 10.1890/04-0922

Hänfling B, Edwards F, Gherardi F (2011) Invasive alien Crustacea: dispersal, establishment, impact and control. BioControl 56:573-595. doi: 10.1007/s10526-011-9380-8

Iken K, Bluhm BA, Gradinger R (2005) Food web structure in the high Arctic Canada Basin: evidence from $\delta^{13}C$ and $\delta^{15}N$ analysis. Polar Biol 28:238-249. doi: 10.1007/s00300-004-0669-2

Iken K, Brey T, Wand U, Voigt J, Junghans P (2001) Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Prog Oceanogr 50:383-405. doi: 10.1016/s0079-6611(01)00062-3

Ingram T, Harmon LJ, Shurin JB (2009) Niche evolution, trophic structure, and species turnover in model food webs. Am Nat 174:56-67. doi: 10.1086/599301

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. J Anim Ecol 80:595-602. doi: 10.1111/j.1365-2656.2011.01806.x

Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. Plos One 7:e31757. doi: 10.1371/journal.pone.0031757

Jackson MC, Jones T, Milligan M, Sheath D, Taylor J, Ellis A, England J, Grey J (2014) Niche differentiation among invasive crayfish and their impacts on ecosystem structure and functioning. Freshw Biol 59:1123-1135. doi: 10.1111/fwb.12333

Jennings S, Dinmore TA, Duplisea DE, Warr KJ, Lancaster JE (2001) Trawling disturbance can modify benthic production processes. J Anim Ecol 70:459-475. doi: 10.1046/j.1365-2656.2001.00504.x

Jennings S, Pinnegar JK, Polunin NV, Warr KJ (2002) Linking size-based and trophic analyses of benthic community structure. Mar Ecol Prog Ser 226:77-85. doi: 10.3354/meps226077

Jennings S, van der Molen J (2015) Trophic levels of marine consumers from nitrogen stable isotope analysis: estimation and uncertainty. ICES J Mar Sci 72:2289-2300. doi: 10.1093/icesjms/fsv120

Jørgensen LL (2005) Impact scenario for an introduced decapod on Arctic epibenthic communities. Biol Invasions 7:949-957. doi: 10.1007/s10530-004-2996-1

Jørgensen LL, Ljubin P, Skjoldal HR, Ingvaldsen RB, Anisimova N, Manushin I (2014) Distribution of benthic megafauna in the Barents Sea: baseline for an ecosystem approach to management. ICES J Mar Sci:106. doi: 10.1093/icesjms/fsu106

Jørgensen LL, Nilssen EM (2011) The invasive history, impact and management of the red king crab (*Paralithodes camtschaticus*) off the coast of Norway. In: Galil BS, Clark PF, Carlton JT (eds) In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. Springer Science + Business Media B.V., Netherlands. doi: 10.1007/978-94-007-0591-3_18

Jørgensen LL, Primicerio R (2007) Impact scenario for the invasive red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (Reptantia, Lithodidae) on Norwegian, native, epibenthic prey. Hydrobiologia 590:47-54. doi: 10.1007/s10750-007-0756-9

Jørgensen T, Løkkeborg S, Fernö A, Hufthammer M (2007) Walking speed and area utilization of red king crab (*Paralithodes camtschaticus*) introduced to the Barents Sea coastal ecosystem. In: Almeida P, Quintella B, Costa M, Moore A (eds) Developments in Fish Telemetry, Book 195. Springer Netherlands. doi: 10.1007/978-1-4020-6237-7_3

Kanapathippillai P, Berg E, Dos Santos J, Gulliksen B, Pedersen T (1994) The food consumption of cod, *Gadus morhua* L., in a high-latitude enhancement area. Aquacult Fish Manage 25:65-76.

