Ecosystem effects of red king crab invasion -a modelling approach using Ecopath with Ecosim

by
Jannike Falk-Petersen

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Norwegian College of Fishery Science
University of Tromsø

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SUMMARY

Knowledge on effects of the invasive red king crab (*Paralithodes camtschaticus*) on the Barents Sea ecosystem is limited. Due to the information available on benthos the Ecopath model of Sørfjord, Northern Norway, was used to investigate possible trophic changes with introduction of king crab to the model. A literature study of the king crab was conducted to find information on diet, mortality, consumption rate and other life history parameters required by the model. A short introduction to biological invasions was also included. The Ecopath with Ecosim software was used as a modelling tool to investigate factors allowing for growth of king crab as well as potentially controlling their biomass. Possible food-web effects of king crab invasion on the Sørfjord ecosystem was also investigated. Knowledge gaps identified through the exercise and management implications were discussed. A biomass of 1.2 t km^{-2} small and 2.8 t km^{-2} large king crabs was introduced to the Sørfjord model. The modelling exercise indicated that a resource opportunity, in the form of benthic production, could allow for growth of the king crab in Sørfjord. Mammals could have a negative impact on large king crab abundance through predation, while fish predation is expected to have minor effects on king crab biomass. King crabs are expected to have a negative effect on the benthic community through predation, but limited impact on the pelagic community. King crab abundance could be controlled by fishing large king crabs. A change in fishing of other commercial fish species is not expected to have an impact on king crab biomass. Knowledge gaps identified from this exercise includes population structure, biology and food preference of king crab. Production and interactions within the native benthic community should also be investigated further to understand possible impacts of king crab invasion.

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1. INTRODUCTION

1.1. OBJECTIVES

During the 1960s Russian scientists introduced the red king crab (*Paralithodes camtschaticus*) to the Barents Sea. Over a period of 10 years king crabs were caught mainly in the Sea of Japan outside Vladivostok and released in the Kola fjord. The motive of the introduction was to improve the coastal fishery economy as the crab is a highly valuable commercial species (Orlov and Ivanov 1978). Since the introductions the crab population has grown and expanded its distribution down the Norwegian coast (Figure 1) (Jørgensen et al. *in press*).

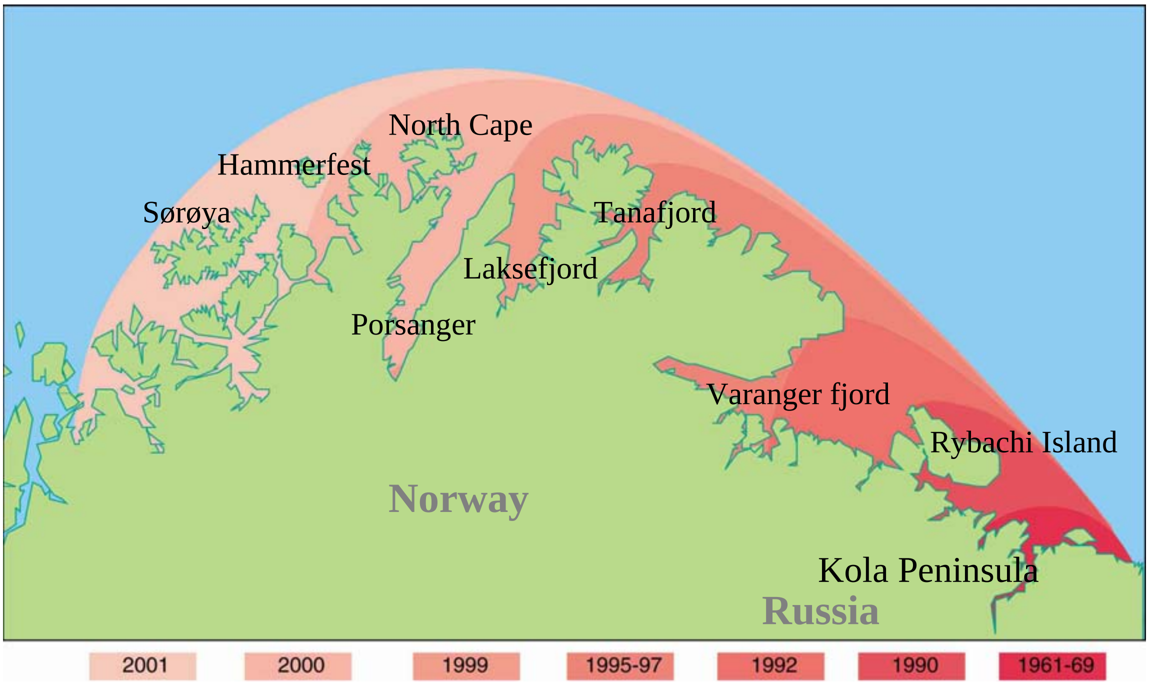

Figure 1. Generalised distribution and spread of the red king crab from area of release (read) and westward expansion (Sundet 2002).

The Norwegian government is working towards ecosystem management of the Norwegian marine resources. An emphasis is put on sustainable management of the ecosystem securing social and economic interests including the possible threat of introduced species. Norway also has high ambitions when it comes to following up international treaties including those concerning protection of biodiversity (Anonymous 2002). An overview of the many treaties, conventions and instruments of relevance to Norway concerning alien species is to be found in Hopkins (2001).

The red king crab is an invasive species in the Barents Sea. Being a large, bottom feeding omnivore of high mobility it may be hypothesised that it will have a significant impact on the ecosystem.

The focus of research has until today been on population biology, distribution and modification of harvesting tools to reduce bycatch of king crabs in traditional fisheries. Diet, temperature tolerance, parasites and symbionts have also been studied as well as the effect of king crab on scallop beds. The management plan of king crab in Norwegian waters expresses its concern regarding the consequences of the crab as an introduced species. This has been followed up by the Institute of Marine Research by focusing on ecosystem effects of king crab. The future focus of research will be on the biology of king crab, their impact on survival of capelin eggs and effect of king crab on the existing habitats and consequences for species interactions (Godø et al. 2003).

While there have been a number of speculations, knowledge on the effect of king crab invasion on the Barents Sea ecosystem is limited. There is a lack of information on what was there prior to invasion and the understanding of factors structuring the ecosystem is restricted (Godø et al. 2003). The possible ecological consequences of king crab invasion is an important factor in the debate concerning how Norway should manage the Barents Sea ecosystem.

Ecosystem analysis of the Barents Sea has so far focused on the pelagic species (Bax et al. 1991, Sakshaug et al. 1994, Tjelmeland and Bogstad 1997, Tjelmeland and Bogstad 1998, Dommasnes et al. 2002), while data on benthic communities is limited (Nilsen 2001). Ecopath with Ecosim (EwE) is a software for constructing and analysing trophic flows in a system as well as exploring impacts of fishing and environmental disturbances. While Ecopath can be considered an analytic tool, Ecosim can be used to predicting changes in abundance of system components over time. Ecosim has successfully been used to predict changes caused by fishing in the Gulf of Thailand (Christensen 1998) as well as rejecting trophic interactions as the main force causing structural changes of the Bering Sea from 1950s to 1980s (Trites et al. 1999, Christensen and Walters *in press*).

Based on Ecopath the Sørfjod model was constructed (Pedersen, T., Nilsen, M., Nilssen, E.M. and Berg, E. *unpubl*.). Due to the information available on benthic production (Nilsen 2001) the Sørfjord model is useful as a base looking at possible trophic changes associated with king crab invasion. The Sørfjord is also a relatively closed system making it well suited for ecosystem analysis with an Ecopath type model.

In this study an extensive literature review was conducted to find the input data required by the model on diet as well as mortality, consumption rate and other life history parameters of king crab. The biology of the king crab is initially described as it is an important key to predict possible effects of the crabs on an invaded system. A short introduction to the literature on invasive species will follow giving a presentation of some of the issues of concern with respect to invasive species.

Ecopath has previously been used to compare a system before and after invasion (Moreau et al. 1993), but is most commonly used to evaluate past and future effects of fishing. In this work, however, Ecopath and Ecosim will be used as a modelling tool to investigate possible trophic impacts of king crab invasion as well as identifying factors that could control the king crab population. Due to the relatively comprehensive benthic data material of the Sørfjord model an attempt to quantify the importance of bottom-up and top-down control can be made. The strength of these links can further indicate if the effects of king crab invasion will be limited to the trophic levels it feeds on or cause significant changes at higher trophic levels. It can also give an indication of the potential of higher trophic levels to control king crab abundance. Identifying factors controlling king crab abundance can help explaining its success as an invader. The output of the Ecopath and Ecosim analysis will be used to determine what groups in the system may be most vulnerable to king crab invasion.

The use and limitations of Ecopath with Ecosim for investigating ecosystem consequences of king crab invasion will be evaluated. Implications for management of the king crab based on the outcome of the modelling exercise will also be discussed. The knowledge gaps that may be important to fill in order understand ecosystem effects of king crab invasion as identified through the modelling exercise will be pointed out.

The objective of this thesis is to identify factors potentially controlling king crab biomass as well as factors allowing for their growth. Possible food-web effects of king crab invasion on the Sørfjord ecosystem will also be investigated. The implications of the findings for management as well as knowledge gaps identified through the analysis will be discussed.

1.2 BIOLOGY OF THE RED KING CRAB

King crabs (Family Lithodidae Samouelle) are among the world's largest arthropods of the genus *Paralithodes* (Martin and Davis 2001, Zaklan 2002).

