Effects of the invasive red king crab on food web structure and ecosystem properties in an Atlantic fjord

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ABSTRACT: Since the 1990s, the density of the invasive red king crab *Paralithodes camtschaticus* has increased dramatically in coastal areas in northern Norway. We investigated its direct and indirect effects on food web structure and ecosystem properties (e.g. species biomasses and production) in the Porsanger Fjord in the study period 2009–2011 using 5 subarea Ecopath food web models. The 5 baseline models with different red king crab densities were compared and the food web effects of crab removal were explored through simulations in Ecosim. King crabs were important as benthic predators and exerted strong top-down effects on long-living invertebrates such as predatory gastropods, asteroids, detritivorous echinoderms and herbivorous sea urchins. The crab experienced little predation from fish or other predators at higher trophic levels, thus food web effects of the red king crab generally stayed within the benthic compartment. Red king crab removal decreased system omnivory and resulted in higher food web biomass–low turnover systems, with relatively lower production:biomass ratios of benthic invertebrates. Other ecosystem properties (e.g. total production, consumption, ascendancy and overhead) were little affected by crab abundance and suggest stable systems. Effects of crab removal were less significant in baseline models with low initial crab biomass, and high benthic production by detritivores in the inner fjord may buffer future predation in this area. Indirect effects of crab predation included a positive cascade effect on macroalgae due to predation on herbivorous sea urchins and a negative effect on benthic-feeding birds, indicating competition for invertebrate prey.

KEY WORDS: *Paralithodes camtschaticus* · Food web model · Coastal ecosystem · Invasion · Trophic impact · Predation · Barents Sea · Benthic invertebrates

INTRODUCTION

Large decapods may play important structuring roles in benthic communities (Boudreau & Worm 2012). There are many examples of invasion of decapod species resulting in top-down effects through direct predation or indirect trophic cascades (Snyder & Evans 2006, Blamey et al. 2010), sometimes with consequences for ecosystem functioning and services (e.g. fisheries) (Grosholz et al. 2000, Hänfling et al. 2011). The transfer of the red king crab *Paralithodes camtschaticus* from its native habitat in the Pacific to the Kola coast along the Barents Sea in the 1960s is one of the most signifi-

cant ecological experiments of the past 50 yr. The crab was transferred by Soviet scientists in order to establish a commercial fishery (Orlov & Ivanov 1978). Since then, this species has expanded westwards, and in the mid-1990s the crab entered the Varangerfjord on the north-eastern Norwegian coast (Jørgensen et al. 2011). Today, the crab is densely distributed along the entire coast and fjords of Finnmark (Windsland et al. 2014).

The red king crab is a large anomuran crab, reaching body weights of up to 10 kg (Wallace et al. 1949). Being a generalist opportunistic predator, it feeds on numerous benthic invertebrates, including in- and epifaunal molluscs, polychaetes, other crustaceans and echinoderms (Falk-Petersen et al. 2011, Fuhrmann et al. 2017). Species composition of benthic invertebrates has changed since its invasion; abundances of echinoderms and most bivalves have decreased while some small polychaetes have increased (Oug et al. 2011, 2018). Other documented ecological impacts of this decapod include reduced density and biomass of benthic invertebrates (Britayev et al. 2010), a shift in size composition towards smaller, motile organisms, effects on sediment quality (Oug et al. 2011) and predation on demersal fish eggs (Mikkelsen & Pedersen 2012). Despite a considerable interest in understanding the impact of the red king crab on the benthic ecosystem (Gudimov et al. 2003, Jørgensen & Primicerio 2007, Jørgensen & Nilssen 2011, Oug et al. 2011), indirect food web effects (e.g. competition) remain poorly studied, and overall impacts on the ecosystem structure and stability are unknown. Concerns persist that the crab may alter the fishery for other species.

This study was conducted in the Porsanger Fjord (70.1−70.9° N, 25−26.5° E), an open fjord that experienced a major increase in red king crab density in the period 2000−2006, and by 2008, the crab had become the most important species in the local fishery. While the middle areas of the fjord were heavily invaded at the time of study (2009−2011), red king crabs had not yet advanced into the inner part.

Using extensive field observations (see Supplement 1 at www.int-res.com/articles/suppl/m596p013_supp.pdf), we constructed Ecopath with Ecosim (EwE) models (Christensen & Pauly 1992, Christensen & Walters 2004) to analyse the Porsanger Fjord ecosystem in the period 2009−2011. Ecopath is based on a mass-balance food web model and can be used to analyse and quantify energy flow, food web structure and ecosystem properties linked to ecosystem functioning, stability and resilience (e.g. system omnivory, ascendency and overhead). These food web models have proven useful in evaluating ecosystem consequences of invasive species (Arias-González et al. 2011, Langseth et al. 2012, Pinnegar et al. 2014) and management measures such as the removal of invasive species (Wong & Dowd 2014).

In this study, we analysed the role of red king crab in Porsanger Fjord and its impact on food web structure and ecosystem properties, with an emphasis on benthic invertebrates, which are much less mobile than most plankton, fish, birds and mammals. While individual red king crabs may move over large distances, the majority show a certain site fidelity within the fjords (Windsland et al. 2014, Fuhrmann et al. 2017). We constructed baseline mass-balance models using EwE for 5 subareas along the fjord with varying king crab abundance and different benthic invertebrate communities. More specifically, the objectives of this study were to: (1) compare food web structure and ecosystem properties between these areas, (2) evaluate food web consequences of crab removal using a model scenario for each baseline model and (3) investigate direct and indirect effects of crab predation on other ecological groups.

MATERIALS AND METHODS

Study area

Porsanger Fjord is located in Finnmark County (Fig. 1). It has an area of 1877 km^2 and is one of the largest fjords in northern Norway, opening northwards into the Barents Sea. It has a maximum depth of 300 m at the entrance, with the inner part being shallower (maximum 110 m depth) and separated by a sill from the outer part. Freshwater run-off occurs mainly in this inner area from 3 rivers. The outer fjord is characterized by Atlantic water. The water column is usually well mixed compared to other northern Norwegian fjords (Mankettikkara 2013). During spring and summer, the surface water becomes stratified due to river run-off and heating. Bottom temperatures range from an annual average of ca. 5°C in the outer fjord to Arctic conditions around 0°C in the inner eastern fjord, and spring temperatures may be close to −1.8°C in that area (Mankettikkara 2013). The inner fjord may experience seasonal ice cover in winter and spring (see also Supplement 3 at www.int-res.com/articles/suppl/m596p013_supp.pdf).

In Porsanger Fjord, macroalgae form unique intertidal kelp formations in the inner western fjord (Sivertsen & Bjørge 2015). Sublittoral macroalgae have
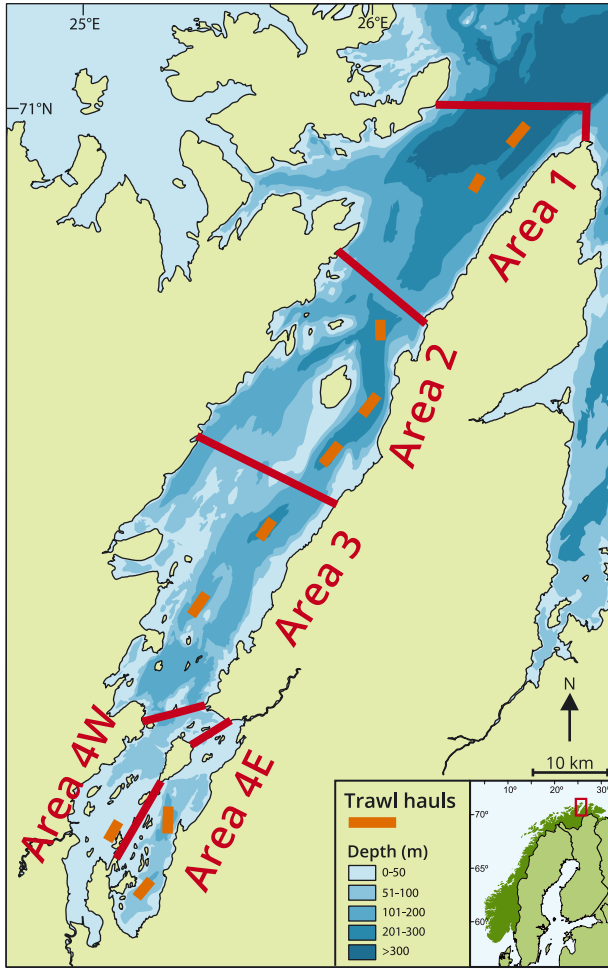
Fig. 1. Porsanger Fjord, Norway, with Subareas 1, 2, 3, 4W and 4E. Orange bars show bottom trawl locations. The inner arctic Subareas 4E and 4W have low bottom temperatures (ca. 0°C), while Subarea 1 has the warmest bottom temperature

been subject to downgrazing by sea urchins (*Strongylocentrotus* spp.), leaving barren grounds in some localities of the outer and middle fjord (Sivertsen & Bjørge 2015). The inner fjord has cold bottom temperatures throughout the year and provides habitat for a number of Arctic benthic invertebrate species (Oug & Fuhrmann 2013) such as Iceland scallops *Chlamys islandica* (Wiborg 1963).

Red king crabs, mainly large mature males, are fished commercially using baited pots. Porsanger Fjord is the westernmost part of the quota-regulated area for the red king crab fishery, where it is managed as a sustainable fishery resource (Hjelset et al. 2012, Falk-Petersen & Armstrong 2013). During the study period, 2009−2011, the large gadoids Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus* and saithe *Pollachius virens* were also targets for fish-

ery exploitation. Commercial trawling for groundfish and deep-water shrimp *Pandalus borealis* was prohibited in Porsanger Fjord during the study period.

Red king crab abundance and biomass and community composition of benthic invertebrates (Fuhrmann et al. 2015, 2017) and other groups vary along the fjord. The fjord was divided into 5 subareas based on differences in density of red king crab, benthic invertebrate community composition and production and on topography (Fig. 1) and hydrography. One baseline food web model was balanced for each subarea.

Food web models using EwE

Ecopath is a model of resources in the system and their interactions over a certain time, assuming mass balance over (usually) 1 yr. It consists of a set of linear equations describing the production term of Eq. (1) and ensuring energy balance of all groups i in the ecosystem (Christensen et al. 2005):

$$B_i \left(\frac{P}{B} \right)_i = \sum_j B_j \left(\frac{Q}{B} \right)_j DC_{ji} + Y_i + E_i + BA_i + B_i \left(\frac{P}{B} \right)_i (1 - EE_i)$$

(1)

where B_i is the biomass of group i in g C m^{-2}, $(P/B)_i$ is the production:biomass ratio of group i, B_j is the biomass of predator j in g C m^{-2}, $(Q/B)_j$ is the consumption:biomass ratio of the predator j, DC_{ji} is the proportion of prey i in the diet of predator j, Y_i is the catch of group i (in g C m^{-2} yr^{-1}), E_i is the export of biomass for the respective group (in g C m^{-2} yr^{-1}), BA_i is the biomass accumulation of group i (in g C m^{-2} yr^{-1}), and EE_i is the ecotrophic efficiency, which is the proportion of production of group i that is consumed, caught by fisheries or exported from the whole system. For each group i, energy balance is established when consumption by group i equals production, respiration and unassimilated food of i (Winberg 1956). Dietary compositions, catches Y_i, the proportion of unassimilated food $(U/Q)_i$ and detritus fate produced are needed for each group i. U/Q values for detritivorous and omnivorous groups may be lower than the default value in Ecopath (see Supplement 4). One missing parameter, i.e. B_i, $(P/B)_i$, $(Q/B)_i$ or EE_i, can be estimated by the model (Christensen et al. 2005), but biomasses for top predators are needed, since they constrain parameters of lower trophic-level (TL) groups through predation. Feeding selection indices and search rates for given predators and prey are calculated by Ecopath based on the diet and biomass values (Supplement 2).