Keats DW, Steele DH, South GR (1987) The role of fleshy macroalgae in the ecology of juvenile cod (*Gadus morhua* L.) in inshore waters off eastern Newfoundland. Can J Zool 65:49-53. doi: 10.1139/z87-008

Kędra M, Renaud PE, Andrade H, Goszczko I, Ambrose Jr WG (2013) Benthic community structure, diversity, and productivity in the shallow Barents Sea bank (Svalbard Bank). Mar Biol 160:805-819. doi: 10.1007/s00227-012-2135-y

Kortsch S, Primicerio R, Fossheim M, Dolgov AV, Aschan M (2015) Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. Proc R Soc Biol Sci Ser B 282:20151546. doi: 10.1098/rspb.2015.1546

Källgren EK, Pedersen T, Nilssen EM (2014) Food resource partitioning between three sympatric fish species in Porsangerfjord, Norway. Polar Biol 38:583-589. doi: 10.1007/s00300-014-1611-x

Lafferty KD, Kuris AM (1996) Biological Control of Marine Pests. Ecology 77:1989-2000. doi: 10.2307/2265695

Langseth BJ, Rogers M, Zhang H (2012) Modeling species invasions in Ecopath with Ecosim: An evaluation using Laurentian Great Lakes models. Ecol Model 247:251-261. doi: 10.1016/j.ecolmodel.2012.08.015

Layman CA, Allgeier JE (2012) Characterizing trophic ecology of generalist consumers: a case study of the invasive lionfish in The Bahamas. Mar Ecol Prog Ser 448:131-141. doi: 10.3354/meps09511

Layman CA, Araujo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR, Matich P, Rosenblatt AE, Vaudo JJ, Yeager LA (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Reviews 87:545-562. doi: 10.1111/j.1469-185X.2011.00208.x

Layman CA, Quattrochi JP, Peyer CM, Allgeier JE (2007a) Niche width collapse in a resilient top predator following ecosystem fragmentation. Ecol Lett 10:937-944. doi: doi 10.1111/j.1461-0248.2007.01087.x

Le Bourg B, Bănaru D, Saraux C, Nowaczyk A, Le Luherne E, Jadaud A, Bigot JL, Richard P (2015) Trophic niche overlap of sprat and commercial small pelagic teleosts in the Gulf of Lions (NW Mediterranean Sea). J Sea Res 103:138-146. doi: 10.1016/j.seares.2015.06.011

Leinaas HP, Christie H (1996) Effects of removing sea urchins (*Strongylocentrotus droebachiensis*): Stability of the barren state and succession of kelp forest recovery in the east Atlantic. Oecologia 105:524-536. doi: 10.1007/bf00330016

Liao IC, Chien Y-H (2011) The pacific white shrimp, *Litopenaeus vannamei*, in Asia: The world’s most widely cultured alien Crustacean. In: Galil BS, Clark PF, Carlton JT (eds) In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. Springer Science + Business Media B.V., Netherlands. doi: 10.1007/978-94-007-0591-3_17

Libralato S, Christensen V, Pauly D (2006) A method for identifying keystone species in food web models. Ecol Model 195:153-171. doi: 10.1016/j.ecolmodel.2005.11.029

Lin H, Wang J, Liu K, He X, Lin J, Huang Y, Zhang S, Mou J, Zheng C, Wang Y (2016) Benthic macrofaunal production for a typical shelf–slope–basin region in the western Arctic Ocean. Cont Shelf Res 113:30-37. doi: Benthic macrofaunal production for a typical shelf–slope–basin region in the western Arctic Ocean

Lockwood JL, Hoopes MF, Marchetti MP (2013) Invasion ecology. John Wiley & Sons, West Sussex, UK

Long WC, Popp J, Swiney KM, Van Sant SB (2012) Cannibalism in red king crab, *Paralithodes camtschaticus* (Tilesius, 1815): Effects of habitat type and predator density on predator functional response. J Exp Mar Biol Ecol 422:101-106. doi: 10.1016/j.jembe.2012.04.019

MacDonald JA, Roudez R, Glover T, Weis JS (2007) The invasive green crab and Japanese shore crab: behavioral interactions with a native crab species, the blue crab. Biol Invasions 9:837-848. doi: 10.1007/s10530-006-9085-6

Mankettikkara R (2013) Hydrophysical characteristics of the northern Norwegian coast and fjords. Doctoral thesis, University of Tromsø, Norway. http://www.ub.uit.no/munin/bitstream/10037/5426/3/thesis.pdf.