The red king crab has been recorded at a wide range of depths from intertidal and shallow rocky habitats of about 4 meters to about 510 meter depths (Rodin 1989, Klitin and Nizyayev 1999). Temperature tolerance has been recorded to range from -1.7 to +18ºC with an optimum of +2 to +7ºC. The crab has been found in water of salinities of 28-30 ppt and higher (Orlov and Karpevich 1965, Rodin 1989). Experiments of incremental exposure to dilute seawater showed that adults are less tolerant to low salinities (12ppt) than juveniles (10ppt). Adults also showed poor performance in volume regulation and recovery (Thomas and Rice 1992).

The habitat of the mature king crab is determined by a mating-molting and a feeding migratory pattern. In late winter/early spring the crabs migrate shoreward to reproduce while in winter they move to deeper waters to feed (Marukawa 1933, Stone et al. 1992). There is not agreement in the literature as to what govern the feeding migration. Stone et al. (1992) point out that food availability is less in deeper waters. They found that photoperiod was well correlated with depth distribution. Temperature and salinity could also regulate movements especially during summer when shallow waters hold unfavourable temperatures and salinities. Large-scale movement is normally undertaken as a group. The crab has been recorded to move over 10 kilometres in a day (Marukawa 1933). A tag and recapture study by Hayes and Montgomery (1963) found king crabs 110 miles from the point of release. In areas of large variation in depth migrations may be limited as suitable habitats and environmental conditions are available within a small geographical area (Wallace et al. 1949).

At about the age of 5 the king crabs reach sexual maturity. Otto et al. (1989) determined size of maturity for females in different areas to range from 65.7 to 105 mm carapace length (CL). Rafter (1996) found CL at maturity to be 100 mm for females and 108.2 mm for males in the Varanger fjord, Norway. A practical average of 100 mm has been suggested by Powell and Nickerson (1965a).

When the crabs reach 5 years sexual segregation starts to emerge. In summer mature males move into deeper waters, while females remain in shallow waters. Mature females stay in water near 4 ºC, presumably to ensure optimal temperatures for the eggs to hatch prior to spawning. The males on the other hand, conserve energy in waters near 1,5ºC. Migration data of ovigerous females in Auk Bay, Alaska, indicates that from mid-June through mid-November the crabs aggregate and feed in relatively deep waters (mean depth 52.6m) below the summer thermocline. When the thermocline breaks down the crabs migrate to intermediate depths (mean depth 27.5m) where they release eggs fertilized in the previous spawning season. In May the females move to shallow coastal areas (mean depth <25m) to molt and mate. The males will join the females in shallow water where they clasp and guard females for up to 16 days prior to spawning (Stone et al. 1992, Stone et al. 1993, Loher et al. 1998). Spawning crabs prefer kelp areas where *Alaria, Costaria,* and *Laminaria* are common probably because they provide protection to the female during ecdysis (Powell and Nickerson 1965a). After spawning the adult crabs migrate back to deeper waters (>40m) (Stone et al. 1993).

The larvae hatch in early winter and spring and pass through four zoeal stages and a glaucothoe (the last larval phase in crabs) that settle and metamorphose into the first benthic instar (Nakanishi 1985, Paul et al. 1989). The inter molt period is influenced by water temperature with full larval development requiring an average of 469 degree days. The intermolt period is 9 days at 8 ºC and 24 days at 2 ºC, while growth is impaired at temperatures above approximately 10 ºC. Experiments suggest that steadily increasing sea surface temperatures through the planktonic phase results in the most rapid development. This is because the later stage zoeae perform better at higher temperatures than early stages (Nakanishi 1985). In addition to high temperatures other factors known to affect mortality rates of king crab larvae include stormy conditions and prey availability (Paul et al. 1979, Ishimaru 1936 as in Paul and Paul 1980).

Settlement occurs mainly in late July and August in near shore habitats. Characteristic habitats include cobble to boulders, shale outcroppings and biogenic structures including filamentous bryozoans, erect colonial ascidians and sponges, tibicolous polychaetes, mussel beds and filamentous algae. These structures provide refuge from predation a well as food (Powell and Nickerson 1965b, Sunberg and Clausen 1977). At this stage the king crabs 1 to 12 months old are 2.5 to 12 mm in carapace length (CL) respectively. Crabs 9 to 19 mm are commonly found on barnacle encrusted dock pilings between rays of starfish. It is believed that the crabs feed upon food particles dislodged by their commensal hosts (Powell and Nickerson 1965b).

The crabs leave their hidings between 12 and 24 months of age and form pod communities consisting of up to about 3000 individuals. The pods are believed to serve as protection against predators and provide biological organization and control. Pods have been observed from December throughout September. They consist of crabs of 17 to 69 mm CL, which are crabs from 2 up to 3-4 years old. The pods are disbanded either to allow the crabs to feed or to change location. In the fourth year when the crabs are 60-97 mm the pods merge and form large piles of crabs. These have been observed to comprise up to 500 000 crabs (Powell and Nickerson 1965b, Dew 1990).

At the larva stage the king crab is subject to predation by a number of planktivorous fish (Livingston et al. 1993, Wespestad et al. 1994). After settlement the king crabs are preyed upon by various fish. As the crab increases in size, the numbers of potential predators decrease although in a soft shelled state the crabs are more vulnerable (Gray 1964, Jewett 1978, 1982, Livingston et al. 1986, Loher et al. 1998). Other organisms that are believed to feed on juvenile king crab include horse crabs, sculpins and may be octopus (Powell and Nickerson 1965b). Sea otters have been observed feeding on mature king crab (Feder and Jewett 1981).

Prey of king crab larvae includes diatoms, nauplii, copepods and copepoids (Kurata 1960, Paul et al. 1979, Abrunhosa and Kittaka 1997). After settlement the diet of the crab consists of a range of benthic organisms including polychaetes, crustaceans, molluscs, echinoderms, ascidians and fish (Tarvierdieva 1979, Feder and Jewett 1981, Rafter 1996).

The king crab does not feed to capacity, but browses slowly or intermittently (Cunningham 1969). The smallest size groups (98-120 mm CL) had the highest feeding index and highest intestinal fullness. King crabs feed alternatively as active predators and filter feeders. They capture food by seizure and tear apart larger animals or scoop up and filter out small invertebrates and microfauna from the substratum. Filtering of the substratum could lead to accidental intake of sand and minute infaunal animals. The majority of the stomachs of the crabs in the study contained 3-4 of the major animal groups simultaneously and occasionally algae (Cunningham 1969). A number of studies suggest that the king crab is an opportunistic feeder feeding on the most available benthos (Cunningham 1969, Feder and Paul 1980). Dietary studies of king crab have to a large extent been qualitative. The diet table below illustrates the diversity of food organisms king crab has been found to prey on (Table 1).

Table 1. Food items found in stomach of king crab. P (present) marks items found.

Reference	McLaughlin and Hebard 1961	Bright 1967		Cunningham 1969	Tarverdieva 1976		Tarvierdieva 1979	Feder and Paul 1980	Feder et al. 1980	Jewett and Feder 1982	Jewett et al. 1989	Rafter 1996	Gerasimova 1997	
Area of study	Southeastern Bering Sea	Cook Inlet, Alaska		Bristol Bay, Bering Sea	Bristol Bay, Bering Sea		Bristol Bay, Bering Sea	Cook Inlet, Alaska	Southeastern Bering Sea	Kodiak Island, Alaska	Norton Sound, Alaska	Varanger fjord, Barents Sea	Varanger fjord, Barents Sea	
Size of crab **Food component**	Size range 63-193mm CL	Juveniles	Adults		shell width 80-130mm	shell width more than 130	armour width: 126-184mm		CL 2.89-5.04 (post larval king crab)		Mainly large crabs (90-100mm CL)	CL 32-201mm	<150mm (CW)	>150mm (CW)
Foraminifera		P				P	P	P	P		P	P		
Coelenterata	P													
Hydrozoa		P	P		P	P	P	P	P		P	P	P	P
Polychaeta	P			P	P	P	P	P		P		P	P	P
Fam. Lumbrineridae											P			
Fam. Oweniidae											P			
Fam. Pectinariidae											P			
Fam. Polynoidae	3										P			
Fam. Sabellidae											P			
Travisia sp.											P			
Sternaspis scutata											P			
Siphunculoidea (class)												P	P	P
Priapuloidea (class)													P	P
Unid. Polychaeta											P			
Polychaete setae									P					
Nematoda						P								
Sipunculoidea						P								
Mollusca	P			P		P	P			P			P	P
Bivalvia					P	P			P	P		P	P	P
Fam. Cardiidae											P			
Cardiomya sp.											P			
Clinocardium ciliatum			P					P						
Clinocardium sp.											P			
Cyclocardia crebricostata											P			
Liocyma fluctosa											P			
Macoma spp.								P						
Macoma spp.			P								P			
Mya spp.											P			
Pandora spp.											P			
Serripes groenlandicus											P			
Spisula polynyma								P						
Tellina nuculoides								P						
Fam. Glycymerididae														
Glycymeris subobsoleta								P						
Fam. Mytilidae			P					P			P			
Musculus sp.											P			
Modiolus Modiolus								P						
Fam. Nuculanidae											P			
Nuculana fossa								P						
Yoldia sp.											P			
Lyonsia sp.											P			
Crenella decussata											P			
Fam. Pectenidae			P											
Chlamys spp.								P						
Fam. Nuculidae		P	P								P			
Nucula tenuis								P						
Fam. Veneridae			P											
Unid. Bivalvia								P			P			
Gastropoda			P		P	P				P		P	P	P
Fam. Buccinidae														
Neptunea lyrata								P						
Fam. Naticidae														
Cylichana alba											P			
Polinices spp.								P						

Table 1. continue.