An Ecopath model forms the basis for Ecosim. In Ecosim, it is possible to simulate scenarios with the perturbation of parameters, e.g. fishing mortality for given groups, and analyse the effects on the food web (Christensen & Walters 2004). Ecosim is based on a system of coupled ordinary differential equations that simulate changes in biomass over time. The biomass dynamic of group i is defined by the equation

$$\frac{dB_i}{dt} = (P/Q)_i \sum_j Q_{ji} - \sum_j Q_{ij} - (MO_i + F_i)B_i \quad (2)$$

where B_i is the biomass of group i, $(P/Q)_i$ is the production:consumption ratio or the net growth efficiency, MO_i is the non-predation (other) natural mortality rate, and F_i is the fishing mortality rate. The consumption rate (Q_{ji}) is the consumption by group j on group i, and Q_{ij} is the consumption by group i on group j.

Model input

Each subarea model comprised 62 ecological groups (Table 1; Supplement 4) representing primary producers, detritus groups, benthic and pelagic consumers as well as mammal and bird predators, with similar diet, habitat, predators and life-history traits within groups. The models had 3 detritus groups: discarded catch (offal, i.e. intestines and heads of fish), detritus from macroalgae and detritus from all other sources. A detailed overview of the input data for each group is given in Supplement 5. Biomasses were averaged for each year and each subarea and are expressed in g C m^{-2}. Wet weight (WW) or dry weight was converted into carbon units using group-specific factors (Supplement 5). All rates were estimated on an annual basis (yr^{-1}), and for migratory species (birds and some mammals) values for the time spent in the study area were averaged over the whole year. A field campaign to collect data for pelagic and benthic invertebrates, fish and the seal groups was conducted during 2009–2011. Thus the models express the average conditions during this period. For composite groups with >1 species, the estimated dietary proportions for each species were weighted with the measured proportion of biomass of the species.

For the mammal groups, abundance estimates were based on local sighting surveys, telemetry or

Table 1. Overview of groups in the Ecopath models for subareas (see Fig. 1) in Porsanger Fjord, Norway. The group number is given in parentheses. For details on group composition, see Table S1 in Supplement 4

Main group category	Group name and number
Mammals	Grey seals (1), harbour seals (2), whales (3), otters (4)
Birds	Piscivorous benthic feeding birds (5), pelagic diving birds (6), surface-feeding birds (7), benthic invertebrate-feeding birds (8)
Fish	Large cod[a] (9), small cod[a] (10), large saithe[a] (11), small saithe[a] (12), large haddock[a] (13), small haddock[a] (14), small gadoids (15), halibut (16), other large flatfish (17), other small flatfish (18), other large demersal fish (19), other small demersal fish (20), cottids (21), small pelagic fish (22), herring (23), salmon (24), sea trout (25), Arctic charr (26)
Zooplankton and invertebrate nekton	Small krill (27), large krill (28), small zooplankton (29), microzooplankton (30), heterotrophic nanoflagellates (31), scyphomedusae (32), chaetognaths (33), other large zooplankton (34), pandalid shrimps (35)
Red king crab	Large red king crab[b] (36), medium red king crab[b] (37), small red king crab[b] (38)
Predatory benthic invertebrates	Crangonid shrimps (39), other large crustaceans (40), predatory asteroids (41), predatory gastropods (42), predatory polychaetes (43), other predatory benthic invertebrates (44)
Detritivorous and herbivorous benthic invertebrates	Detritivorous polychaetes (45), small benthic crustaceans (46), small molluscs (47), large bivalves (48), detritivorous echinoderms (49), *Ctenodiscus crispatus* (50), large epibenthic suspension feeders (51), other benthic invertebrates (52), herbivorous echinoids (53)
Bacteria	Bacteria (54)
Macroalgae and benthic microalgae	Kelp (55), annual macroalgae (56), littoral macroalgae (57), benthic microalgae and recruiting macroalgae (58)
Phytoplankton	Phytoplankton (59)
Detritus	Discarded catch (60), detritus from macroalgae (61), detritus from all other sources (62)

[a]Multi-stanza group in models for Subareas 1, 2 and 3
[b]Multi-stanza group in all subareas

literature values from regional data (Supplement 5). For seals, data from scat and stomach analysis were available, while for whales and otters, dietary input was mostly obtained from the literature. Individual body masses (WW), P/B (or mortality rates/survival rates used in calculations of P/B) and Q/B for species in these groups were taken from literature reports (Supplement 5).

In order to capture ontogenetic shifts in diet, predation mortality and exploitation patterns, species can be split into 'multi-stanza' groups in EwE (Christensen & Walters 2004, Heymans et al. 2016). In 'multi-stanza' groups, values are required for age of transition between stanza (stage-like age-groups), the total mortality rate per stanza, the von Bertalanffy K parameter and a value for the weight at maturity as a fraction of weight at infinity. Value for predation, diet and catches of each stanza are also needed. In the models for the 3 outer subareas, the gadoid species cod, saithe and haddock were split into small (<35 cm in length) and large (≥35 cm) multi-stanza groups, and input for the small groups was estimated by the Ecopath multi-stanza procedure (Christensen & Walters 2004). In the models for the inner 2 areas, biomasses of large fishes were very low, and these fish groups were represented by non-stanza groups. Red king crabs were split into 3 stanza: <70 mm carapace length (CL), CL between 70 and 130 mm and CL >130 mm.

Data from bottom trawl hauls were supplemented by data from pelagic trawl hauls, hydroacoustical abundance estimation for small pelagic fishes and herring, beach seine hauls for littoral fishes, sampling by fishing rods and epibenthic trawl, underwater video and fishery statistics. Input values for catch and landings of cod and other exploited marine fish species were calculated from local biomass values, and fishing mortality rates were estimated in regional stock assessments, assuming that other species had the same fishing mortality as cod. This is reasonable, as the other fish species (except anadromous salmonids) were largely caught as bycatch in the cod fishery. Biomass for salmonids was based on official catch statistics and number of smolts produced in the rivers. Dietary input values for the fish groups were largely based on stomach samples. Occurrences of red king crab in predator stomachs were observed in cod in Subarea 3 and in spotted wolffish *Anarhichas minor* in Subarea 1 (see Supplements 5 & 6), but were generally rare. In total, 927 fish stomachs from 8 fish species were analysed in addition to information from published literature.

Input values for zooplankton and nekton groups were largely based on regional average values from the literature (Supplement 5). Biomass values of small zooplankton (mainly copepods) and chaetognaths were based on values of abundance from Zhou et al. (2005), who surveyed Ullsfjord during 1995. The biomass of small and large krill (euphausiids) and other large zooplankton was estimated using the model, as was the biomass of pandalid shrimps except for in the 2 inner areas, where calculations were based on catch per unit effort from otter trawls. Input values for bacteria, heterotrophic nanoflagellates and microzooplankton were calculated using the same approach as used for the Sørfjord model of Pedersen et al. (2008) (Supplement 5), based on investigations in 1997 in Ullsfjord and neighbouring fjords (Archer et al. 2000).

Phytoplankton biomass levels are similar within subareas in Porsanger Fjord (Eilertsen & Frantzen 2007), but no primary production estimates exist for the fjord (see Supplement 5). The value for pelagic primary production (130 g C m^2 yr^{-1}) was based on studies in north Norwegian fjords and is equal to the value used in the Sørfjord model (Pedersen et al. 2008). The biomass of littoral and subtidal macroalgae was estimated from surveys in Porsanger Fjord during 2008–2012 (Supplement 5).

The 3 red king crab stanzas differ with regard to prey composition (Fuhrmann et al. 2017) and predator composition, and only the large red king crab stanza was exposed to commercial fishery. Abundance of the 2 largest groups, with a CL >70 mm, was estimated by sampling with a 6 m wide beam trawl (see Fuhrmann et al. 2015). Abundance of the small red king crab group was calculated within the multistanza procedure by back-calculation, with the largest group with known abundance as the leading group, assuming that the population had stable individual growth rates, mortality rates (natural and fishing mortality) and recruitment. Dietary information for king crabs was based on stomach samples supported by stable isotope analysis. Since prey items were often fragmented and quantification was difficult, proportions were initially based on frequency of occurrence and adjusted according to data from the literature and to achieve mass balance.

Benthic invertebrates were sampled by van Veen grab (infauna) and epibenthic sledge (patchy epibenthos). The 4 groups of predatory invertebrate benthos and other large crustaceans were mainly epibenthic, and biomass was estimated using data from epibenthic trawl hauls or by using the model (Supplement 5). The biomasses of infaunal groups (detriti-

vorous polychaetes, small molluscs, detritivorous echinoderms and other benthic invertebrates) were estimated from grab samples (see Fuhrmann et al. 2015). Annual *P/B* ratios were estimated using the artificial neural network model of (Brey 2012) (see also Supplement 5). Biomasses of small benthic crustaceans and large bivalves were estimated using the Ecopath model since these groups partly consisted of motile fauna and species living on hard bottoms in shallow water that were not well sampled by grab.

Herbivorous sea urchins, mainly *Strongylocentrotus droebachiensis*, were abundant in water less than 15 m deep in the shallow areas within the fjord. The abundance of herbivorous sea urchins was estimated using an aquascope at depths shallower than 4 m, underwater video between 4 and 25 m and by epibenthic trawl hauls in deeper water.

For invertebrate groups, the dietary compositions were based on information in the literature (see Pedersen et al. 2008, 2016) and complemented with information from stable isotope analysis from Porsanger Fjord (Supplement 5). An overview of diet proportions for all consumer groups is given in Supplement 6.

Network indices and summary statistics

The TL of each consumer group *j* (*TL_j*) in EwE is calculated from prey composition and is expressed as:

$$TL_j = 1 + \sum_{j=1}^{n} DC_{ij} \times TL_i \qquad (3)$$

where DC_{ij} is the proportion of prey *i* in the diet of predator *j* and TL_i is the TL of prey group *i*.

Several summary statistics were calculated to describe ecosystem energetics and flows: total biomass, total production, total consumption and exports (Ulanowicz 1986). Export is the amount of biomass that leaves the modelled system, e.g. as detritus or as fishery catches. Transfer efficiencies were calculated from trophic flows between adjacent TLs.