McCann KS (2000) The diversity-stability debate. Nature 405:228-233. doi: 10.1038/35012234

Michelsen HK (2011) Prey selection of the red king crab (*Paralithodes camtschaticus*) preying on lumpfish eggs (*Cyclopterus lumpus*), sea urchins (*Strongylocentrotus droebachiensis*) and scallops (*Chlamys islandica*). Master thesis, University of Tromsø, Norway. http://hdl.handle.net/10037/3392.

Middelburg J (2014) Stable isotopes dissect aquatic food webs from the top to the bottom. Biogeosciences 11:2357-2371. doi: 10.5194/bg-11-2357-2014

Mikkelsen N (2013) Predation on the demersal fish eggs of capelin *Mallotus villosus* and lumpsucker *Cyclopterus lumpus* in relation to recruitment. Doctoral thesis, University of Tromsø, Norway. http://hdl.handle.net/10037/5428.

Mikkelsen N, Pedersen T (2012) Invasive red king crab affects lumpsucker recruitment by egg consumption. Mar Ecol Prog Ser 469:87-99. doi: 10.3354/meps09917

Miljødirektoratet (2004) Råd til utforming av marin verneplan for marine beskyttede områder i Norge. Rådgivende utvalg for marin verneplan 30. juni 2004. In Norwegian. http://www.miljodirektoratet.no/old/dirnat/multimedia/1831/Endelig_tilradning.pdf.

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the Global Threat of Invasive Species to Marine Biodiversity. Front Ecol Environ 6:485-492. http://www.jstor.org/stable/20440991

Morissette L (2007) Complexity, cost and quality of ecosystem models and their impact on resilience: a comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence. Doctoral thesis, University of British Columbia, Canada. doi: 10.14288/1.0074903.

Newsome SD, del Rio CM, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. Front Ecol Environ 5:429-436. doi: 10.1890/060150.01

Newsome SD, Yeakel JD, Wheatley PV, Tinker MT (2012) Tools for quantifying isotopic niche space and dietary variation at the individual and population level. J Mammal 93:329-341. doi: 10.1644/11-mamm-s-187.1

Nilsen M, Pedersen T, Nilssen EM (2006) Macrobenthic biomass, productivity (P/B) and production in a high-latitude ecosystem, North Norway. Mar Ecol Prog Ser 321:67-77. doi: 10.3354/meps321067

Nilsen M, Pedersen T, Nilssen EM, Fredriksen S (2008) Trophic studies in a high-latitude fjord ecosystem-a comparison of stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) and trophic-level estimates from a mass-balance model. Can J Fish Aquat Sci 65:2791-2806. doi: 10.1139/F08-180

Nilssen EM (2003) Kongekrabbe i Barentshavet - Biologi og utbredelse. In Norwegian. Ottar, Tromsø museum, University of Tromsø. 4:7-12.

Nilssen KT, Grotnes PE, Haug T (1992) The effect of invading harp seals (*Phoca groenlandica*) on local coastal fish stocks of north Norway. Fisheries Research 13:25-37. doi: 10.1016/0165-7836(92)90031-n

Norderhaug K, Christie H, Fossa J, Fredriksen S (2005) Fish-macrofauna interactions in a kelp (*Laminaria hyperborea*) forest. J Mar Biol Assoc U K 85:1279-1286. doi: 10.1017/S0025315405012439

Norderhaug KM, Christie HC (2009) Sea urchin grazing and kelp re-vegetation in the NE Atlantic. Mar Biol Res 5:515-528. doi: 10.1080/17451000902932985

Norkko A, Villnas A, Norkko J, Valanko S, Pilditch C (2013a) Size matters: implications of the loss of large individuals for ecosystem function. Sci Rep 3. doi: 10.1038/srep02646

Norkko A, Villnäs A, Norkko J, Valanko S, Pilditch C (2013b) Size matters: implications of the loss of large individuals for ecosystem function. Scientific Reports 3:2646. doi: 10.1038/srep02646

Nyström P (1999) Ecological impact of introduced and native crayfish on freshwater communities: European perspectives. Crustac Issues 11:63-86.