Reference/ **Food component**	McLaughlin and Hebard 1961	Bright 1967		Cunningham 1969	Tarverdieva 1976		Tarvierdieva 1979	Feder and Paul 1980	Feder et al. 1980a	Jewett and Feder 1982	Jewett et al. 1989	Rafter 1996	Gerasimova 1997	
Fam. Trochidae											P			
Margarites sp.											P			
Solariella spp.								P			P			
Fam. Turridae														
Oenopota spp.								P						
Gastropod eggs								P				P		
Unid. Gastropoda								P			P			
Scaphopoda													P	P
Crustacea										P		P	P	P
Order Amphipoda					P	P	P	P			P	P	P	
Photis spaskii											P			
Balanus spp. (U.Klasse. Cirripedia)						P		P		P	P		P	P
Calanoidea (copepods)														
Chionoecetes bairdi (tanner crabs)										P	P			
Cumacea											P			
Decapoda	P					P	P		P		P	P		
Halacaridae (sea mites)											P			
Harpacticoida									P					
Isopoda							P				P			
Majidae (spider crabs)											P			
Ostracoda (mussel shrimp)									P		P			
Paguridae								P			P		P	P
Pandalus spp. (U. orden Caridea)								P		P				
Pinnixa occidentalis										P				
P. camtschatica													P	P
Unid. Crustacea	P							P	P	P	P			
Echiurida														
Echiurus echiurus											P			
Echinodermata	P			P			P			P			P	P
Asteroidea						P	P	P	P	P	P	P	P	P
Pycnopodia helianthoides			P											
Echinoidea					P	P	P					P	P	P
Ophiuroidea						P	P	P		P	P	P	P	P
Strongylocentrotus droebachiensis		P	P							P	P			
Echinarachnius parma											P			
Holothuroidea		P	P											
Unid. echinoidea											P			
Unid. echinodermata									P		P			
Other echinoderms										P				
Pogonophora					P	P	P							
Bryozoa		P	P					P			P	P		
Flustrella									P					
Ascidiae					P	P	P							P
Tunicata												P		
Pisces, bones, scales				P			P			P	P	P	P	P
Fish roe													P	P
Porifera		P				P			P		P			
Diatoms		P	P						P					
Silicoflagellates									P					
Tintinnida (ciliates)									P					
Unid. Animal material										P	P			
Remains of plants	P	P	P	P		P	P	P	P	P	P		P	P
Brown algae												P		
Red algae												P		
Digested weight						P	P							
Unid. Material								P	P	P		P		
Unid.tissue									P					
Unid. Org material									P					
Slime							P							
Sand					P	P	P		P	P	P			
Nylon rope fiber									P					

1.3 BIOLOGICAL INVASIONS

There is a lack of consistency in the use of terminology concerning invasive species (Ehrlich 1986, Williamson and Fitter 1996a, IUCN 2000, Lawrence 2000, Mack et al. 2000, Manchester and Bullock 2000, Prieur-Richard and Lavorel 2000, Hopkins 2001). Invasion has been defined as the whole process from arrival of a new species into a community to establishment, maintenance and further spread (Prieur-Richard and Lavorel 2000). Mack et al. (2000) differentiate between immigrants and invaders where the latter have become abundant and widespread. In addition invaders were defined as having a negative effect on the environment. Although invasive species are associated with the above, this introduces a large degree of subjectivity to the term. Manchester and Bullock (2000) for example, argue that introduced species can have negative, positive and no impact upon native biota.

Biotic invasives and their descendants have been referred to as alien, non-indigenous, non-native, foreign, exotic, adventive, introduced, transferred, transplanted and introduced (IUCN 2000, Mack et al. 2000, Hopkins 2001). A native, or indigenous, species is defined as a species, subspecies or lower taxon occurring within its natural past or present range and dispersal potential (IUCN 2000). All these terms will be used interchangeably. Table 2 shows definitions of terms related to different levels of invasion success modified from Williamson and Fitter (1996b).

Table 2. Definitions and terms related to levels of invasion success. (Modified from Williamson 1996, Wiliamson and Fitter 1996b, Manchester and Bullock 2000).

Imported	-brought into the country, contained.
Introduced	-found in the wild, feral, casual, released but not breeding successfully, population not necessarily self-maintaining.
Established	-with a self-sustaining population, naturalized, feral and breeding successfully, released and breeding successfully.
Pest	-with a negative economic effect.
Escaping	-transition from imported to introduced.
Establishing	-transition from introduced to established.
Becoming a pest	-transition from established to pest.

Biological invasions are not a new phenomenon or solely human induced. But through increased mobility man has significantly extended the geographic scope, rate and numbers of species involved (di Castri 1989). Today biological invasions are considered major agents of global change and one of the main threats to marine systems. Although most invaders have minor consequences those that do succeed may have economic, environmental and ecological effects (Elton 1958, Vitousek 1990, Williamson 1996, Vitousek et al. 1996, Mack et al. 2000, Hopkins 2001, ICES 2001).

The three major categories for introductions include accidental introductions, species imported for a limited purpose that escape, and deliberate introductions (Levin 1989). Digging of canals, accidental transport on ships and deliberate introductions are important vectors causing change in the distribution of species in the ocean (Carlton and Geller 1993, Minchin and Gollasch 2002).

King crab is only one of many species that have been introduced for economic reasons. Today many introductions are the foundation of important industries in their new area, while others have proven disastrous. Releases of exotic species have caused problems such as pests, pathogens and weeds in forestry, agriculture and aquaculture as well as endangered and caused extinction of native species. Introduction of exotics is regarded as one of the largest threat to biodiversity (Elton 1958, Soulé 1990, McNeely 2001).

Economic damages due to biological invasions can be very large. The damage can be both due to interspecific interaction between the exotic and native species and through effects on ecologically important species, habitats or ecosystems (Williamson 1996, Mack et al. 2000). There have been attempts to measure the costs of biological invasion as well as the value of biodiversity for comparison with alternative use of the resource. This is a task that is difficult, many will say impossible, and full of controversies. It could nevertheless be used as a tool to shed some light on the costs and benefits involved (Barbier 2001, Nunes and van den Bergh 2001). It is clear that the cost of introductions can be great and in many instances it is not carried by those who benefit from the exotics. This can be a source of conflict (Elton 1958, Ewel et al. 1999, Mack et al. 2000, McNeely 2001). In many instances decisions concerning introductions are ultimately a political issue of economic gains and public emotions versus the value of preventing biological damage (Soulé 1990, Jenkins 1999, Mack et al. 2000).

Invasive species can be fought at three stages with each stage being more difficult and costly. Invaders can be prevented from entering a new area, eradicated when first detected or attempts can be made to control their population size once established (Elton 1958, Mack et al. 2000). Control, management and eradication programs for exotic species can be very controversial and involve many competing interests. These programmes may involve destructive mechanical and chemical methods as well as biological control agents. The latter could result in the release of another pest (Elton 1958, Mack et al. 2000). Invaders are rarely eradicated once established and the success of control is dependent on commitment rather than the tools used. Long term, ecosystem wide strategies have proven the most effective (Mack et al. 2000).

Exotics may do well in a new environment due to the lack of predators, competitors, parasites and/or abundance of spatial and dietary resources as well as more favourable abiotic conditions. Behavioural traits may also determine the success of invasives. Many invasions are facilitated by human-caused disturbance of native communities (Williamson and Fitter 1996b, Holway and Suarez 1999, Mack et al. 2000, Hopkins 2001).

Based on Vitousek (1990) Crooks (2002) identified three major effects of exotics on ecosystems. These include the alteration of flow, availability and quality of 1) nutrient resources within biogeochemical cycles, 2) trophic resources within food webs and 3) physical resources. Through predation, competition or breaking links in the system, invasive species can cause extinction or stress native species. The result can be a system with simpler and less sustainable community structure. Reduced biodiversity has also been found to lead to higher vulnerability to pests and diseases (Begon et al. 1996, Sakai et al. 2001). A number of introductions have caused major structural changes in food web structures. Examples include the impact of zebra mussel (*Dreissena polymorpha*) on freshwater systems in Europe and North America (Strayer et al. 1998, Aldridge et al. *in* *press*), the Nile perch (*Lates nioticus*) on the Lake Victoria ecosystem (Moreau et al. 1993) and the opossum shrimp (*Mysis relicta*) in freshwater lakes in the United States and Canada (Spencer et al. 1991).

A number of crustaceans have occupied new areas (ICES 2001) among them the European shore crab. The European shore crab (*Carcinus maenas*) originally from the European Atlantic waters is now established on the Atlantic and Pacific coasts of U.S.A, in Brazil, Panama, Hawaii, Ceylon, Australia and South Africa. It is known as an aggressive predator controlling its prey populations both in its native and introduced areas. In South Africa the crab is restricted to sheltered localities which make up a small part of the coast. The crab is not expected to compete with or displace indigenous crab species as dietary and habitat preferences differentiate. It could, however, be a threat to South African lagoon systems where many important mariculture centres and conservation areas are situated. In North America crab invasion has been followed by a decline of benthic invertebrates and shorebird species. It is also a pest of commercial bivalve culture operations (Le Roux et al. 1990, Griffits et al. 1992, Grosholz and Ruiz 1996).

Only a small number of studies have attempted to quantify the impacts of marine invasive species on the native biota. Even fewer have measured the effects on multiple trophic levels. Grosholz et al. (2000) monitored a Californian coastal system over 9 years to determine the impacts of the nonindigenous *Carcinus maenas* on the marine food web. It was found that the crab had both direct and indirect effects on the abundance of a number of native species.

Knowledge of the ecological impact of introduced species in marine systems is limited compared to the understanding of their effects on terrestrial and freshwater communities (Grosholz et al. 2000, ICES 2001). Studies of marine invasions usually have poor predictive power as they seldom combine wide-ranging descriptive data and quantitative or experimental results. The ability to predict which species will have serious impacts is important to understand ecosystem structure and functioning and aid in management and control efforts (Grosholz and Ruiz 1996).