A number of ecosystem indicators, describing structure and emergent properties, were calculated as part of the network analysis in Ecopath (Supplement 2). The biomass residence time (Christensen 1995) is defined as the system biomass as a proportion of the sum of all output and was calculated as Biomass/(Respiration + Export). The omnivory index (OI) measures the variance of TLs in each consumer's diet and represents how specialized (smaller values) a group is (Christensen & Pauly 1993). The system OI

(SOI) is defined as the average OI of all consumers weighted by the logarithm of each consumer's food intake (Christensen & Walters 2004). The SOI quantifies how trophic interactions are distributed over TLs and usually increases with a 'web like' structure.

The connectance index (C) is calculated as the number of realized food web links divided by the number of possible links, including detritus as a food source. It depends strongly on how groups are defined, but can be used to compare similarly structured models.

The predation impact of the red king crab was evaluated by examining mortality of prey groups. We identified indirect competitive effects by calculating niche overlap with other predators in the system based on diet input (modified in Ecopath from Pianka 1973, see Christensen et al. 2005). In addition, the mixed trophic impact (MTI) was calculated in Ecopath, defined as the effect of a biomass change in one group on other groups, including all direct and indirect impacts (see Supplement 2). Through the MTI, it is possible to estimate the overall effect of a group *i* on the ecosystem, described as the total impact (*e_i*) (Libralato et al. 2006) (Eq. 6 in Supplement 2).

Model balancing and uncertainty

Before and during balancing, the PREBAL procedure described by Link (2010) was applied to check if input values were within accepted ecological constraints (Figs. S4–S6 in Supplement 7, and Heymans et al. 2016). Furthermore, we followed the approach outlined by Pedersen et al. (2008) when balancing the models. This was done manually by ensuring that EE was ≤1 for the top predators and large fish groups, for which we had local biomass data (Supplement 7).

For groups where dietary information was scarce and the consumption was higher than the production of some prey in their diet (i.e. prey EE > 1), we inspected if feeding selectivities and searching rates of a predator were similar for similar prey groups. If a predator had very high search rates and feeding selectivity for a prey with EE > 1, the proportion in the diet of the prey was reduced and the proportions of other prey with EE < 1 were increased. During balancing, the proportions of 'detritus from all other sources' were increased in the diets of the red king crab groups (mostly in the 2 largest groups) to satisfy the consumption needs (see Supplement 7). Gross efficiencies (*P/Q*) were checked as being in accordance with data in the literature, and we checked that the values for respiration/assimilation were <1

(Supplement 7). We did not attempt to estimate import of detritus between subareas because empirical data on this were unavailable, but Ecopath estimated total export in each baseline model. The models were constructed using version 6.5.14040.0 of EwE (http://ecopath.org).

Since Subarea 3 had the highest abundance of red king crab and potentially the largest ecosystem effects, results and analysis are presented in more detail for this subarea. The uncertainty in the input values to the Ecopath baseline model for Subarea 3 was assessed and described using the pedigree routine (Supplement 8). Pedigree indices are uncertainty scores for each input variable and value in Ecopath and were based on either measured uncertainty given as confidence intervals or assessed from the type and source of the input value. An uncertainty level is associated with a pedigree index, and an uncertainty analysis was undertaken by loading the assessed pedigree indices with associated confidence intervals for the input values into the Monte Carlo routine in Ecosim (see Heymans et al. (2016)). The Monte Carlo routine included 100 trials, and each trial had up to 10 000 runs. In each run, input values to Ecopath models were randomly sampled from uniform distributions, with the width of distributions corresponding to the pedigree-specified input uncertainty level. Only the first balanced Ecopath model was retained in each trial. From the 100 retained Ecopath-model values, 95 % percentile confidence intervals (CIs) for biomasses of the groups were calculated. Calculated 95 % CIs (upper CI − lower CI)/2 are given as % of the median for biomass values based on the Monte Carlo uncertainty analysis.

Crab removal scenario analysis

To test whether simulated removal of red king crab biomass affected other groups, dynamic Ecosim simulations were run for each subarea model (Supplement 9). Each scenario lasted 68 yr and had 2 phases. The first phase was a stabilising spin-up phase from Year 1 to 29, with the same fishing mortality rate as in the baseline Ecopath models. The second phase involved removal of red king crab by heavy fishing from Year 30 to 68. Here, the fishing mortality for the large red king crab was about twice (1.5 yr⁻¹) the base fishing mortality rate (0.85 yr⁻¹) from the balanced baseline Ecopath models. In addition, the medium and small king crab groups, which are unexploited in the real commercial fishery, were fished with a fishing mortality of 1.2 and 0.8 yr⁻¹, respectively.

The crab removal scenarios were run with the default values for 'vulnerability' (v) settings ($v = 2$) for the linkages between red king crab and their prey. $v = 2$ implies mixed top-down and bottom-up control. Alternative scenarios with alternative settings for the linkages between red king crab and prey (with v between 1 = bottom-up control and 10 = top-down control) but with all other v set to 2, were tested. Other alternative scenarios with settings for v of 5 and 10 for all groups in the models including red king crabs were also tested. The other parameters needed for Ecosim simulations (e.g. maximum relative feeding time, feeding time adjustment rate and others, see Christensen et al. 2005) were kept at default values (Supplement 9).

We retained the food web model outputs from near steady-state conditions for each subarea before (at Year 25) and after crab removal (Year 65) and examined the changes in (1) food web properties (system values for production, consumption, biomass residence time, P/B, ascendency and overhead, as well as biomass, production and P/B values for the main benthic invertebrate categories, and (2) biomasses of other ecological groups (Fig. S11 in Supplement 9).

To assess uncertainty in the output of the crab removal scenario, the Monte Carlo procedure in EwE was applied and 100 scenario trials were run for Subarea 3, which was the subarea with the highest crab density and largest expected effects. We calculated if the percentage changes of values for system properties and group biomasses differed significantly before and after crab removal, in Years 25 and 65, respectively. The values were calculated from the output from Ecopath models retrieved from the Ecosim runs in Years 25 and 65. The 100 scenario values of each statistic were treated as bootstrap samples, and 95 % CIs were estimated (Efron & Tibshirani 1993). CIs for percentage change not overlapping with 0 indicated statistical significance.

RESULTS

Food web structure and ecosystem properties

The mass-balanced baseline food web models for the subareas of Porsanger Fjord spanned 5 TLs, with detritus, phytoplankton and macroalgal groups at TL 1, benthic invertebrate groups between TL 2.0 and 3.3, and harbour seals, grey seals and otters at the highest TL between 4.5 and 5 (Fig. 2, Table 2). The red king crab groups had a TL close to 3 (Fig. 2), with the highest TL occupied by small red king crabs

due to a lower proportion of 'detritus from all other sources' than the larger crab groups (see Supplement 7).

Low TL groups, namely phytoplankton and bacteria, dominated total production and consumption. Total primary production (TL 1) was about 135 g C m^{-2} yr^{-1} in all subareas, with the exception of 4W, where high macroalgal production (35.1 g C m^{-2} yr^{-1}) raised total primary production to 165.1 g C m^{-2} yr^{-1} (Table 3). Biomasses of macroalgae groups and herbivorous echinoids were highest in Subarea 4W, and both decreased towards the outer part of the fjord with the lowest biomass in Subarea 1 (Fig. S12 in Supplement 9). The inner fjord Subareas 4E and 4W were characterized by high total biomass, long biomass residence times (>86 d) and lower system P/B values (6.9 and 3.3 yr^{-1}) than the mid- and outer fjord subareas with P/B around 11 yr^{-1} (Table 3).

Benthic invertebrate biomass was much higher in the inner subareas, mostly due to higher abundance of detritivorous polychaetes, *Ctenodiscus crispatus* (Subarea 4E) and large bivalves (Subareas 4E and 4W) (Fig. 3C, Table 3). Accordingly, benthic invertebrate production was highest in Subarea 4E, with detritivores constituting the major part (Table 3). Benthic invertebrate P/B values ranged from 0.49 to 0.90 yr^{-1}. These were higher in areas with high red

king crab biomasses. Red king crabs had the highest biomasses (0.10–0.13 g C m^{-2}) in Subareas 2 and 3 in the middle of the fjord and the lowest biomass in the inner Subareas 4E and 4W (Fig. 3A). The biomass of other large crustaceans was similar to king crab biomasses in the middle fjord (Subareas 2 and 3), but higher in the outer (Subarea 1) and inner fjord (Subareas 4E and 4W). Cod and other large demersal fishes dominated biomasses of higher TL fish in the outer and middle fjord (Subareas 1–3). Cottids dominated in the inner fjord (4E and 4W) (Fig. 3B). Herring (TL 3.4) were mostly restricted to the inner fjord, and pandalid shrimps had a TL of 2.9 and a much higher biomass in Subarea 4E compared to the rest of the fjord (Fig. 3D).

Predation

In the baseline models, red king crabs fed on a total of 16 other groups with a large variation in biomass and TLs, ranging from kelp and detritus (TL 1), detritivores, grazers (TL ≈ 2) and predatory invertebrates, such as predatory gastropods and predatory asteroids (TL ≈ 3) (Fig. 4A,B). Consumption by benthic invertebrate predators, including red king crab, made up 0.6–1.4% of the total consumption in all
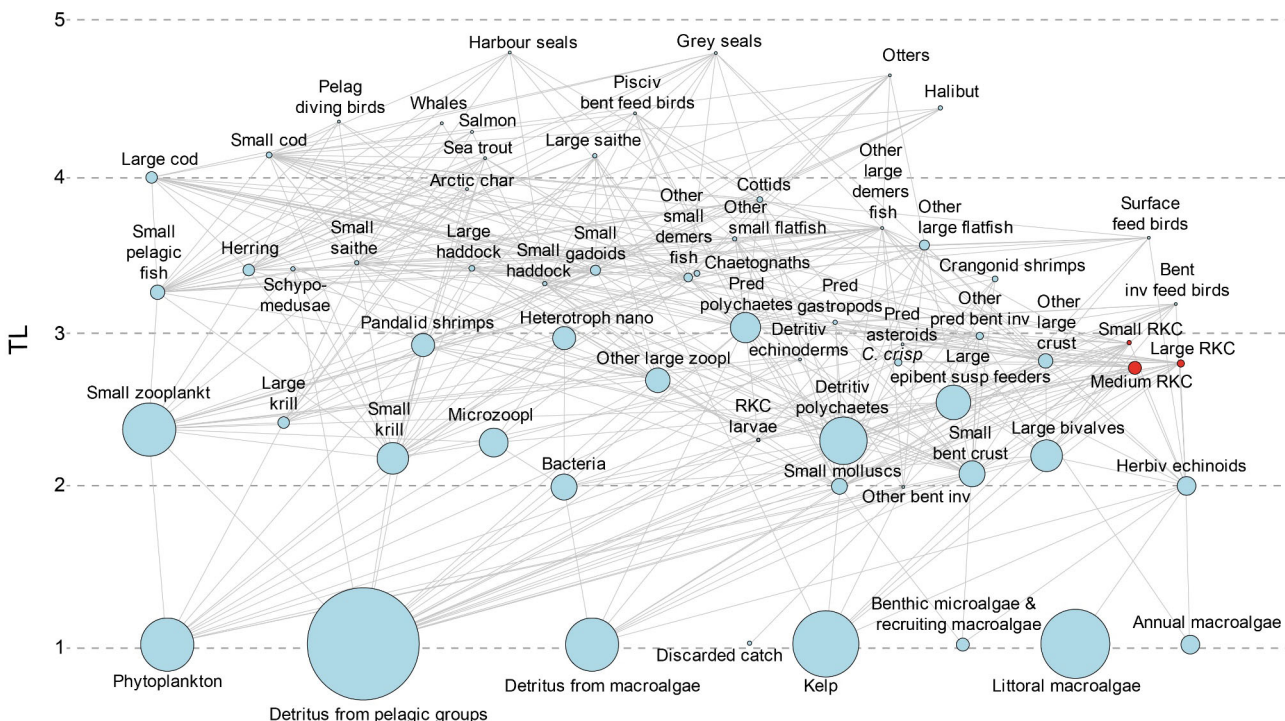