O'Farrell S, Bearhop S, McGill RA, Dahlgren CP, Brumbaugh DR, Mumby PJ (2014) Habitat and body size effects on the isotopic niche space of invasive lionfish and endangered Nassau grouper. Ecosphere 5:art123. doi: 10.1890/ES14-00126.1

Orlov YI, Ivanov BG (1978) On the introduction of the Kamchatka king crab *Paralithodes camtschatica* (Decapoda: Anomura: Lithodidae) into the Barents Sea. Mar Biol 48:373-375. doi: 10.1007/bf00391642

Ortiz M, Berrios F, Campos L, Uribe R, Ramirez A, Hermosillo-Núñez B, González J, Rodriguez-Zaragoza F (2015) Mass balanced trophic models and short-term dynamical simulations for benthic ecological systems of Mejillones and Antofagasta bays (SE Pacific): Comparative network structure and assessment of human impacts. Ecol Model 309:153-162. doi: 10.1016/j.ecolmodel.2015.04.006

Oug E, Cochrane S, Sundet J, Norling K, Nilsson H (2011) Effects of the invasive red king crab (*Paralithodes camtschaticus*) on soft-bottom fauna in Varangerfjorden, northern Norway. Mar Biodiv 41:467-479. doi: 10.1007/s12526-010-0068-6

Oug E, Fuhrmann M (2013) Bunndyrsamfunn i foreslått marint verneområde i indre Porsangerfjorden. Artssammensetning og biomasse før invasjon av kongekrabben 2011. In Norwegian. http://rapp.niva.no/symfoni/RappArkiv8.nsf/URL/E68D0D19FC647D2CC1257BE1002A7015/$FILE/6556-2013_200dpi.pdf.

Paine R (1974) Intertidal community structure: Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93-120.

Paine RT (1966) Food web complexity and species diversity. The American Naturalist:65-75.

Paine RT (1969) A note on trophic complexity and community stability. The American Naturalist 103:91-93.

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: Toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3-19. doi: 10.1023/a:1010034312781

Pauly D, Christensen V, Walters C (2000) Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. ICES J Mar Sci 57:697-706. doi: 10.1006/jmsc.2000.0726

Pavlova L (2008) Effect of juvenile red king crabs on zoobenthos in Kola Bay (Barents Sea). Dokl Biol Sci 422:312-315. doi: 10.1134/s0012496608050098

Pavlova LV (2009) Estimation of foraging on the sea urchin *Strongylocentrotus droebachiensis* (Echinoidea: Echinoida) by the red king crab *Paralithodes camtschaticus* (Malacostraca: Decapoda) in coastal waters of the Barents Sea. Russ J Mar Biol 35:288-295.

Pedersen T, Nilsen M, Nilssen EM, Berg E, Reigstad M (2008) Trophic model of a lightly exploited cod-dominated ecosystem. Ecol Model 214:95-111. doi: 10.1016/j.ecolmodel.2007.12.012

Pedersen T, Ramsvatn S, Nilssen EM, Nilsen M, Morissette L, Ivarjord T, Systad G, Kolsum I, Fause H (2016) Species diversity affects ecosystem structure and mass flows in fjords. Regional Studies in Marine Science 3:205-215. doi: 10.1016/j.rsma.2015.10.007

Petersen GH, Curtis MA (1980) Differences in energy flow through major components of subarctic, temperate and tropical marine shelf ecosystems. Dana 1:53-64. http://www.aqua.dtu.dk/English/Publications/Dana.aspx

Piepenburg D (2005) Recent research on Arctic benthos: common notions need to be revised. Polar Biol 28:733-755. doi: 10.1007/s00300-005-0013-5