1.4 ECOPATH AND ECOSIM

The Ecopath with Ecosim (EwE Version 5) software is a tool for constructing a model of trophic flows between compartments in an ecosystem. Ecopath offers a network analysis which can provide information on the structure and functions of ecosystems (Wulff et al. 1989, Christensen and Walters *in press*). Ecopath also provides a mixed trophic impact routine that quantifies all direct and indirect trophic effects by summing the negative and positive impacts for each group (Christensen 1995a).

Ecopath is a mass-balance approach describing an ecosystem for a given period of time. Ecosystem changes can be simulated over time using Ecosim, which is a dynamic ecosystem model. Ecosim can be used to explore the dynamics of the system as well as the responses of the system to various fishing patterns and environmental disturbances (Walters et al. 1997, Pauly et al. 2000).

The Ecopath model assumes that for any producer at the time period considered consumption can be described by

Consumption = production + non-assimilated food+ respiration 1)

Production is estimated from

Production = predation mortality + non-predation mortality + net migration + biomass accumulated 2)

Predation mortality (equation 2) can be estimated as consumption by all predators and thus links predators and prey.

Ecopath requires three of the following four input parameters for each of the functional groups in the model: biomass, production/biomass, consumption/biomass and ecotrophic efficiency. Ecotrophic efficiency (EE) expresses the proportion of production of a given group that is used for predation in the system. EE has a scale from 0 to 1 where 1 is complete utilization by other species.

EE = 1 – (non-predation mortality / production rate)

Ecopath sets up as many linear equations as there are groups in the system and solve for unknown values. The EE parameter is the main tool used to balance the model in order to assure that no group is being preyed upon beyond their level of production. Other parameters important to evaluate the model are production/consumption ratio and food electivity (Christensen et al. 2000).

Additional parameters to those listed above needed as input in the Ecopath model include diet composition, assimilation rate, net migration rate, biomass accumulation rate as well as fisheries catch and discards. The data input required to construct the model has commonly been collected in fisheries analysis. By combining these data into one coherent picture the major predator-prey relationships are highlighted. An Ecopath analysis can also help identifying critical data gaps in the knowledge of the ecosystem of concern (Christensen and Pauly 1992, Christensen et al. 2000).

The basics of Ecosim are derived from the Ecopath equation and consist of biomass dynamics expressed in the form of coupled differential equations. It takes into account the trade-off between searching for prey and being exposed to predators. This can be manipulated through changing the vulnerability parameter of prey. The vulnerability parameter ranges from 0 (prey not vulnerable, implying bottom-up control) to 1 (prey vulnerable, implying top-down control). Ecosim requires input of life history parameters and allows for linking of juvenile and adult groups to better represent ontogenetic shifts (Pauly et al. 2000).

2. MATERIALS AND METHODS

2.1 THE SØRFJORD MODEL

An Ecopath model by Pedersen, T., Nilsen, M., Nilssen, E.M. and Berg, E. (*unpubl.*) on the Sørjord system was used as a base model representing a North Norwegian fjord. The model represents an average year and is based on sampling between 1993 and 1996. The Ecopath input and output parameters for the functional groups in the Sørfjord model (Model I) are shown in Table 3, while the diet matrix can be found in Appendix A.

Table 3. Input and output parameters for the Sørfjord model without king crab (Model I). Parameters summarised include trophic level as well as annual biomass, production per biomass (P/B), consumption per biomass (Q/B), ecotrophic efficiency (EE), biomass accumulation (Biomass accum.), assimilation coefficient (Assim. coef.), production per consumption (P/Q) and harvest by cod fleet. Input parameters are shown in black while values estimated by the model are marked in blue.

Group name	Trophic level	Biomass (t/kmý)	P/B (/year)	Q/B (/year)	EE	Biomass accum.	Assim. coef.	P/Q	Harvest (t/kmý)
Cormorants	4.32	0.0009	0.125	37.10	0.533	0.0	0.2	0.003	0.00006
Mammals	4.24	0.01	0.102	35.30	0.490	0.0	0.2	0.003	0.0005
Large cod	3.35	1.81	0.42	3.00	0.869	0.1	0.2	0.140	0.370
Small cod	3.36	0.14	1.70	6.00	0.384	0.0	0.2	0.283	
Large other fish	3.08	0.78	0.50	3.00	0.631	0.0	0.2	0.167	0.150
Small other fish	3.14	0.575	1.70	6.70	0.900	0.0	0.2	0.254	
Herring	3.07	0.22	1.00	6.00	0.900	0.0	0.2	0.167	
Euphausiids	2.11	4.515	2.50	16.70	0.900	0.0	0.3	0.150	
Small zooplankton	2.05	20.0	6.50	26.00	0.359	0.0	0.3	0.250	
Schypomedusae	3.10	0.72	6.50	17.33	0.133	0.0	0.2	0.375	
Chaetognaths	3.05	0.20	3.80	19.00	0.493	0.0	0.2	0.200	
Shrimp	2.59	0.193	2.00	13.30	0.900	0.0	0.2	0.150	
Other large zooplankton	2.00	0.706	2.00	13.30	0.900	0.0	0.2	0.150	
Large decapoda	2.93	0.363	0.50	3.33	0.900	0.0	0.2	0.150	
Predatory benthos	2.89	1.273	0.50	3.33	0.900	0.0	0.2	0.150	
Detrivore polychaetes	2.00	43.0	0.74	4.93	0.105	0.0	0.2	0.150	
Small benthic crustaceans	2.12	4.0	0.50	3.33	0.433	0.0	0.2	0.150	
Small molluscs	2.08	26.0	0.35	2.33	0.634	0.0	0.2	0.150	
Large bivalves	2.00	62.9	0.19	2.11	0.084	0.0	0.2	0.090	
Detrivore echinoderms	2.00	41.0	0.20	2.22	0.284	0.0	0.2	0.090	
Other benthic invertebrates	2.00	2.0	0.50	3.33	0.243	0.0	0.2	0.150	
Phytoplankton	1.00	20.0	60.00	-	0.460	0.0		-	
Detritus	1.00	50.0	-	-	0.493			-	

Sørfjord (69°40’N, 19°40’E) is the inner part of the Ullsfjord-Sørfjord system and is situated in Troms County, Northern Norway (Figure 2). The fjord is about 27 km long with a maximum with and depth of 3 km and 130 m respectively, and covers an area of 55 km^2. It is separated from Ullsfjord by a 300 m wide and 8 m deep sill (Eliassen and Eilertsen 1988). The fjord consists of a well mixed outer basin (max. depth 125 m) with winter and summer temperatures of 3 °C and 9 °C, a shallow mid-fjord basin of 65 m depth and an inner basin with a maximum depth of 130 m. The water column of the two latter areas is stratified during summer with water temperatures below the thermocline of 3 °C, or lower, in winter and a maximum of 6 °C in autumn (Kanapatihippillai et al. 1994).

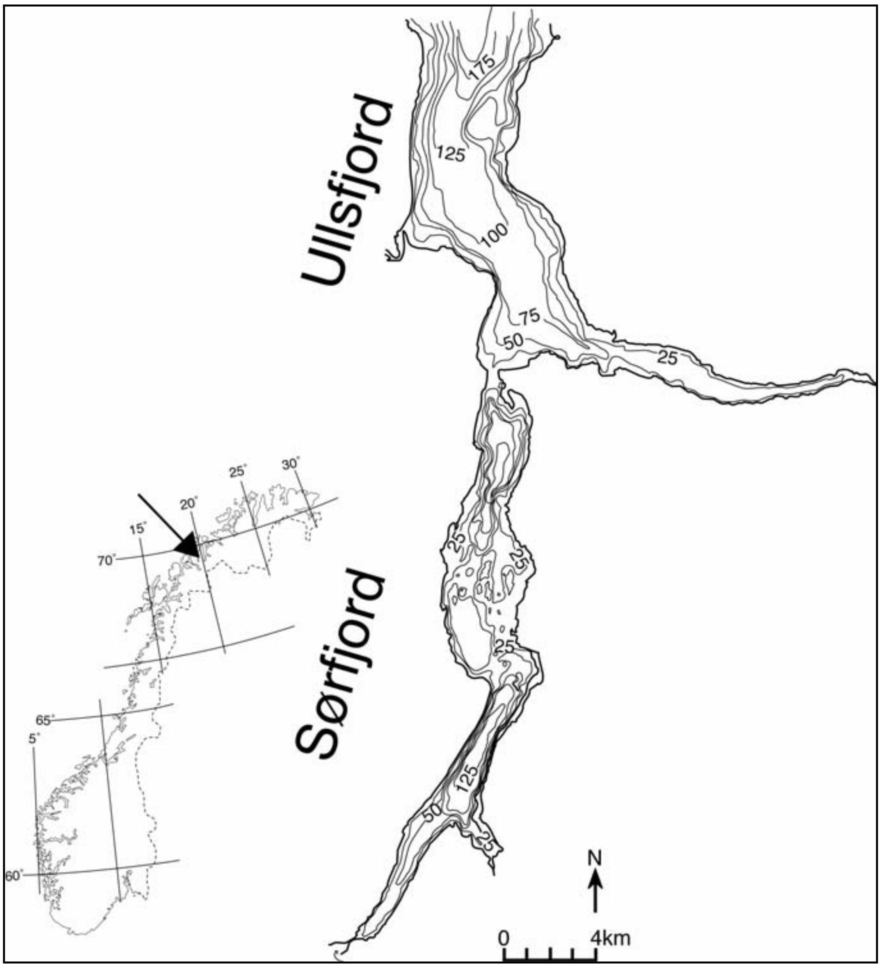

Figure 2. Map of the Sørfjord-Ullsfjord system.

2.2 CONSTRUCTION OF THE SØRFJORD MODEL WITH KING CRAB

A literature study was conducted to identify predators and prey of the king crab as well as other life history parameters relevant for the model. Three life history stages were identified: planktonic, juvenile and mature stage. The planktonic stage was omitted from the model as this stage was not included for the other groups in the Sørfjord model. In addition Ecosim does not allow for linking of more than two groups.