Fig. 2. Food web baseline model of Subarea 3 in Porsanger Fjord. Lines show trophic links between ecological groups. Diameters of circles are scaled proportional to logarithm of group biomass. Left axis shows estimated trophic level (TL). Red king crab (RKC) groups are shown in red

Table 2. Overview of values for the balanced Ecopath model for Subarea 3. Values estimated by the model are shown in **bold italics**. Full descriptions of the groups are given in Table 1 in Supplement 4. TL: trophic level; B: biomass; P: production; Q: consumption; Z: total mortality rate (underlined); EE: ecotrophic efficiency; CL: carapace length

Group	Group name	TL	B (g m^{-2})	Z or P/B (yr^{-1})	Q/B (yr^{-1})	EE	P/Q
1	Grey seals	4.77	0.00049	0.12	16.0	*0.17*	*0.007*
2	Harbour seals	4.77	0.00051	0.09	15.0	*0.87*	*0.006*
3	Whales	4.32	0.00028	0.13	12.8	*0.00*	*0.010*
4	Otters	4.63	0.00012	0.25	68.4	*0.00*	*0.004*
5	Piscivorous benthic birds	4.38	0.00039	0.21	103.0	*0.02*	*0.002*
6	Pelagic diving birds	4.33	0.00000	0.08	135.6	*0.00*	*0.001*
7	Surface-feeding birds	3.59	0.00014	0.13	118.9	*0.00*	*0.001*
8	Benthic invertebrate-feeding birds	3.17	0.00043	0.16	57.6	*0.00*	*0.003*
9	Large cod	3.97	0.076	0.53	3.00	*0.57*	*0.177*
10	Small cod	4.12	0.023	1.20	8.53	*0.96*	*0.141*
11	Large saithe	4.11	0.012	0.53	3.00	*0.56*	*0.177*
12	Small saithe	3.43	0.009	1.20	6.27	*1.00*	*0.191*
13	Large haddock	3.39	0.018	0.53	3.00	*0.52*	*0.177*
14	Small haddock	3.29	0.013	1.20	6.27	*1.00*	*0.191*
15	Small gadoids	3.38	*0.056*	1.20	6.0	0.90	*0.200*
16	Halibut	4.41	0.008	0.53	3.0	*0.00*	*0.177*
17	Other large flatfish	3.54	0.060	0.53	3.0	*0.04*	*0.177*
18	Other small flatfish	3.58	0.006	1.20	6.0	*0.82*	*0.200*
19	Other large demersal fish	3.65	*0.003*	0.53	3.0	0.90	*0.177*
20	Other small demersal fish	3.34	*0.050*	1.20	6.0	0.90	*0.200*
21	Cottids	3.83	*0.014*	1.29	3.9	0.90	*0.328*
22	Small pelagic fish	3.24	*0.107*	1.00	6.0	0.90	*0.167*
23	Herring	3.38	0.079	1.00	4.0	*0.17*	*0.250*
24	Salmon	4.26	0.000092	0.28	3.1	*0.85*	*0.090*
25	Sea trout	4.10	0.000008	0.48	3.1	*0.52*	*0.155*
26	Arctic char	3.90	0.000003	1.28	6.3	*0.26*	*0.201*
27	Small krill	2.18	*0.498*	2.50	16.7	0.90	*0.150*
28	Large krill	2.41	*0.071*	2.35	16.7	0.90	*0.141*
29	Small zooplankton	2.37	2.0	6.50	26.0	*0.52*	*0.250*
30	Microzooplankton	2.28	0.4	36.50	121.7	*0.64*	*0.300*
31	Heterotrophic nanoflagellates	2.95	0.26	36.50	121.7	*0.89*	*0.300*
32	Schypomedusae	3.39	0.011	6.50	23.5	*0.22*	*0.277*
33	Chaetognaths	3.36	0.020	3.80	19.0	*0.10*	*0.200*
34	Other large zooplankton	2.69	*0.302*	1.20	8.0	0.90	*0.150*
35	Pandalid shrimps	2.91	*0.267*	1.20	8.0	0.90	*0.150*
36	Large king crab >130 mm CL	2.85	0.037	1.00	3.34	*0.84*	*0.299*
37	Medium king crab	2.76	0.086	0.35	4.50	*0.09*	*0.078*
38	Small king crab <70 mm CL	2.92	0.011	0.50	9.18	*0.89*	*0.054*
39	Crangonid shrimps	3.33	0.019	0.39	2.6	*0.37*	*0.150*
40	Other large crustaceans	2.80	*0.116*	0.50	3.3	0.90	*0.150*
41	Predatory asteroids	2.91	0.001	0.19	1.3	*0.96*	*0.150*
42	Predatory gastropods	3.05	0.012	0.52	3.5	*0.95*	*0.150*
43	Predatory polychaetes	3.02	0.430	0.90	6.0	*0.84*	*0.150*
44	Other predatory benthic invertebrates	2.97	0.036	0.80	4.0	*0.97*	*0.200*
45	Detritivorous polychaetes	2.30	1.398	1.51	7.6	*0.99*	*0.200*
46	Small benthic crustaceans	2.08	*0.325*	1.51	10.0	0.90	*0.150*
47	Small molluscs	2.00	0.119	1.07	7.1	*0.97*	*0.150*
48	Large bivalves	2.20	*0.484*	0.19	2.4	0.90	*0.080*
49	Detritivorous echinoderms	2.30	0.001	0.40	5.0	*0.88*	*0.080*
50	*Ctenodiscus crispatus*	2.80	0.026	0.15	1.9	*0.80*	*0.080*
51	Large epibenthic suspension feeders	2.54	*0.626*	0.16	2.0	*0.90*	*0.080*
52	Other benthic invertebrates	2.00	0.002	0.64	4.3	*0.35*	*0.150*
53	Herbivorous echinoids	2.01	0.183	0.42	4.2	*0.98*	*0.100*
54	Bacteria	2.00	*0.316*	143.00	340.5	0.80	*0.420*
55	Kelp	1.00	4.500	0.76	0.0	*0.10*	
56	Annual macroalgae	1.00	0.174	1.50	0.0	*0.21*	
57	Littoral macroalgae	1.00	5.090	0.49	0.0	*0.02*	
58	Benthic microalg & recruit macroalg	1.00	*0.083*	6.80	0.0	0.90	
59	Phytoplankton	1.00	2.000	65.00	0.0	*0.65*	
60	Discarded catch	1.00	0.010	0.00	0.0	*0.46*	
61	Detritus from macroalgae	1.00	2.000	0.00	0.0	*0.51*	
62	Detritus from all other sources	1.00	67.000	0.00	0.0	*0.91*	

Table 3. Summary statistics and ecosystem properties of baseline Ecopath models constructed for the various subareas. *P/B*: production per biomass. **Bold** values indicate values outside the 95% confidence intervals for Subarea 3 given in Table S19

	Subarea				
	1	2	3	4E	4W
Primary production (g C m⁻² yr⁻¹)	135.4	136.3	136.8	137.2	165.1
Export (g C m⁻² yr⁻¹)	**0.1**	8.2	12.9	**0.8**	19.2
Sum of all consumption (g C m⁻² yr⁻¹)	292.0	289.1	279.1	**347.3**	277.1
Sum of all flows into detritus (g C m⁻² yr⁻¹)	**105.2**	142.1	143.2	156.6	162.2
Biomass residence time (d)	58.4	55.7	55.6	**86.9**	**192.8**
Sum of all production (g C m⁻² yr⁻¹)	218.9	227.3	225.4	235.8	250.3
Total biomass (excl. detritus) (g C m⁻²)	21.6	20.4	20.4	**34.2**	**74.6**
P/B (excl. detritus) (yr⁻¹)	10.1	11.1	11.0	**6.9**	**3.3**
Connectance index	0.111	0.108	0.109	0.107	0.106
System omnivory index	0.205	0.196	0.202	**0.185**	**0.194**
Production by macroalgae (g C m⁻² yr⁻¹)	5.09	5.84	6.19	6.56	**34.85**
Production by fish (g C m⁻² yr⁻¹)	**1.68**	0.50	0.48	**1.11**	0.62
Production of pred. benthic inv. (g C m⁻² yr⁻¹)[a]	0.54	0.55	0.49	**0.32**	**0.31**
Production of detritiv. benthic invertebrates (g C m⁻² yr⁻¹)[a]	2.22	3.24	2.92	**11.26**	3.04
Biomass of benthic invertebrates (g C m⁻²)[a]	3.61	**4.53**	3.81	**14.7**	**6.84**
Total *P/B* (yr⁻¹) for benthic invertebrates[a]	**0.76**	0.84	0.90	0.79	**0.49**
Total catch of fish (g C m⁻² yr⁻¹)	0.107	0.020	0.020	0.000	0.000
Total catch of red king crab (g C m⁻² yr⁻¹)	0.006	0.020	0.030	0.004	0.001
Consumption by red king crab (g C m⁻² yr⁻¹)	**0.10**	**0.41**	0.61	**0.07**	**0.06**
Consumption by all benthic invertebrate predators in % of total consumption	1.17	1.36	1.37	0.64	0.67

[a]Red king crab not included

baseline models (Table 3). Red king crab consumed ca. 1 to 18% (0.06–0.61 g C m⁻², Table 3) of the production of benthic invertebrates in the various subareas. The medium red king crab group had the highest biomass and consumption among the king crab groups (Table 2). In the middle fjord (Subarea 3), where crabs were highly abundant, they mostly consumed herbivorous echinoids, kelp, detritivorous polychaetes, large epibenthic suspension feeders and detritus from pelagic groups (carrion) (Fig. 4). Predation impact by the red king crab was most significant for prey groups with low production (Fig. 4), mainly *C. crispatus*, large epibenthic suspension feeders, herbivorous echinoids, predatory gastropods, predatory asteroids and other large crustaceans, in which they caused high predation mortality relative to total mortality (Fig. 5A). In comparison, in the inner subareas with low king crab biomass (4E and 4W), the predation mortality induced by red king crab was in general much lower (Fig. 5B).

Small and large cod were the most important predators on red king crabs in the Ecopath model for Subarea 3 in Porsanger Fjord (Fig. 4), with a predation mortality of 0.24 yr⁻¹ on small red king crab. 'Other large demersal fish' was the only other predator group feeding on red king crab (Fig. 4, Supplements 5 & 6), and the crab comprised only a low proportion of their diet.