Pimm SL (1982) Food webs. Springer, Netherlands

Pinnegar JK, Tomczak MT, Link JS (2014) How to determine the likely indirect food-web consequences of a newly introduced non-native species: A worked example. Ecol Model 272:379-387. doi: 10.1016/j.ecolmodel.2013.09.027

Planque B, Fromentin JM, Cury P, Drinkwater KF, Jennings S, Perry RI, Kifani S (2010) How does fishing alter marine populations and ecosystems sensitivity to climate? J Marine Syst 79:403-417. doi: 10.1016/j.jmarsys.2008.12.018

Polovina JJ (1984) Model of a coral reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3:1-11. doi: 10.1007/BF00306135

Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:703-718. doi: 10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montana CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179-189. doi: 10.1007/s00442-006-0630-x

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the Quest for Keystones. Bioscience 46:609-620. doi: 10.2307/1312990

Quijon PA, Snelgrove PVR (2005) Predation regulation of sedimentary faunal structure: potential effects of a fishery-induced switch in predators in a Newfoundland sub-Arctic fjord. Oecologia 144:125-136. doi: 10.1007/s00442-005-0017-4

Rafter E, Nilssen E, Sundet J (1996) Stomach content, life history, maturation and morphometric parameters of red king crab, *Paralithodes camtschaticus*, from Varangerfjord area, North Norway. ICES CM 1996/K:10:16.

Ramsvatn S (2013) Investigating coastal ecosystem structure and dynamics using Ecopath mass-balance modelling and stable isotope data. Doctoral thesis, University of Tromsø, Norway. http://hdl.handle.net/10037/5175.

Ramsvatn S, Pedersen T (2012) Ontogenetic niche changes in haddock *Melanogrammus aeglefinus* reflected by stable isotope signatures, δ^{13}C and δ^{15}N. Mar Ecol Prog Ser 451:175-185. doi: 10.3354/meps09604

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. Ecol Monogr 83:263-282. doi: 10.1890/13-0183.1

Richardson DM, Pyšek P (2008) Fifty years of invasion ecology – the legacy of Charles Elton. Divers Distrib 14:161-168. doi: 10.1111/j.1472-4642.2007.00464.x

Richardson DM, Pyšek P, Carlton JT (2011) A compendium of essential concepts and terminology in invasion ecology. In: Richardson DM (ed) Fifty years of invasion ecology: The legacy of Charles Elton. Wiley Blcakwell, West Sussex, UK.

Robertson AI (1979) The relationship between annual production: Biomass ratios and lifespans for marine macrobenthos. Oecologia 38:193-202. doi: 10.1007/bf00346563

Rombouts I, Beaugrand G, Artigas LF, Dauvin JC, Gevaert F, Goberville E, Kopp D, Lefebvre S, Luczak C, Spilmont N, Travers-Trolet M, Villanueva MC, Kirby RR (2013) Evaluating marine ecosystem health: Case studies of indicators using direct observations and modelling methods. Ecol Indic 24:353-365. doi: 10.1016/j.ecolind.2012.07.001

Rosenberg R (1995) Benthic marine fauna structured by hydrodynamic processes and food availability. Neth J Sea Res 34:303-317. doi: 10.1016/0077-7579(95)90040-3

Ruiz G, Fofonoff P, Steves B, Dahlstrom A (2011) Marine crustacean invasions in North America: a synthesis of historical records and documented impacts. In: Galil BS, Clark PF, Carlton JT (eds) In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. Springer Science + Business Media B.V., Netherlands. doi: 10.1007/978-94-007-0591-3_6

Sainte-Marie B, Chabot D (2002) Ontogenetic shifts in natural diet during benthic stages of American lobster (*Homarus americanus*), off the Magdalen Islands. Fishery Bulletin 100:106-116. http://fishbull.noaa.gov/1001/sai.pdf