Two functional groups, large and small king crab, were introduced into Model I. In order to emphasise the possible trophic impacts the king crab may have on the ecosystem, their biomasses were increased to the maximum level where it could be avoided that ecotrophic efficiency (EE) of any group became larger than unity. The largest biomass of king crab obtained for the model to balance was 2.8 t/km y^{-1} and 1.2 t/km y^{-1} for large and small king crab respectively. The model was run under the assumption that the predators of king crab feed upon them according to relative biomass available. This gave very low electivity values of cod and other fish as predators on small king crab. Feeding electivity values are output of Ecopath expressing the food preference of consumers. Electivity values range from -1 (total avoidance) to 1 (exclusive feeding) (Christensen et al. 2000). The food preference of the fish groups for small king crab was much lower than for large decapods. The proportion of small king crab in the diets of these groups was therefore adjusted up so that electivity values resembled those of large decapods. When balancing the model it was noted that it was very sensitive to changes in diet input. A 0.01 increase in the proportion of large king crab in diet of large cod, for example, increased EE of large king crab about 20% from 0.512 to 0.607. The balanced Ecopath model for Sørfjord model with king crab (Model II) is shown in Table 4 and the diet matrix in Appendix B.

Table 4. Input and output parameters for Sørfjord model with king crab (Model II). Parameters summarised include trophic level as well as annual biomass, production per biomass (P/B), consumption per biomass (Q/B), ecotrophic efficiency (EE), biomass accumulation (Biomass accum.), assimilation coefficient (Assim. coef.), production per consumption (P/Q) and harvest by cod and king crab fleets. Input parameters are shown in black while values estimated by the model are marked in blue.

Group name	Trophic level	Biomass (t/kmý)	P/B (/year)	Q/B (/year)	EE	Biomass accum.	Assim. coef.	P/Q	Harvest (t/kmý)
Cormorants	4.36	0.0009	0.125	37.10	0.533	0.0	0.2	0.003	0.00006
Mammals	4.19	0.01	0.102	35.30	0.490	0.0	0.2	0.003	0.0005
Large cod	3.40	1.81	0.42	3.00	0.789	0.1	0.2	0.140	0.370
Small cod	3.41	0.14	1.70	6.00	0.333	0.0	0.2	0.283	
Large other fish	3.11	0.78	0.50	3.00	0.553	0.0	0.2	0.167	0.150
Small other fish	3.16	0.525	1.70	6.70	0.900	0.0	0.2	0.254	
Herring	3.07	0.22	1.00	6.00	0.900	0.0	0.2	0.167	
Euphausiids	2.11	4.217	2.50	16.70	0.900	0.0	0.3	0.150	
Small zooplankton	2.05	20.0	6.50	26.00	0.356	0.0	0.3	0.250	
Schypomedusae	3.10	0.72	6.50	17.33	0.133	0.0	0.2	0.375	
Chaetognaths	3.05	0.20	3.80	19.00	0.493	0.0	0.2	0.200	
Shrimp	2.59	0.178	2.00	13.30	0.900	0.0	0.2	0.150	
Other large zooplankton	2.00	0.691	2.00	13.30	0.900	0.0	0.2	0.150	
Large decapoda	2.94	0.432	0.50	3.33	0.900	0.0	0.2	0.150	
Predatory benthos	2.89	1.658	0.50	3.33	0.900	0.0	0.2	0.150	
Detrivore polychaetes	2.00	43.0	0.74	4.93	0.247	0.0	0.2	0.150	
Small benthic crustaceans	2.12	4.0	0.50	3.33	0.638	0.0	0.2	0.150	
Small molluscs	2.08	26.0	0.35	2.33	0.918	0.0	0.2	0.150	
Large bivalves	2.00	62.9	0.19	2.11	0.351	0.0	0.2	0.090	
Detrivore echinoderms	2.00	41.0	0.20	2.22	0.790	0.0	0.2	0.090	
Other benthic invertebrates	2.00	2.0	0.50	3.33	0.460	0.0	0.2	0.150	
Large king crab	3.03	2.8	0.20	3.00	0.512	0.0	0.2	0.067	0.010
Small king crab	3.04	1.2	1.00	5.00	0.459	0.0	0.2	0.200	
Phytoplankton	1.00	20.0	60.00	-	0.457	0.0		-	
Detritus	1.00	50.0	-	-	0.497			-	

A short description of the functional groups included in the Sørfjord model including king crab (Model II) follows. Details on the parameters used in the original Sørfjord model can be found in Pedersen, T., Nilsen, M., Nilssen, E.M. and Berg, E. (*unpubl.*).

1. Cormorants

Cormorants (*Phalacrocorax carbo carbo*) are not expected to feed on or be fed upon by king crab.

2. Mammals

This group includes harbour porpoises (*Phocoena phocoena*), harbour seals (*Phoca vitulina*), Eurasian otters (*Lutra lutra)* and harp seals (*Phoca groenlandica* Erxleben).

Harbour porpoises feed on pelagic or semidemersal fishes including herring, capelin, mackerel, sardines, cods and whiting (Tomilin 1967, Rae 1973). Harbor seals have been found to eat fishes, octopus and crustaceans including *Idotea baltica* spp. and *Thysanoessa* spp. (Berg et al. 2002). Pacific sea otters (*Enhydra lutris*) have been observed feeding on mature king crab (Feder and Jewett 1981, Fukuhara 1985). Harp seals feed on herring, cod and pelagic crustaceans including *Thysanoessa* spp., *Parathemisto libellula*, *Pandalus* spp., *Crangon* spp. and *Sabinea septemcarinatus* (Lindstrøm 1998, Nilssen et al. 1992, 1998). King crabs have been observed to be missing legs in areas where seals are common along the North Norwegian coast. This suggests that the king crab is subject to seal predation (Nilssen, E. Norwegian College of Fishery Science, personal communication).

The mammal group will, on the whole, be treated as feeding on large king crab. Under the assumption that king crabs are fed upon according to relative biomass, king crab proportion in the diet of mammals was put to 0.346.

3 and 4. Adult and juvenile cod

As the majority of cod preyed upon are smaller than 35cm this length was used to divide the cod group into small and large cod. Cod in Sørfjord feed on crustaceans including amphipoda and *Hyas* spp (Kanapathippillai et al. 1994). Pacific cod are important predators of soft-shell red king crab (Jewett 1978, Fukuhara 1985, Livingston et al. 1986, Livingston 1989). Smaller crustaceans have been found to be more common in small cod while cod larger than 60 cm gradually shifts to a mixed diet of larger prey, primarily fishes (Daan 1973, Livingston et al. 1986). Livingston (1989) found that cod larger than 60 cm contained whole red king crab (CL 53-160 mm) more often than cod with lengths of 30-59 cm. The percentage of weight of king crab legs in cod diet was generally less than 25%.

The adult cod group prey upon both large and small king crab, but is not preyed upon by king crab. Small cod are less than 35 cm and will have similar diet as large cod, but restricted to smaller organisms. This group is expected to prey upon small king crab.

5 and 6. Large and small other fish

This group consists of haddock (*Melanogrammus aeglefinus*), long rough dab (*Hippoglossoides platessoides*), plaice (*Pleuronectes platessa*), whitch flounder (*Glyptocephalus cynoglossus*), wolffish (*Anarhichas lupus*), redfish (*Sebastes* spp.), whiting (*Merlangius merlangius*) and saithe (*Pollachius virens*). Large and small other fish are longer and shorter than 35 cm respectively.

In this group only wolffish has been observed to feed on adult king crab in aquarium (Gerasimova 1997, personal communication Nilsen, M. Norwegian College of Fishery Science). In its native range the king crab has a number of fish predators. Yellowfin sole (*Limanda aspera*) is thought to be an important predator of zoea and megalops of king crab so are other flatfish including rock sole (*Lepidopsetta bilineata*) and flathead sole (*Hippoglossoides elassodon*). Halibut (*Hippoglossus stenolepis*), sablefish (*Anplopoma fimria*), eelpout (*Lycodes palearis*), skates (*Raja spp.*), sculpins (*Hemilepidotus hemilepidotus, Myoxocephalus spp.*), snailfish (*Liparis spp.*), sockeye salmon (*Oncorhynchus nerka*) and Walleye pollock (*Theragra chalcogramma*) are also potential predators of various stages of king crab (Gray 1964, Healey 1980, Jewett 1982, Haflinger and McRoy 1983, Wespestad et al. 1994, Loher et al. 1998). King crabs of three years and older are too large for most fish to feed on (Jewett and Powell 1981).

Capelin is one of the fish species that has been found in king crab stomachs (Feder and Jewett 1981). There is not agreement in the literature if fish found in king crab stomachs have been eaten alive or dead. Cunningham (1969) found it unlikely that food organisms had been eaten dead. This is supported by the findings of Logvinovich (1945, as in

Cunningham) who rejected that the crabs are scavengers as they did not accept putrefied food organisms during laboratory experiments. McLaughlin and Herbard (1961), on the other hand, found decomposed organisms in crab stomachs indicating that crabs had been feeding upon dead material. Stone et al. (1993) discovered that individual king crabs periodically returned to a cleaning station for local fishermen in Auke Bay. They suggested that the crabs were attracted to this location by the periodic disposal of offal. The crab has also been observed feeding on carcasses of fish (Zhou and Shirley 1997). Bright (1967) fed king crab dead flounder, but the crab did not attempt to catch live fish. Fish is also used successfully as bait in king crab pots.

As a group the "other fish" are likely to prey upon king crab. Large king crab will only be fed upon by large other fish. Due to the relatively high mobility of fish the king crab will not be feeding on fish in the model.