Feeding on multiple TLs, the red king crab groups had among the highest OIs, ranging from 0.37 to 0.43 in the baseline models for the subareas (Fig. S8 in Supplement 8). Accordingly, the SOI was slightly higher in the middle and outer fjord (0.196–0.205), where king crabs were abundant, in comparison to the inner fjord (0.185–0.195) (Table 3). Due to a similar model structure, C did not vary much between subareas.

Niche overlap and MTI

In the baseline models, medium red king crab had a moderate prey niche overlap (>0.20) with 12 other groups, mostly predatory benthic invertebrate groups, benthic and demersal fish groups (other large flatfish and large haddock) and surface- and benthic invertebrate-feeding birds (Fig. S9 in Supplement 8). Cod groups (TL ≈ 4) fed at 1 TL higher than red king crab (Fig. 2), and resource overlap with cod was very low and only present in the small cod size class.

The MTI of red king crabs was negative on most of the benthic invertebrate prey groups (Fig. S10a in Supplement 8), except for a slightly positive impact on large bivalves. Red king crabs also had a positive MTI on benthic microalgae and recruiting macroalgae, annual algae and littoral macroalgae. In gen-
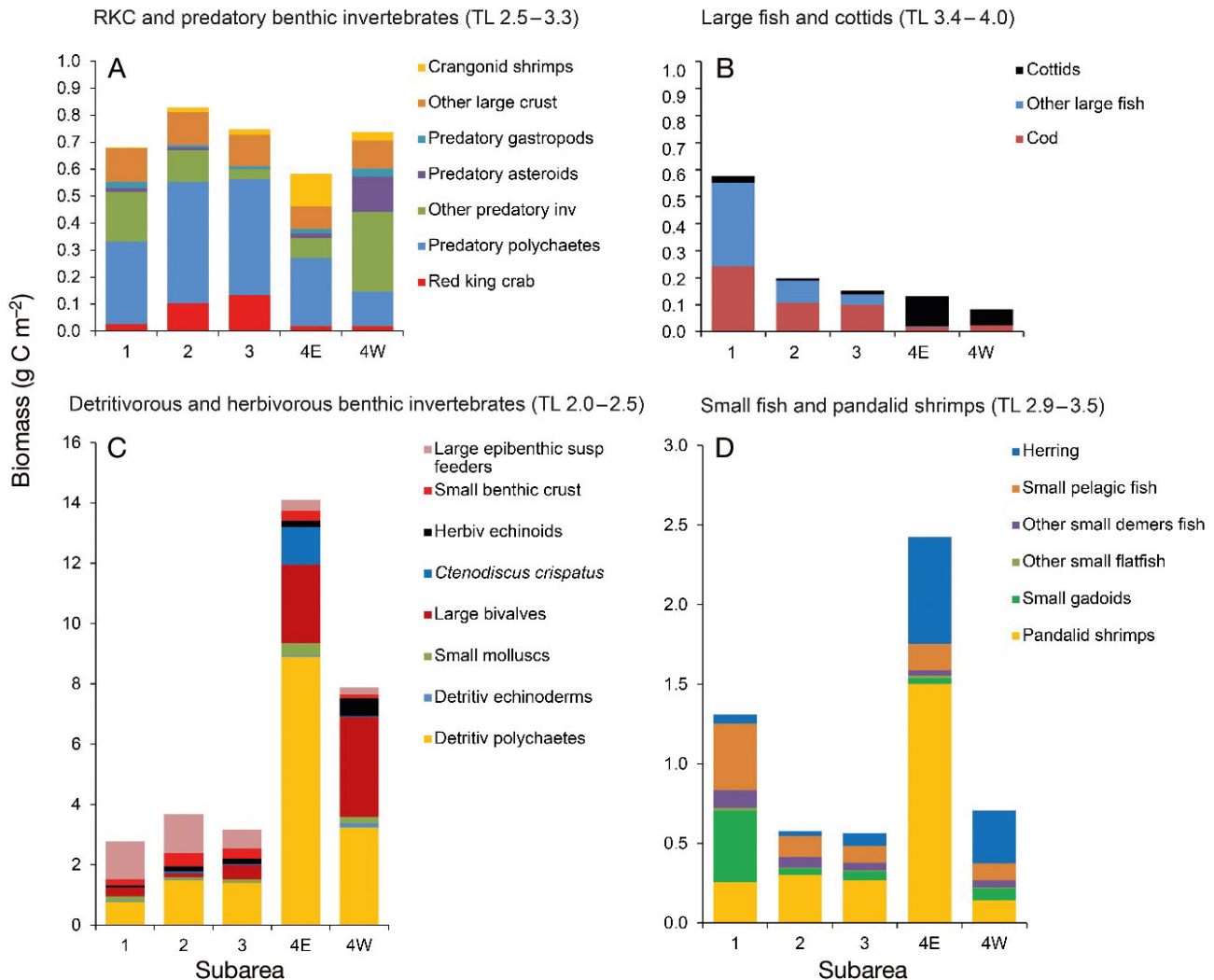
Fig. 3. Biomasses of various groups estimated by the baseline Ecopath models for the subareas within Porsanger Fjord: (A) benthic predators including red king crab (RKC); (B) large fish groups and cottids, 'other large fishes' including the groups large saithe, large haddock, halibut, other large flatfishes and other large demersal fishes; (C) detritivorous and herbivorous benthic invertebrates; (D) pelagic and small fish groups and pandalid shrimps. TL: trophic level
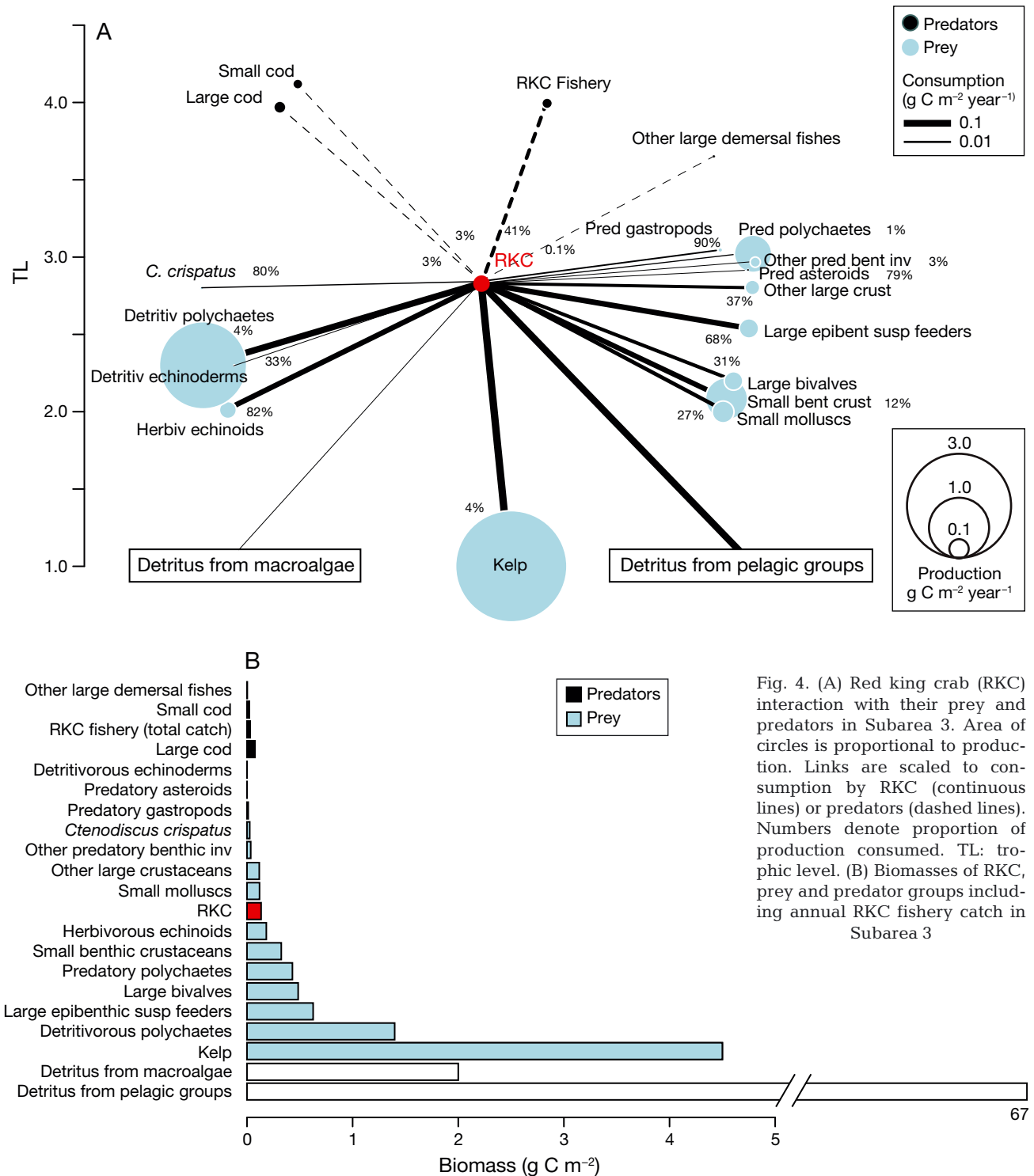
eral, MTI of crabs was low on pelagic groups and high TL vertebrate groups, except for a negative effect on benthic invertebrate- and surface-feeding birds. In comparison, large cod affected a higher number of ecological groups and had a large negative MTI on medium king crab (Fig. S10b in Supplement 8).

The relative total impact calculated for all groups varied markedly among groups and subareas (Fig. 6). Because of high biomass and consumption, medium red king crabs had the highest total impact among the king crab groups, ranking second behind large demersal fish and phytoplankton in the middle fjord (Subareas 2 and 3), respectively. In the inner fjord (Subareas 4E and 4W), the total impact from medium

king crab was low; here, cottids, pandalid shrimps and otters had a high total impact. Other large crustaceans exceeded red king crab impact only in the outer Subarea 1 (Fig. 6).

Uncertainty in baseline models

The baseline model for Subarea 3 had an overall pedigree index of 0.55. The pedigree indices for the input values were lowest (i.e. highest uncertainty) for low TL pelagic groups and for the diet of benthic detritivorous groups (Table S18a in Supplement 8). Low pedigree values were associated with high CIs (Table S18b in Supplement 8). The Monte Carlo

Fig. 4. (A) Red king crab (RKC) interaction with their prey and predators in Subarea 3. Area of circles is proportional to production. Links are scaled to consumption by RKC (continuous lines) or predators (dashed lines). Numbers denote proportion of production consumed. TL: trophic level. (B) Biomasses of RKC, prey and predator groups including annual RKC fishery catch in Subarea 3

uncertainty analysis showed the widest CIs for biomasses of the small cod, saithe, haddock and small gadoid group biomasses which were estimated by the model. Some lower TL groups estimated by the baseline Ecopath model, i.e. phytoplankton and 'benthic microalgae and recruiting macroalgae', also

had CIs higher than 50% of the median. For benthic invertebrates, biomasses of most groups had CIs in the range of 10–40% of the median (Fig. S7 in Supplement 8).