Siikavuopio SI, James P (2013) Effects of temperature on feed intake, growth and oxygen consumption in adult male king crab *Paralithodes camtschaticus* held in captivity and fed manufactured diets. Aquac Res 46:602-608. doi: 10.1111/are.12207

Sivertsen K, Bjørge A (2015) On the brink of the Arctic: Unusual intertidal sub-Arctic kelp associations in the Porsangerfjord, North Norway. Mar Biol Res 11:405-413. doi: 10.1080/17451000.2014.940975

Snelgrove PV (1998) The biodiversity of macrofaunal organisms in marine sediments. Biodivers Conserv 7:1123-1132. doi: 10.1023/A:1008867313340

Snyder WE, Evans EW (2006) Ecological effects of invasive arthropod generalist predators. Annu Rev Ecol Evol Syst 37:95-122. doi: 10.1146/annurev.ecolsys.37.091305.110107

Solan M, Cardinale BJ, Downing AL, Engelhardt KA, Ruesink JL, Srivastava DS (2004) Extinction and ecosystem function in the marine benthos. Science 306:1177-1180. doi: 10.1126/science.1103960

Solomon CT, Carpenter SR, Rusak JA, Vander Zanden MJ (2008) Long-term variation in isotopic baselines and implications for estimating consumer trophic niches. Can J Fish Aquat Sci 65:2191-2200. doi: 10.1139/F08-125

Stachowicz JJ (2001) Mutualism, facilitation, and the structure of ecological communities: Positive interactions play a critical, but underappreciated, role in ecological communities by reducing physical or biotic stresses in existing habitats and by creating new habitats on which many species depend. Bioscience 51:235-246. doi: 10.1641/0006-3568(2001)051[0235:mfatso]2.0.co;2

Starikov YV, Spiridonov VA, Naumov AD, Zuev YA (2015) First record and potential for red king crab *Paralithodes camtschaticus* (Crustacea Decapoda Lithodidae) population establishment in the White Sea. Russ J Biol Invasions 6:118-128. doi: 10.1134/s2075111715020083

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. Environ Conserv 29:436-459. doi: doi:10.1017/S0376892902000322

Stevens BG (2014) Embryo development and hatching of king crabs. In: Stevens BG (ed) King crabs of the world: biology and fisheries management. CRC Press 2014, USA.

Stone RP, O'Clair CE, Shirley TC (1992) Seasonal migration and distribution of female red king crabs in a southeast Alaskan estuary. J Crustac Biol 12:546-560. doi: 10.2307/1548836

Stone RP, O'Clair CE, Shirley TC (1993) Aggregating behavior of ovigerous female red king crab, *Paralithodes camtschaticus*, in Auke Bay, Alaska. Can J Fish Aquat Sci 50:750-758. doi: 10.1139/f93-086

Summerhayes VS, Elton CS (1923) Bear Island. J Ecol 11:216-233. doi: 10.2307/2255864

Sundet JH, Bakanev S (2014) Snow crab (*Chionoecetes opilio*)–a new invasive crab species becoming an important player in the Barents Sea ecosystem. ICES CM. http://www.ices.dk/sites/pub/CM%20Doccuments/CM-2014/Theme%20Session%20F%20contributions/F0414.pdf

Sundet JH, Hoel AH (2016) The Norwegian management of an introduced species: the Arctic red king crab fishery. Marine Policy. In Press. doi: 10.1016/j.marpol.2016.04.041

Sundet JH, Rafter EE, Nilssen EM (2000) Sex and seasonal variation in the stomach content of the red king crab (*Paralithodes camtchaticus*) in the southern Barents Sea. Crustac Issues 12:193-201.