7. Herring

Herring (*Glupea harengus*) may feed on planktonic king crab larvae, but in this model the larval stage of the king crab is excluded.

8. Euphausiids

Thysanoessa inermis and *Thysanoessa raschii* are the main euphausiid species found in Sørfjord. Prey found in the stomach of king crab zoeae captured in nature includes diatoms, barnacle nauplii and crab larvae (Bright 1967). Early life stages of the euphausiid group are likely to be preyed upon by king crab larvae, but in the model the larvae stage is excluded.

9. Small zooplankton

Small zooplankton (<8 mm) are mainly herbivorous copepods, cladocera, ciliates, rotifers and appendicularians. Copepods and copepodids have been used as food in experiments with king crab zoeae. At sufficiently high concentrations the zoeae will consume up to 12 copepods per day (Paul et al. 1979). Copepods have been found in adult king crab stomachs (Jewett and Feder 1982, Jewett et al. 1989). In the model there will be no direct interaction between king crab and small zooplankton as the king crab larvae stage is ignored and the findings of copepods in the adult is not considered significant.

10. Schypomedusae

The common schypomedusae in Sørfjord are *Cyanea capillata* and *Aurelia aurita*. Jellyfish could be eating planktonic king crab stages. Coelenterates have been found in adult king crab stomachs (Tarverdieva 1976, 1979, Feder and Paul 1980, Feder et al. 1980, Jewett et al. 1989, Rafter 1996, Gerasimova 1997). The stage of the coelenterates found is not specified. Assuming the crab feed on the bottom living stage the schypomedusae group will not prey or get preyed on by the king crab stages in this model.

11. Chaetognaths

The dominating species is the carnivorous *Sagiita elegans* that could feed on planktonic king crab. In the model this group will not interact directly with king crab.

12. Shrimp

Pandalus borealis is the dominant species, while *Eualus gaimardii, Eualus pusiolus, Spirontocaris spinus, Pontophilus norvegicus, Crangon crangon* and *Pandalus montagui* are also present. Pandalus spp. have been found in king crab stomachs (Feder and Paul 1980, Jewett and Feder 1982), but due to their mobility they are unlikely to be important prey of king crab.

13. Other large zooplankton

This group consists of zooplankton larger than 8 mm and include pelagic amphipods, mysidae and pelagic polychaetes. These could prey and get preyed upon by larval king crab, but feeding interaction with the king crab groups in the model is unlikely.

14. Large decapods

This group is made up by Brachyurans, mainly *Hyas areneus*, *Hyas coarctatus* and *Carcinus maenas*, and Anomurans, which include hermit crabs and *Munida* spp. Crustaceans of this category are found in king crab stomachs (McLaughlin and Hebard

1961, Tarverdieva 1979, Feder et al. 1980, Feder and Paul 1980, Jewett and Feder 1982, Jewett et al. 1989, Rafter 1996, Gerasimova 1997).

15. Predatory benthos

Predatory molluscs and asteroids, Actinaria and free living errante polychaetes are included in predatory benthos.

16. Detrivore polychaeta

Important taxa in this group are Terebellidae and Flabelligerida. They are sedentary polychaetes that feed on detritus.

17. Small benthic crustaceans

Amphipods, mysiids, cumaceans and other hyperbenthic groups are included in this group. Due to their small size they will not feed on king crab in the model.

18. Small mollusca

This group of detrivores and herbivores includes gastropoda, polyplachophora, small bivalves and scaphopoda.

19. Large bivalves

Large bivalves are large, long lived animals with low mortality rates. Species included are *Artica islandica*, *Musculus niger* and *Chlamys islandica*.

20. Detrivore echinoderms

Detrivore echinoderms are largely made up by *Ctenodiscus crispatus*, but also *Ophiopholis aculeate* and *Ophiura* species.

21. Other benthic invertebrates

This group comprises Priapulidae, Hirudinea, Pycnogonidae, Brachiopoda, Ascidia and sea urchins (Echinodea).

22 and 23. Large and small king crabs

Large king crabs are crabs of 5 years and older while small king crabs are younger than 5 years old. At 5 years they are about 100 mm carapace length (CL) and have attained sexual maturity (Powell and Nickerson 1965a, Otto et al. 1989, Rafter 1996). At this stage it is assumed that the predator prey relationship of the king crab changes due to the size attained as well as change in habitat. It is also assumed that the diet and mortality rate does not differ between the sexes. Relative proportion of small to large crabs was calculated to 30:70 based on length and age data on king crab from Varanger fjord and literature study (Nilssen and Sundet *in prep.*). Calculations are shown in Appendix C.

Production per biomass (P/B) for king crab

The P/B values used in other models for king crab or groups comparable to king crab show great variations.

Bundy et al. (2000) used a P/B of 0.282 yr^{-1} for large crustaceans in an Ecopath model of the Newfoundland-Labrador Shelf. This value was estimated from catch and biomass data on American lobster, snow crab and various non-commercial species. In the Ecopath model of the Northern Gulf of St. Lawrence P/B for snow crab is 0.251 yr^{-1} and takes into account the high mortality of young and low mortality of old males (Morisette 2001). P/B values for various crabs in a study conducted in Chile ranged from 0.5 yr^{-1} to 1.95 yr^{-1} (Ortiz and Wolff 2002). A P/B of 0.6 yr^{-1} for king crab in the Eastern Bering Sea was suggested in Trites et al. (1999), while snow and tanner crabs were given P/B of 1 yr^{-1}. All P/B values were based on the Tanner crab (Paul and Fuji 1989).

P/B as estimated by the model of Brey (1999) for small and large king crab was calculated to 0.232 yr^{-1} and 0.114 yr^{-1} at 5°C. The value for small king crab is quite low both compared to the P/B of large decapods in the Sørfjord model and to the other values found in the literature for crab.

Based on the information listed above a P/B value of 1 yr^{-1} was chosen for small king crab and 0.2 yr^{-1} for large king crab.

Consumption per biomass (Q/B) for king crab

Q/B values for various crabs in a Chilean Ecopath model range from 4.5 yr^{-1} to 9.9 yr^{-1} (Ortiz and Wolff 2002). Morisette (2001) used a value for snow crab of 1.3, while Bundy et al. (2000) used a value of 5.9 for lobsters.

Based on daily ration of adult male king crab (mean weight 2144 g) of 0.31% of their body weight (Tarvierdieva 1979) a Q/B of 1.132 yr^{-1} was calculated. Gerasimova (1997) collected information from Russian studies of food digestion and diurnal ration of king crab. A crab of 362 g has a daily ration of 1.5% of body weight giving a Q/B of [(5.43/362)*365] 5.48 yr^{-1}. A crab of 2710 g has a daily ration of 0.32% of body weight resulting in Q/B of 1.17 yr^{-1}, while crab of 4091 g of daily ration 0.15 yr^{-1} has a Q/B of 0.54 yr^{-1}.

Q/B values calculated based on a feeding and growth study of king crab by Zhou et al. (1998) were significantly higher than values found in other literature. They were as follows:

Ovigerous females of about 1000 g: (59.25 g food/1000 g crab)*365 days = 21.63 yr^{-1}.
Juvenile females of about 530 g: (31.5 g food/530 g crab)*365 days = 21.7 yr^{-1}.
Males of about 900g: (50.85 g food/900 g crab)*365days = 20.62 yr^{-1}.

A rearing study by Rice et al. (1985) found juvenile crabs (3-4 cm CL) to consume 0.011 g herring per day per gram crab. This gives a Q/B value of (0.011*365) 4.015 yr^{-1}. Feeding rate of 6.3 mm (±0.1 mm SE) king crabs was found to be 0.081 g (±0.0076 g SE) per day per gram crab in experiments by Molyneaux and Shirley (1988), giving a Q/B of (0.081*365) 29.565 yr^{-1}.

The Q/B for king crab in Aydin et al. (2002) was 5 yr^{-1} in Eastern Bering Sea and is based on Trites et al. (1999) whose value is based on Tanner crab. An estimate of Q/B in the Western Bering Sea, on the other hand, is based on adult king crab (>80 mm CL) and has a value of 2.27 yr^{-1}. Juvenile king crab (40-80 mm CL) Q/B has been estimated to range from

3.5-5.0 yr^{-1}. The range is due to seasonal study differences (Aydin et al. 2002, Aydin, K.Y., Alaska Fisheries Science Center, personal communication).

Based on the literature study a Q/B value of 3 yr^{-1} for large king crab and 5 yr^{-1} for small king crab were chosen.

Predators and prey of king crab

The literature study revealed that king crab feed on a wide range of organisms (Table 1) and was used to determine prey groups of king crab in the Sørfjord model. An overview of the functional groups of Model II that the king crab feed or get fed upon is shown in Table 5. Cannibalism within small king crabs has been documented by Rounds et al. (1989) and Damsgård et al. (1997). Large king crabs in Norwegian waters have been found to contain juvenile king crabs (Haugan, T.A. Norwegian College of Fishery Science, personal communication).

The diet of the king crab has been suggested to reflect prey availability (Takeuchi 1959, Feder and Paul 1980). In the model it was assumed that the proportion of prey in diet of king crab is reflected by the relative availability, in terms of biomass, of the respective prey groups it feeds on. The proportion of king crab in the diets of its predators was put equal to relative biomass availability of king crab. The diets were then scaled to one.

24. Phytoplankton

Diatoms dominate during the spring bloom, while there is a low abundance of dinoflagellates and coccolithophorids in Sørfjord. Diatoms are an important energy source for stage one king crab zoeae (Bright 1967, Paul et al. 1989). Silicoflagellates have been found in juvenile king crab (Feder et al. 1980).