For ecosystem properties in the baseline model for Subarea 3, 95% CIs were in the range of 10–30% of
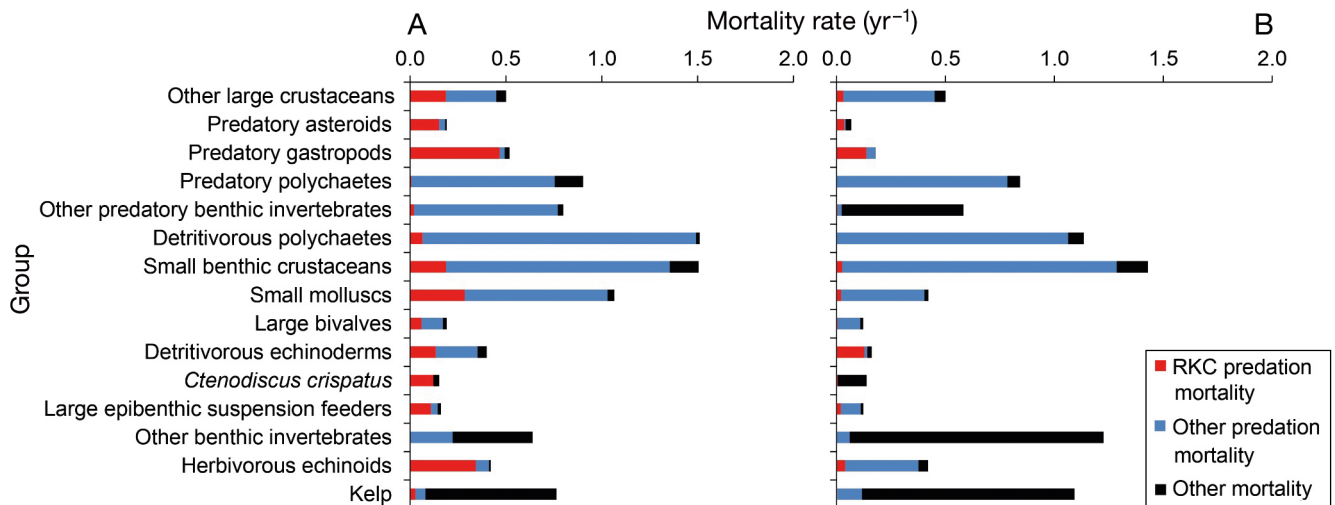
Fig. 5. Predation mortality rates from red king crab (RKC) and other predators compared to other mortality in the baseline models for (A) Subarea 3, with high RKC abundance, and (B) Subarea 4E, with low RKC abundance

the median for most measures, with biomass measures in the lower range and values for consumption and production measures in the upper range (Table S19 in Supplement 8). CIs for export estimates were very high (118% of median). Unconsumed detritus was the main contributor to export, and average export for the subareas was 8.2 g C m^{-2} yr^{-1}. Estimated export varied spatially between low values (<1 g C m^{-2} yr^{-1}, Table 3) for Subareas 1 and 4E and the highest values for Subareas 3 and 4W (13 and 19 g C m^{-2} yr^{-1}), but the uncertainty analysis of Subarea 3 shows wide 95% CIs (Table S19).

Crab removal scenarios

Comparison of scenario models with baseline models showed that group biomass responses (mainly increases in biomasses) of crab removal were stronger in subareas with highest baseline crab biomass (Subareas 2 and 3), but in general were similar across subareas (Fig. 7). For biomass of the ecological groups, simulations for the other subareas showed some exceptions to the responses seen in Subareas 2 and 3, which consisted mostly of the lack of effects of red king crab removal on biomass of benthic invertebrate-feeding birds, herbivorous echinoids and benthic algae groups in the inner 2 subareas (Fig. 7). Generally, there were fewer and smaller effects in the outer Subarea 1. Overall, fish and mammal groups were little affected by changes in crab biomass. The Ecosim simulations widely supported results obtained from the MTI analysis. After the removal of crab biomass in Subarea 3, there were marked increases in the biomasses of some of the prey groups and competitors (Fig. S11 in Supplement 8). These were predatory gastropods, *C. crispatus*, predatory asteroids, large epibenthic suspension feeders, benthic invertebrate-feeding birds, herbivorous echinoids, surface-feeding birds and other large
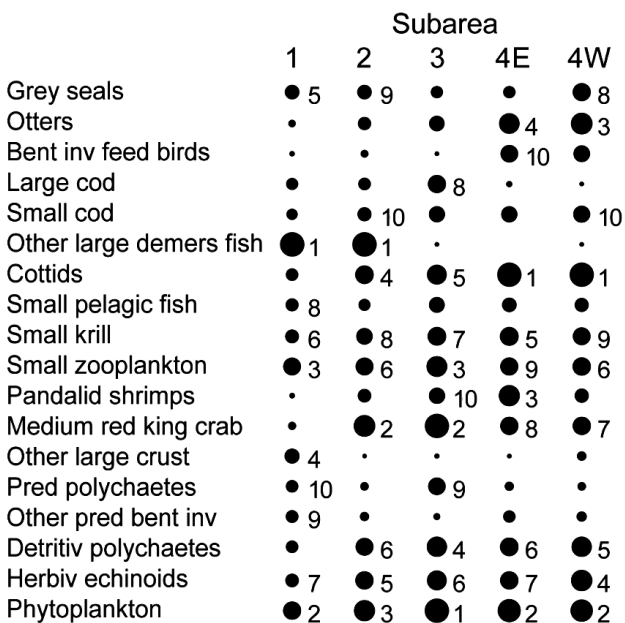

Fig. 6. Total impact of groups per subarea in the baseline models. Total impacts are relative to the maximum impact measured in each subarea, and circles are scaled to total impact. Only groups which rank at least 10 in total impact are shown, and numbers show rank of the respective group in each subarea

crustaceans (Fig. 7). In contrast, benthic microalgae and recruiting macroalgae decreased in biomass (Fig. 7).

For Subarea 3, Monte Carlo analysis showed that the simulated crab removal caused small but significant (p < 0.05) changes in median values for total system consumption (−0.2%), production (−0.2%), biomass residence time (3.5%), biomass (3.5%) and P/B (−3.6%) and for the production of detritivorous benthic invertebrates (2.2%) (Table 4). Changes were larger and significant for the SOI (−8.0%), production of predatory benthic invertebrate groups (10.5%), the biomass of benthic invertebrates (22.0%), and the P/B for benthic invertebrate groups (−15.5%) (Table 4). Production of fish, production of macroalgae, ascendency and overhead showed small and insignificant changes (Table 4). Changes in ecosystem properties due to crab removal were similar in Subareas 3 and 2, but were generally lower in the other subareas for most metrics (Table 4). However, the SOI decreased in all subareas when crabs were removed (Table 4).

Changing the vulnerability settings for crab interactions (from 1.2 to 5) in simulations did not have a large effect on the observed biomass changes of other groups. In simulations with v = 10 for all interactions in the models, short-term cycles were pronounced for multi-stanza fish groups, but trends for long-lived benthic invertebrates were similar to the baseline simulation with v = 2.

DISCUSSION

The Ecopath baseline models revealed differences in food web structure and properties along the fjord. The inner cold subareas, with low red king crab biomass, were characterized by high benthic biomass and production, accompanied by lower benthic P/B values and higher biomass residence times in comparison to the outer areas. The red king crab fed on numerous benthic prey species at different TLs, but it had little significance as prey, and direct or indirect interaction with fish groups was low. The crab removal scenarios indicated that the red king crab mostly affected the benthic compartment, with small effects on most overall ecosystem properties. However, the removal of red king crab increased benthic invertebrate biomass, biomass residence times and production, and decreased system omnivory and benthic P/B values. Both crab removal scenarios and trophic impact analysis of the baseline models indicated that red king crabs exert a strong top-down

	Subarea				
	1	2	3	4E	4W
Large red king crab >130					
Medium red king crab					
Small red king crab <70					
Grey seals					
Whales					
Surface feed birds					
Bent inv feed birds					
Other large flatfish					
Other large demers fish					
Salmon					
Crangonid shrimps					
Other large crust					
Pred asteroids					
Pred gastropods					
Other pred bent inv					
Small molluscs					
Large bivalves					
Detrivore echinoderms					
Ctenodiscus crispatus					
Large epibent susp feed					
Herbivore echinoids					
Annual macroalgae					
Benthic microalgae					

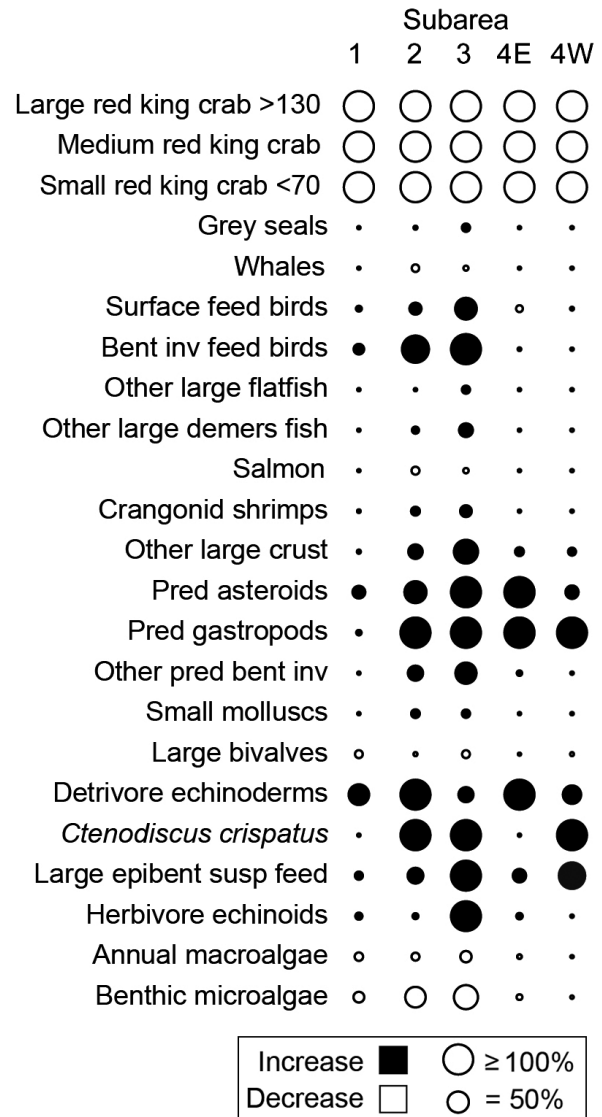| Increase ■	○ ≥100%
Decrease □	○ = 50%

Fig. 7. Effects of simulated complete removal of red king crab biomass shown as changes in biomasses of groups between scenario models after (Year 65) and before (Year 25) simulated complete removal of red king crab biomass. Open (filled) circles show decrease (increase) in biomass. Only groups with >10% change in one subarea are shown. Circle area is proportional to percentage change in biomass, and a 100% increase corresponds to a doubling

control on several, mostly long-lived, benthic invertebrate groups. Crab removal also had indirect effects, and the decrease in benthic algae was due to reduced crab predation on sea urchins, while the increase in biomass of invertebrate-feeding birds was likely because of reduced competition with red king crab for benthic prey.