Tagliapietra D, Cornello M, Pessa G (2007) Indirect estimation of benthic secondary production in the Lagoon of Venice (Italy). Hydrobiologia 588:205-212. doi: 10.1007/s10750-007-0663-0

Thatje S, Anger K, Calcagno JA, Lovrich GA, Pörtner H-O, Arntz WE (2005) Challenging the cold: crabs reconquer the Antarctic. Ecology 86:619-625. doi: 10.1890/04-0620

Thompson RM, Hemberg M, Starzomski BM, Shurin JB (2007) Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. Ecology 88:612-617. doi: 10.1890/05-1454

Townsend M, Lohrer A, Rodil I, Chiaroni L (2015) The targeting of large-sized benthic macrofauna by an invasive portunid predator: evidence from a caging study. Biol Invasions 17:231-244. doi: 10.1007/s10530-014-0722-1

Tumbiolo ML, Downing JA (1994) An empirical model for the prediction of secondary production in marine benthic invertebrate populations. Mar Ecol Prog Ser 114:165-165. doi: 10.3354/meps114165

Ulanowicz RE (1986) Growth and development: ecosystems phenomenology. Springer Verlag, New York, USA

Valentine-Rose L, Rypel AL, Layman CA (2011) Community secondary production as a measure of ecosystem function: a case study with aquatic ecosystem fragmentation. Bull Mar Sci 87:913-937. doi: 10.5343/bms.2010.1043

Valls A, Coll M, Christensen V (2015) Keystone species: toward an operational concept for marine biodiversity conservation. Ecol Monogr 85:29-47. doi: 10.1890/14-0306.1

Vander Zanden MJ, Casselman JM, Rasmussen JB (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. Nature 401:464-467. doi: 0.1038/46762

Vandermeer J (2006) Omnivory and the stability of food webs. J Theor Biol 238:497-504. doi: 10.1016/j.jtbi.2005.06.006

Vasconcellos M, Mackinson S, Sloman K, Pauly D (1997) The stability of trophic mass-balance models of marine ecosystems: a comparative analysis. Ecol Model 100:125-134. doi: 10.1016/S0304-3800(97)00150-6

Villasante S, Arreguín-Sánchez F, Heymans JJ, Libralato S, Piroddi C, Christensen V, Coll M (2016) Modelling marine ecosystems using the Ecopath with Ecosim food web approach: New insights to address complex dynamics after 30 years of developments. Ecol Model 331:1-4. doi: 10.1016/j.ecolmodel.2016.04.017

Virnstein RW (1977) The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58:1200-1217. doi: 10.2307/1935076

Walters C, Christensen V, Pauly D (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev Fish Biol Fish 7:139-172.

Ward EJ, Semmens BX, Phillips DL, Moore JW, Bouwes N (2011) A quantitative approach to combine sources in stable isotope mixing models. Ecosphere 2:1-11. doi: 10.1890/ES10-00190.1

Weis JS (2010) The role of behavior in the success of invasive crustaceans. Mar Freshw Behav Physiol 43:83-98. doi: 10.1080/10236244.2010.480838

Welsh DT (2003) It's a dirty job but someone has to do it: the role of marine benthic macrofauna in organic matter turnover and nutrient recycling to the water column. Chem Ecol 19:321-342. doi: 10.1080/0275754031000155474

Whiteledge TE, Reeburgh WS, J W (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Deep-Sea Res 32:85-95.

Windsland K (2014) The invasive red king crab (*Paralithodes camtschaticus*): Mortality, individual growth and dispersal in Norwegian waters. Doctoral thesis, University of Tromsø, Norway. http://munin.uit.no/handle/10037/6735?show=full.

Windsland K, Hvingel C, Nilssen EM, Sundet JH (2014) Dispersal of the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters: a tag-recapture study. ICES J Mar Sci 71:1966-1976. doi: 10.1093/icesjms/fst241

Wong MC, Dowd M (2013) Role of invasive green crabs in the food web of an intertidal sand flat determined from field observations and a dynamic simulation model. Estuaries and Coasts 37:1004–1016. doi: 10.1007/s12237-013-9728-7

Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH (2005) Body size in ecological networks. Trends Ecol Evol 20:402-409. doi: 10.1016/j.tree.2005.04.005

Worm B, Duffy JE (2003) Biodiversity, productivity and stability in real food webs. Trends Ecol Evol 18:628-632. doi: 10.1016/j.tree.2003.09.003

6 Papers