25. Detritus

This group consists of dead organic material as well as bacteria. The king crab is expected to eat detritus when feeding by scooping up and filtering material. Since the model primarily is used to explore potential predator-prey relationships of the king crab, the crab will not be feeding on detritus in this model.

Table 5. Predators and prey of small and large king crab in Model II.

Groups	Prey of small king crab	Prey of large king crab	Predators of small king crab	Predators of large king crab
Cormorants				
Mammals				+
Large cod			+	+
Small cod			+	
Large other fish			+	+
Small other fish			+	
Herring				
Euphausiids				
Small zooplankton				
Schypomedusae				
Chaetognaths				
Shrimp				
Other large zooplankton				
Large decapoda	+	+	+	
Predatory benthos	+	+		
Detrivore polychaetes	+	+		
Small benthic crustaceans	+	+		
Small molluscs	+	+		
Large bivalves		+		
Detrivore echinoderms	+	+		
Other benthic invertebrates	+	+		
Juvenile king crab			+	
Adult king crab	+	+	+	
Phytoplankton				
Detritus				

2.3 ECOPATH OUTPUT ANALYSIS

Biomass, ecotrophic efficiency and predation mortality rate for the various groups in Model I and Model II were compared. Predator and prey overlap matrixes of Model II were made into a similarity tree using an unweighted arithmetic average clustering analysis in SYSTAT (version 10.2). The mixed trophic impact analysis summarises the direct and indirect impacts of predation and competition on groups in the model. The matrix shows how an increase in the biomass of one group affects the biomass of another group. The mixed trophic impact routine was run for Model II. A sensitivity analysis included in

Ecopath was run on Model II to test what effect a change in basic input parameters have on the output parameters for each group.

2.4 ECOSIM MODEL INPUTS

Small and large cod, small and large other fish and small and large king crab were linked. The default values were kept for minimum and maximum time as juvenile, recruitment power parameter, base fraction of food intake used for reproduction and fraction of increase in food intake used for growth. The default assumption that feeding time can at the most double was kept. Unless stated the default values of the software were chosen for the other parameters of the model.

Age at transition to adult group (>35cm) for cod was set to 4 years (Berg and Pedersen 2001). A curvature parameter (K) of the von Bertalanffy growth function (VBGF) of 0.14 yr^{-1} was used based on Berg and Pedersen (2001). An equation for weight at age by Brander (1995) was used to estimate average adult weight (2.92 kg for 6 year olds) and weight at transition (1.53 for 4 year olds) assuming a temperature of 5 °C. The ratio of average adult weight to weight at transition was calculated to 1.91.

For the other fish group, data on the female long rough dab (*Hippoglossoides platessoides*) in Storura, Sørfjord, were used (Mikalsen 1995). The ratio of average adult weight (about 340 g for 13 year olds)/ weight at transition (about 180 g for 9 year olds) was calculated to 1.89. K of the VBGF is 0.119 yr^{-1}. Age at transition to adult was 9 years for long rough dab. This was not considered representative of the group as it includes many short lived species. An age of transition of 4 was therefore chosen.

Age of transition to adult group for king crab was 5. The ratio of average adult weight/weight at transition and K of the VBGF was calculated from king crab data from Varanger fjord to be 4.11 yr^{-1} and 0.133 respectively (Appendix C).

2.5 ECOSIM MODEL RUNS

The Ecosim models with king crab were run for different scenarios for up to 100 years. A change in fishing effort was kept constantly high until most of the parameters were relatively stable. Fishing mortality rate is a product of catchability times fishing effort. The default value in Ecosim of density independent catchability was kept. A change in fishing effort therefore resulted in an equivalent change in fishing mortality. The following scenarios were run:

II A. To investigate the effects of fishing out large king crab, fishing effort was increased 300 fold from year 10 until year 70. Initial fishing mortality of large king crab was 0.004 yr^{-1} and increased to 1.2 yr^{-1} when fishing effort was increased.

II B. Effects of increasing outtake of large cod and large other fish was investigated. A 3 fold increase in cod fishery from year 10 to year 80 increased fishing mortality of cod from 0.204 yr^{-1} to 0.612 yr^{-1}. Fishing mortality of large other fish increased from 0.192 $yr^{-1}$to 0.576 yr^{-1}. The bycatch of cormorants and mammals in the cod fishery resulted in an increase in fishing mortality for these groups from 0.067 yr^{-1} and 0.05 yr^{-1} to 0.201 yr^{-1} and 0.15 yr^{-1} respectively.

II Ba. Run II B was repeated excluding bycatch of mammals to see if changes in Model II B could be attributed to increased fishing mortality of mammals.

II C. The effects of an increase in king crab biomass was investigated. A scenario with high initial fishing mortality for small (0.5 yr^{-1}) and for large (0.1 yr^{-1}) king crab with a fishery of 0.28 t km^{-2} yr^{-1} for small and 0.6 t km^{-2} yr^{-1} large king crab. The system was run for 80 years with a complete stop in fishery from year 10 to 60. This scenario was investigated further to look at mechanisms behind king crab biomass changes. Relative change in total mortality and predation mortality rate, feeding time and consume per biomass as well as change in predator and prey composition with variation in king crab abundance were investigated.

II D. Ecosim assumes that the biomasses of the groups in the system are determined by a mix of bottom-up and top-down control with a default vulnerability parameter of 0.3. The vulnerability parameter of Ecosim is determined by the trade off between searching for prey and being exposed to predators. A number of factors affect the vulnerability parameter including risk sensitive behaviour of predators and prey, the availability of refuge, size of prey and mobility (Christensen et al. 2000, Ecopath with Ecosim Version 5 help guide). Some of the groups in the Sørfjord system are not expected to seek refuge. The effect of increased predator control of the less mobile groups was therefore explored. A vulnerability of 1 to king crab predation was set for predatory benthos, large bivalves and detrivore echinoderms.

A schematic presentation of the Ecopath and Ecosim scenarios analysed is shown in figure 3.

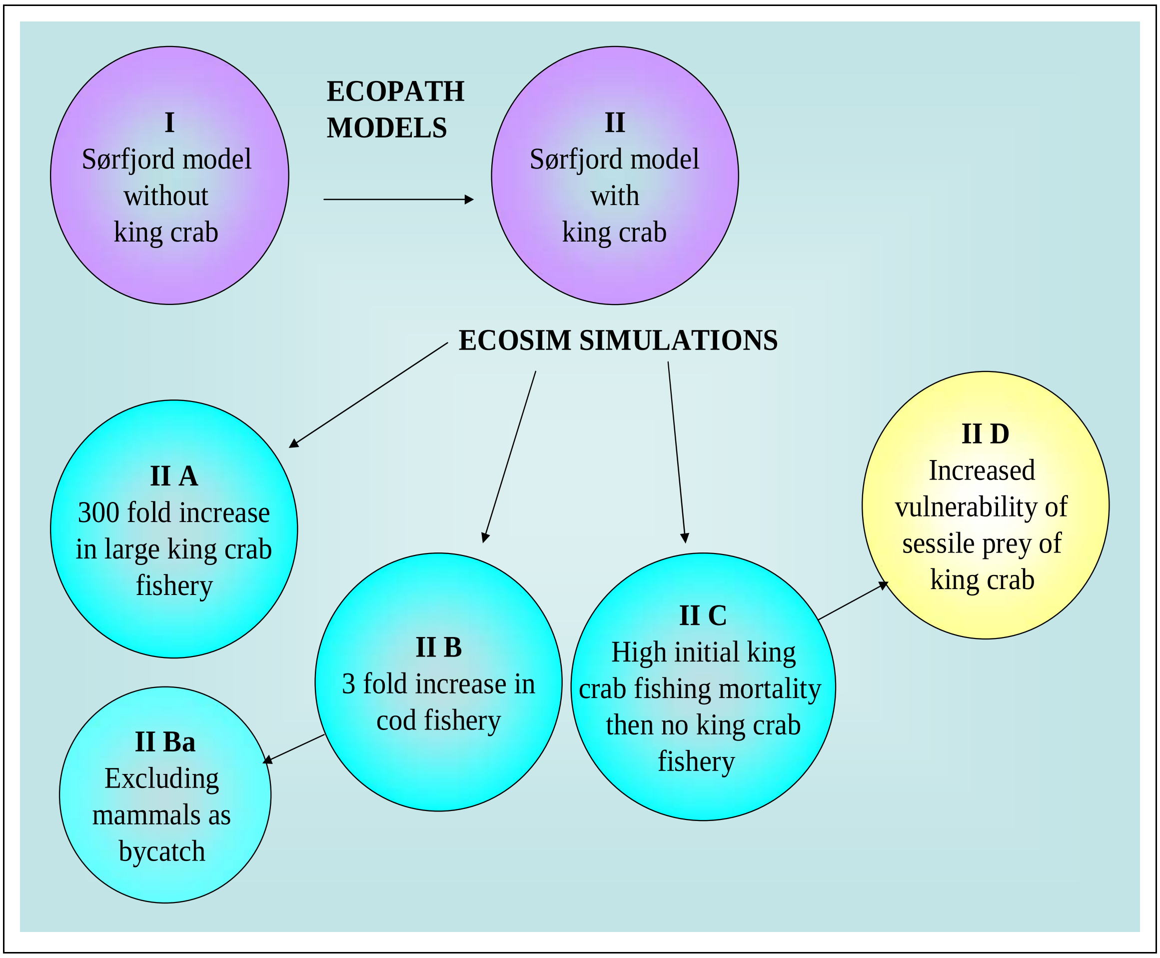

Figure 3. Ecopath and Ecosim scenarios analysed.

3. RESULTS

3.1 ECOPATH MODEL OUTPUTS

Ecopath model outputs for Model I and Model II is shown in Table 3 and 4 in chapter 2.1 and 2.2. Large and small king crabs have a trophic level of 3.03 and 3.04 respectively. Ecotrophic efficiency (EE) of small king crab is lower than large decapoda, a group small king crabs could be expected to share many features with.