The Monte Carlo uncertainty analysis showed that the level of uncertainty of the output biomass

Table 4. Percent changes of ecosystem properties after red king crab removal (Year 65) in comparison to baseline models (Year 25). Full names of groups are given in Table 1. *P/B*: production per biomass. For Subarea 3, percentage change of median of 100 Monte Carlo scenario trials is given in brackets, along with the significance probability for 95% confidence intervals not overlapping with zero; *p < 0.05, ns: not significant. Original units of variables are given in Table 3

| | Subarea | | | | |
	1	2	3	4E	4W
Primary production	0.0	−0.1	−0.1 (0.0 ns)	0.0	0.0
Export	0.6	−0.3	−0.7 (−0.1 ns)	−20.4	2.1
Sum of all consumption	−0.1	−0.2	−0.3 (−0.2 ns)	0.0	0.4
Sum of all flows into detritus	−0.1	−0.2	−0.2 (−0.1 ns)	−0.1	0.4
Biomass residence time	0.5	4.6	5.2 (3.5*)	1.0	0.3
Sum of all production	0.0	−0.2	−0.2 (−0.2*)	0.0	0.1
Total biomass (excluding detritus)	0.5	4.6	5.1 (3.5*)	0.9	0.2
P/B (excluding detritus)	−0.5	−4.6	−5.1 (−3.6*)	−0.9	−0.2
Connectance index	0.0	0.0	0.0 (0.0 ns)	0.0	0.0
System omnivory index	−6.4	−10.5	−8.3 (−8.0*)	−5.2	−7.1
Production by macroalgae	−0.1	0.0	−0.5 (−0.1 ns)	−0.1	0.0
Production by fish	0.1	−0.6	1.3 (1.3 ns)	0.0	1.2
Production of pred. benthic inv.	0.7	6.3	10.8 (10.5*)	2.3	4.4
Production of detritiv. benthic inv.	0.6	−0.3	2.6 (2.2*)	−0.1	0.8
Biomass of benthic invertebrates	4.1	24.3	30.6 (22.0*)	2.2	1.7
Total *P/B* for benthic invertebrates[a]	−3.3	−18.9	−20.5 (−15.5*)	−2.2	−0.6
Ascendancy	0.0	−0.1	−0.3 (−0.1 ns)	0.0	0.5
Overhead	0.0	0.1	0.1 (0.1 ns)	0.0	−0.2

[a]Red king crab not included

tion, production and biomass showed only small changes in response to simulated crab removal. These measures are mostly affected by the production and consumption of pelagic groups and bacteria (input values for plankton groups were similar in all subareas), and not affected by the crab. Since consumption by invertebrate benthic predators, including red king crabs, accounted for only a small part of the total consumption, the effects of red king crabs on ecosystem properties were small. In the crab removal scenarios, overall ecosystem energetics therefore seem to be resilient towards changing crab abundances. These results are comparable with the small changes in system properties seen after simulated removals of invasive green crab on the east coast of North America (Wong & Dowd 2014).

The total system *P/B* ratios (ca. 10 yr^{-1}) for the baseline models of the outer 3 subareas in Porsanger Fjord are similar to the system *P/B* ratio for the Chukchi Sea (ca. 10 yr^{-1}) but somewhat lower than values for the Barents Sea (16 yr^{-1}) and in the native areas for red king crab in the Eastern Bering Sea (22 yr^{-1}) and Gulf of Alaska (26 yr^{-1}) (Whitehouse et al. 2014). However, when the coastal macroalgal groups were excluded, system *P/B* values for most subareas in Porsanger Fjord were similar to the value for the Barents Sea, except for Subarea 4E, which had a lower *P/B* ratio of ca. 9 yr^{-1}. This was due to the low *P/B* values of benthic invertebrates, which made up 43% of the total biomass in this subarea compared to <23% in the other subareas. The general high biomass and production of benthic invertebrates (mostly detritivores), pandalid shrimps and small fish in the inner cold Subareas 4E and 4W is probably a combined result of prevailing environmental conditions (e.g. large food supply via macroalgae detritus) and low predation mortality due to low abundance of predators such as red king crab and cod.

The export from the Ecopath models for Porsanger Fjord consisted mainly of unconsumed detritus, and the average of the subarea export estimates (8.2 g C m^{-2} yr^{-1}) from the Ecopath models for Porsanger Fjord is in the range of the estimates of carbon burial

values for single groups was similar to the level of uncertainty of the input values. This is in line with earlier studies (Essington 2007, Pedersen et al. 2008, 2016) and, for the benthic invertebrate groups that were the main focus of this study, there were few signs of error propagation in the model output, probably because most groups had input biomass values that were based on local field sampling. No long-time series for benthic invertebrate biomasses was available that could be used for fitting of Ecosim models to estimate vulnerabilities, thus vulnerability settings are uncertain. The moderate variability in the scenario results when different vulnerabilities for interactions involving red king crab were assumed suggests that this may not have affected the short-term responses of crab removal results adversely. However, the short-term cycling observed in simulations with high vulnerability settings for all groups stresses the need for biomass time series and long-term monitoring of prey and predator responses.

Impacts on food web structure and properties

Relative to the baseline models along the fjord, overall ecosystem properties such as total consump-

rates in the sediments for the Barents Sea (6 g C m^{-2} yr^{-1}) (Carroll et al. 2008) and an Atlantic influenced fjord at Svalbard (15 g C m^{-2} yr^{-1}) (Zaborska et al. 2018). Since export estimates were imprecise, empirical measurements of water and detritus export between subareas are needed to validate transport between subareas.

Benthic biomass concentration in large, long-lived animals with lower *P/B* ratios in this inner area could mean slower recovery from future disturbance; however, high production by polychaetes may buffer some predation effects of future invasion by crabs (see below). Numerous observations point to red king crab predation increasing *P/B* ratios of the benthic compartment. We found higher *P/B* ratios for prey groups in the 2 middle fjord Subareas 2 and 3, where king crabs were abundant, and benthic *P/B* ratios decreased after simulated removal of red king crabs in all subareas. Our study suggests that crab predation shifts benthic community size composition, which is closely linked to *P/B* and turnover, towards short-lived small invertebrate prey species that benefit from crab predation (Oug et al. 2011). Fuhrmann et al. (2015) suggested that the higher *P/B* of benthic invertebrates in the middle and outer part of Porsanger Fjord could already be an indication of predation.

Generalist feeders create a number of links in a food web and may affect ecosystem structure substantially, usually leading to increased connectance (Kortsch et al. 2015). The red king crab had a high OI and contributed to high overall SOI in the baseline models for the 3 outer subareas, and SOI also decreased in all subareas when crabs were removed. The effect of omnivory in food webs has been discussed in relation to ecosystem stability (Gellner & McCann 2012), but is not consistent. To assess whether an increase in red king crabs affects ecosystem stability, further monitoring of the benthic community and modelling of perturbation effects on ecosystem resistance and resilience are needed.

Predation effects on individual groups

The significant increase in biomass of some long-lived invertebrate prey groups in all subareas following the simulated removal of king crab biomass suggests that these prey groups may be particularly vulnerable to predation from red king crabs. In support of this, several of these groups, including predatory gastropods (e.g. *Buccinum undatum*), predatory asteroids (e.g. *Asterias rubens*), the mud

star *Ctenodiscus crispatus* and other detritivorous echinoderms, had much higher biomass in baseline models of the inner subareas of Porsanger Fjord with low biomass of red king crab at the time of investigation.

Predatory asteroids and gastropods have been consumed by red king crabs both in laboratory experiments and in the field (Jorgensen 2005, Jørgensen & Primicerio 2007) (Supplement 5) and were common prey in all dietary investigations of red king crab in its native and invaded areas (Britayev et al. 2010, Falk-Petersen et al. 2011). In fjord arms of the Varanger Fjord which were invaded during the mid-1990s, the asteroid *C. crispatus* had virtually disappeared by 2007 and many sedentary polychaetes and large bivalve species have decreased in abundance (Oug et al. 2011). Large predatory gastropods such as *B. undatum* and *Neptunea* sp. may be especially vulnerable to red king crab predation, since they do not have pelagic larvae and thus have limited ability to recruit in areas with low adult abundance. Predatory polychaete biomass was high in the outer subareas, despite high abundance of king crab, probably due to these species being motile and able to escape predation (Oug et al. 2011).

Some benthic prey groups (detritivorous polychaetes, small benthic crustaceans, large bivalves, small molluscs) showed no or little change in biomass in response to simulated crab removal. Higher production in some of these groups buffered predation by the crab in the model. Large bivalves are an important prey for red king crabs (Falk-Petersen et al. 2011), and concerns that king crab predation may affect *Chlamys islandica* beds have been raised (Jorgensen 2005, Boudreau & Worm 2012). Scenarios suggested that crab predation on large bivalves was to some extent replaced by predation from recovering stocks of other large crustaceans, predatory gastropods and predatory asteroids, with the net result of small change in total predation mortality rate when the crab was removed. In addition, the initial proportion of large bivalves in the diet of red king crabs in the baseline models, prior to adjustment, was relatively small, due to the fact that they were rarely found in crab stomachs. This may have been a result of misidentification, since crabs are able to ingest soft tissue without hard shells, or simply low abundance in nature due to previous invasion.

Red king crabs have been shown to prey on benthic fish eggs, e.g. lumpfish *Cyclopterus lumpus* (Mikkelsen & Pedersen 2012), and benthic sculpin eggs may also be vulnerable to predation. Sculpins (cottids) are an ecologically important group in Por-

sanger Fjord, with high total impact (see Fig. 6), and a negative impact on their recruitment may have consequences for ecosystem structure and predators in the system.

The smallest red king crab size group had the highest estimated TL in the Ecopath models among the red king crab groups (TL = 2.9 in Subarea 3), mainly due to a lower proportion of 'detritus from all other sources' than in the larger crab groups. This apparently contradicts TL estimation based on stable isotope signatures, where small crabs had a marginally lower TL compared to larger size groups (Fuhrmann et al. 2017). However, the stable isotope signatures of carrion will resemble the higher TL groups' carrion sources and this may explain why the largest red king crab groups had slightly lower TL estimated by Ecopath (TL = 2.8–2.9) than by stable isotopes (TL = 3.1) (Fuhrmann et al. 2017).

Red king crab as prey

The low predation rate on red king crabs suggests that it is of minor importance as prey for other species, in contrast to the invasive green crab *Carcinus maenas*, which also plays an important ecosystem role as prey (Wong & Dowd 2014). In predator stomach data from Porsanger Fjord including the cod groups and large demersal fishes, there were few records of king crabs. Atlantic cod was the most important predator of red king crabs in Subarea 3, and the MTI analyses indicated that cod has an impact on small and medium red king crab. In the native range of the red king crab in the Bering Sea, Pacific cod *Gadus macrocephalus* is the major predator of king crabs, but predation from mammals may also occur (Lee et al. 2010). Furthermore, cannibalism in red king crabs has been recorded in Varangerfjord (Haugan 2004), but its importance is at present uncertain. In summary, red king crabs were not important as a food source other than for human consumption.

Indirect effects: suppression of herbivory and competition

The crab removal simulations revealed a potential negative impact of red king crab predation on herbivorous echinoids in the middle areas of Porsanger Fjord where crab densities were highest (see Figs. 5 & 7). Red king crab is an important predator of herbivorous echinoids, as demonstrated in field investi-

gations from Russian waters (Gudimov et al. 2003, Pavlova 2009) and laboratory studies (Jørgensen & Primicerio 2007). In other systems, predation from large decapods on sea urchins may cause a cascading increase in macroalgae (Pinnegar et al. 2000, Blamey et al. 2010, Boudreau & Worm 2012). In Norway, artificial reduction of green sea urchin *Strongylocentrotus droebachiensis* abundance in overgrazed barren ground resulted in rapid regrowth of kelp (Leinaas & Christie 1996). The negative effect of king crab removal on the group 'microalgae and recruiting macroalgae' would likely be followed by a decrease in larger macroalgae, including kelp. However, the Ecopath version applied in this study did not have the option for multi-stanza groups in primary producers, so the possible indirect effect from crabs on 'large' kelp could not be evaluated realistically in simulations.

The small effects of red king crab removal on fish, mammals and pelagic groups suggest that these groups are in general not adversely affected by crabs. Atlantic cod, which is a dominant predator in coastal areas, feeds on benthic invertebrates in their shallow nursery areas (Kanapathippillai et al. 1994, Svåsand et al. 2000). Cod seem to prefer mobile crustaceans and free-living predatory polychaetes (Kanapathippillai et al. 1994), and red king crab predation does not seem to affect these groups heavily. We speculate that increased macroalgal cover as a result of king crab predation on sea urchins may enhance the shallow nursery areas of coastal cod (Michaelsen 2012), thereby affecting cod recruitment positively. Thus, the indirect effects from red king crab may be large given that they enhance regrowth of macroalgae. For the other benthos-feeding fish, such as the haddock and flatfishes, any indirect impacts of red king crab predation may depend on whether these fish groups can adapt to changes in the species and size composition of the benthic invertebrate prey, but so far competitive effects on the most abundant fish species seem to be modest.

The increase in benthic invertebrate-feeding birds and surface-feeding birds following the removal of red king crab in the middle Subareas 2 and 3 of Porsanger Fjord, is most likely to be due to competition for herbivorous echinoids and other large crustaceans (see diet input in Supplement 6, Table S17), which were affected negatively by king crab predation. However, the lack of a positive effect from king crab removal on these mobile bird groups in the inner Subareas 4E and 4W suggests that the prey production in these areas was sufficient for both the king crab and bird populations.

CONCLUSIONS

Red king crabs play a major role in the benthic part of the food web of Porsanger Fjord due to their relative high biomass and the ability to feed on large long-lived benthic prey utilized by few other predators. Food web responses to crab predation are likely to be top-down effects induced by medium- and larger-sized crabs, since these are not particularly important as prey for other predators. The strongest predation effects were found for larger long-lived benthic invertebrates, whose absence is likely to be the first indicator of a predation impact. Cascading effects, such as the mediation of macroalgal growth, and competitive effects with benthic-feeding sea birds may be possible, but need further empirical validation. The crab removal scenarios showed that food web responses to crab invasion may differ spatially, but most overall ecosystem properties likely remain unaffected. However, the scenarios supported the finding that red king crab predation affects benthic production processes (increased *P/B* rates), inducing lower biomass and higher turnover, with unknown consequences for stability and resilience towards future perturbations.

LITERATURE CITED

Archer SD, Verity PG, Stefels J (2000) Impact of microzooplankton on the progression and fate of the spring bloom in fjords of northern Norway. Aquat Microb Ecol 22: 27–42

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

Blamey LK, Branch GM, Reaugh-Flower KE (2010) Temporal changes in kelp forest benthic communities following an invasion by the rock lobster *Jasus lalandii.* Afr J Mar Sci 32:481–490

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

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

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

Carroll J, Zaborska A, Papucci C, Schirone A, Carroll ML, Pempkowiak J (2008) Accumulation of organic carbon in western Barents Sea sediments. Deep Sea Res II 55: 2361–2371

Christensen V (1995) Ecosystem maturity—towards quantification. Ecol Model 77:3–32

Christensen V, Pauly D (1992) ECOPATH II—a system for balancing steady-state ecosystem models and calculating network characteristics. Ecol Model 61:169–185

Christensen V, Pauly D (eds) (1993) Trophic models of aquatic ecosystems. ICLARM Conference Proceedings 26. ICLARM, Manila

Christensen V, Walters CJ (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecol Model 172: 109–139

Christensen V, Walters C, Pauly D (2005) Ecopath with Ecosim: a user's guide. Fisheries Centre, University of British Columbia, Vancouver

Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman and Hall Inc., New York, NY

Eilertsen HC, Frantzen S (2007) Phytoplankton from two sub-Arctic fjords in northern Norway 2002–2004: I. Seasonal variations in chlorophyll *a* and bloom dynamics. Mar Biol Res 3:319–332

Essington TE (2007) Evaluating the sensitivity of a trophic mass-balance model (Ecopath) to imprecise data inputs. Can J Fish Aquat Sci 64:628–637

Falk-Petersen J, Armstrong CW (2013) To have one's cake and eat it too: managing the alien invasive red king crab. Mar Resour Econ 28:65–81

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

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

Fuhrmann MM, Pedersen T, Nilssen EM (2017) Trophic niche of the invasive red king crab *Paralithodes camtschaticus* in a benthic food web. Mar Ecol Prog Ser 565: 113–129

Gellner G, McCann K (2012) Reconciling the omnivory-stability debate. Am Nat 179:22–37

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

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. Dokl Bio Sci 393:539–541

Hänfling B, Edwards F, Gherardi F (2011) Invasive alien Crustacea: dispersal, establishment, impact and control. BioControl (Dordr) 56:573–595

Haugan TA (2004) Bunnsamfunn og næringsvalg hos kongekrabbe, *Paralithodes camtschaticus* (Tilesius, 1815), på noen lokaliteter i Finnmark. MSc thesis, Norwegian College of Fisheries Science, University of Tromsø

Heymans JJ, Coll M, Link JS, Mackinson S, Steenbeek J, Walters C, Christensen V (2016) Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. Ecol Model 331:173–184

Hjelset AM, Nilssen EM, Sundet JH (2012) Reduced size composition and fecundity related to fishery and inva-

sion history in the introduced red king crab (*Paralithodes camtschaticus*) in Norwegian waters. Fish Res 121–122: 73–80

Jørgensen LL (2005) Impact scenario for an introduced decapod on Arctic epibenthic communities. Biol Invasions 7: 949–957

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, Dordrecht, p 521–536

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

Jørgensen LL, Renaud PE, Cochrane SKJ (2011) Improving benthic monitoring by combining trawl and grab surveys. Mar Pollut Bull 62:1183–1190

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 Manag 25(Suppl 1):65–76

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 B 282:20151546

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

Lee SI, Aydin KY, Spencer PD, Wilderbuer TK, Zhang CI (2010) The role of flatfishes in the organization and structure of the eastern Bering Sea ecosystem. Fish Sci 76: 411–434

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

Libralato S, Christensen V, Pauly D (2006) A method for identifying keystone species in food web models. Ecol Model 195:153–171

Link JS (2010) Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. Ecol Model 221:1580–1591

Mankettikkara R (2013) Hydrophysical characteristics of the northern Norwegian coast and fjords. PhD dissertation, University of Tromsø

Michaelsen C (2012) Habitat choice of juvenile coastal cod: the role of macroalgae habitats for juvenile coastal cod (*Gadus morhua* L.) in Porsangerfjorden and Ullsfjorden in Northern Norway. MSc thesis, University of Tromsø

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

Orlov YI, Ivanov B (1978) On the introduction of the Kamchatka king crab *Paralithodes camtschatica* (Decapoda: Anomura: Lithodidae) into the Barents Sea. Mar Biol 48: 373–375

Oug E, Fuhrmann MM (2013) Bunndyrsamfunn i foreslått marint verneområde i indre Porsangerfjorden. Artssammensetning og biomasse før invasjon av kongekrabben 2011. RAPPORT L.NR. 6556-2013. NIVA, Grimstad

Oug E, Cochrane SKJ, Sundet JH, Norling K, Nilsson HC (2011) Effects of the invasive red king crab (*Paralithodes camtschaticus*) on soft-bottom fauna in Varangerfjorden,

northern Norway. Mar Biodivers 41:467–479

Oug E, Sundet JH, Cochrane SK (2018) Structural and functional changes of soft-bottom ecosystems in northern fjords invaded by the red king crab (*Paralithodes camtschaticus*). J Mar Sys 180:255–264

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

Pedersen T, Ramsvatn S, Nilssen EM, Nilsen M and others (2016) Species diversity affects ecosystem structure and mass flows in fjords. Reg Stud Mar Sci 3:205–215

Pianka ER (1973) The structure of lizard communities. Ann Rev Ecol Syst 4:53–74

Pinnegar JK, Polunin NVC, Francour P, Badalamenti F and others (2000) Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. Environ Conserv 27:179–200

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

Sivertsen K, Bjørge A (2015) On the brink of the Arctic: unusual, intertidal sub-Arctic kelp associations in the Porsangerfjord. Mar Biol Res 11:405–413

Snyder WE, Evans EW (2006) Ecological effects of invasive arthropod generalist predators. Annu Rev Ecol Evol Syst 37:95–122

Svåsand T, Kristiansen TS, Pedersen T, Salvanes AGV, Engelsen R, Nævdal G, Nødtvedt M (2000) The enhancement of cod stocks. Fish Fish 1:173–205

Ulanowicz RE (1986) Growth and development: ecosystem phenomenology. Springer-Verlag, New York, NY

Wallace M, Pertuit C, Hvatum A (1949) Contribution to the biology of the king crab (*Paralithodes camtschatica* Tilesius). Fishery Leaflet 340. U.S. Department of the Interior, Fish and Wildlife Service, Washington, DC

Whitehouse GA, Aydin K, Essington T, Hunt GLJ (2014) A trophic mass balance model for the eastern Chukchi Sea with comparisons to other high-latitude systems. Polar Biol 37:911–939

Wiborg KF (1963) Some observations on the Iceland scallop *Chlamys islandica* (Muller) in Norwegian waters. Fiskeridir Skr Ser Havunders 13:38–53

Winberg GG (1956) Rate of metabolism and food requirements of fishes. Fish Res Board Can Trans Ser 194:1–239

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

Wong MC, Dowd M (2014) Role of invasive green crabs in the food web of an intertidal sand flat determined from field observations and a dynamic simulation model. Estuaries Coasts 37:1004–1016

Zaborska A, Włodarska-Kowalczuk M, Legeżyńska J, Jankowska E, Winogradow A, Deja K (2018) Sedimentary organic matter sources, benthic consumption and burial in west Spitsbergen fjords–signs of maturing of Arctic fjordic systems? J Mar Syst 180:112–123

Zhou M, Zhu Y, Tande KS (2005) Circulation and behavior of euphausiids in two Norwegian sub-Arctic fjords. Mar Ecol Prog Ser 300:159–178