With introduction of king crab into Model I follows an increase in biomass estimates of large decapods and predatory benthos, while small other fish, euphausiids, shrimp and other large zooplankton biomasses decrease. EE of detrivore polychaetes, small benthic crustaceans, small molluscs, large bivalves, detrivore echinoderms and other benthic invertebrates increase significantly when king crab is introduced to the system. Large other fish and the cod groups show a decline in EE (Figure 4). Alternative Ecopath model estimate putting biomass of large decapods and predatory benthos constant gave EEs that exceeded unity for these groups.

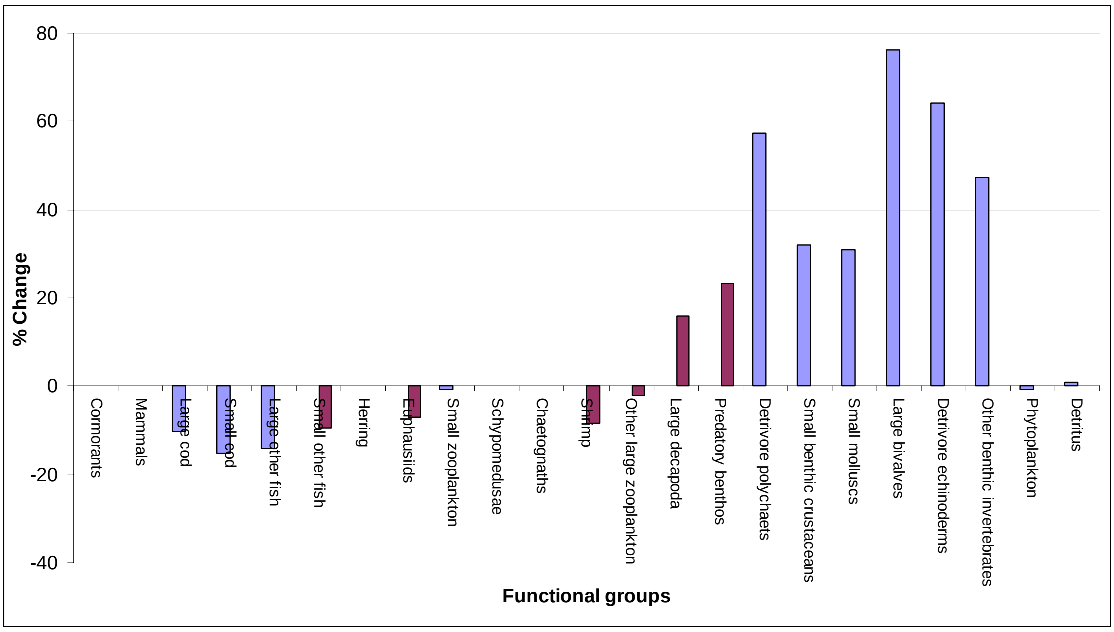

Figure 4: Percentage change in ecotrophic efficiency (blue) and biomass (red) with king crab introduced to Model I.

The benthic groups whose ecotrophic efficiencies were calculated by the model show a large increase in predation mortality rate with introduction of king crab. The mortality rate of large bivalves increased by over 300%, while the mortality rate of detrivore polychaetes and detrivore echinoderms increased by over 100%. The same benthic groups whose predation mortality increased showed a decrease in other mortality rate. Large and small cod and large other fish show a decrease in predation mortality rate and an increase in other mortality rate (Figure 5).

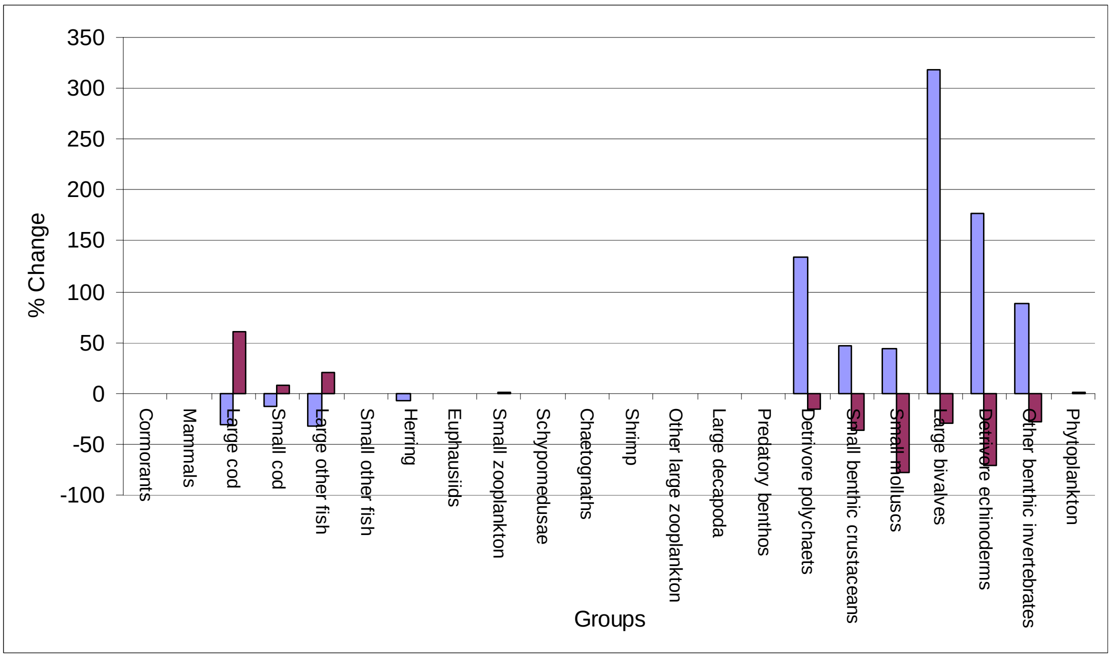

Figure 5: Percentage change in predation mortality (blue) and other mortality (red) with king crab introduced into Model I.

The percentage predation mortality rate caused by king crab on their prey in Model II is shown in Figure 6. King crab causes almost 70% of the predation mortality rate of large bivalves and over half of the predation mortality rate of detrivore echinoderms and detrivore polychaetes.

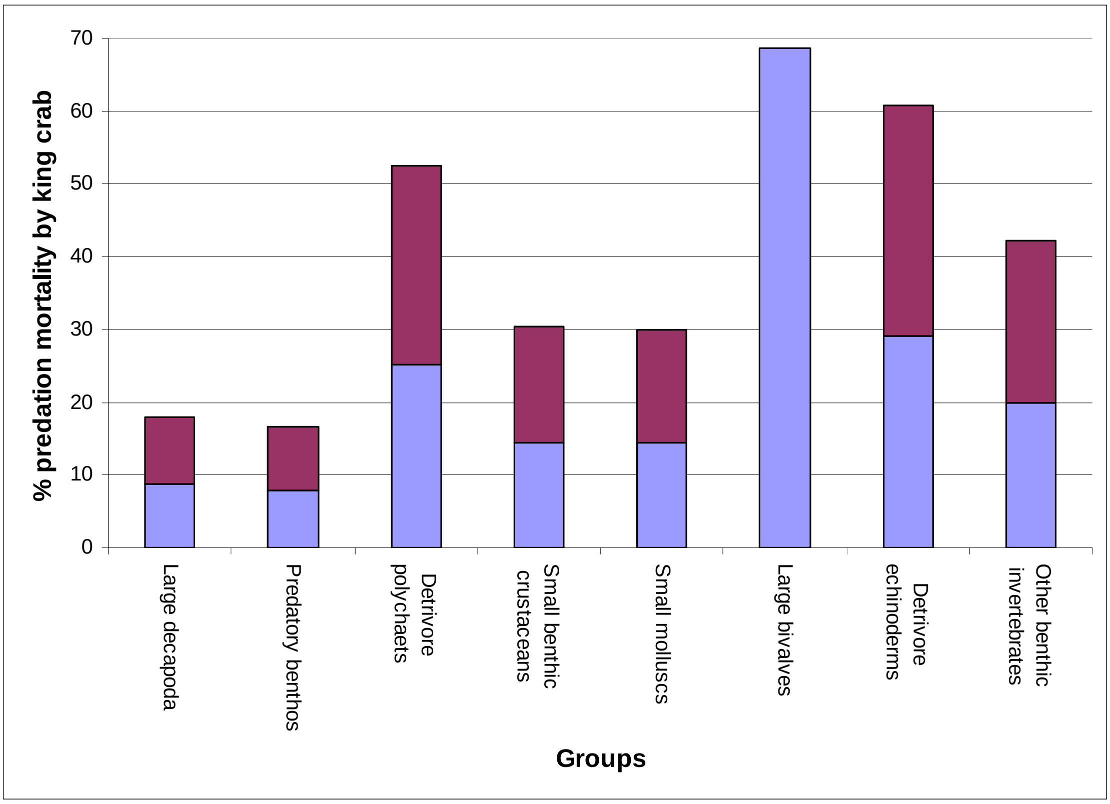

Figure 6: Proportion of predation mortality rate caused by small king crab (red) and large king crab (blue) on their prey groups in Model II.

Predation mortality rates of prey of mammals, cod and other fish is generally reduced when king crab is introduced into Model I. Prey of large decapods and predatory benthos experienced an increase in predation mortality rate. The biomasses of these two groups were estimated by the model. Predation mortality rates in Model I and II are shown in Table 1D and 2D in appendix D.

Small and large king crabs have the largest prey overlap with large decapods and predator benthos. The cod and other fish groups have some similarity in diet to king crab (Figure 7). Large king crab have similar predators, or source of predation mortality, to large other fish and large cod. Small king crab have similar predators to large decapods, herring, small other fish and small cod (Figure 8).

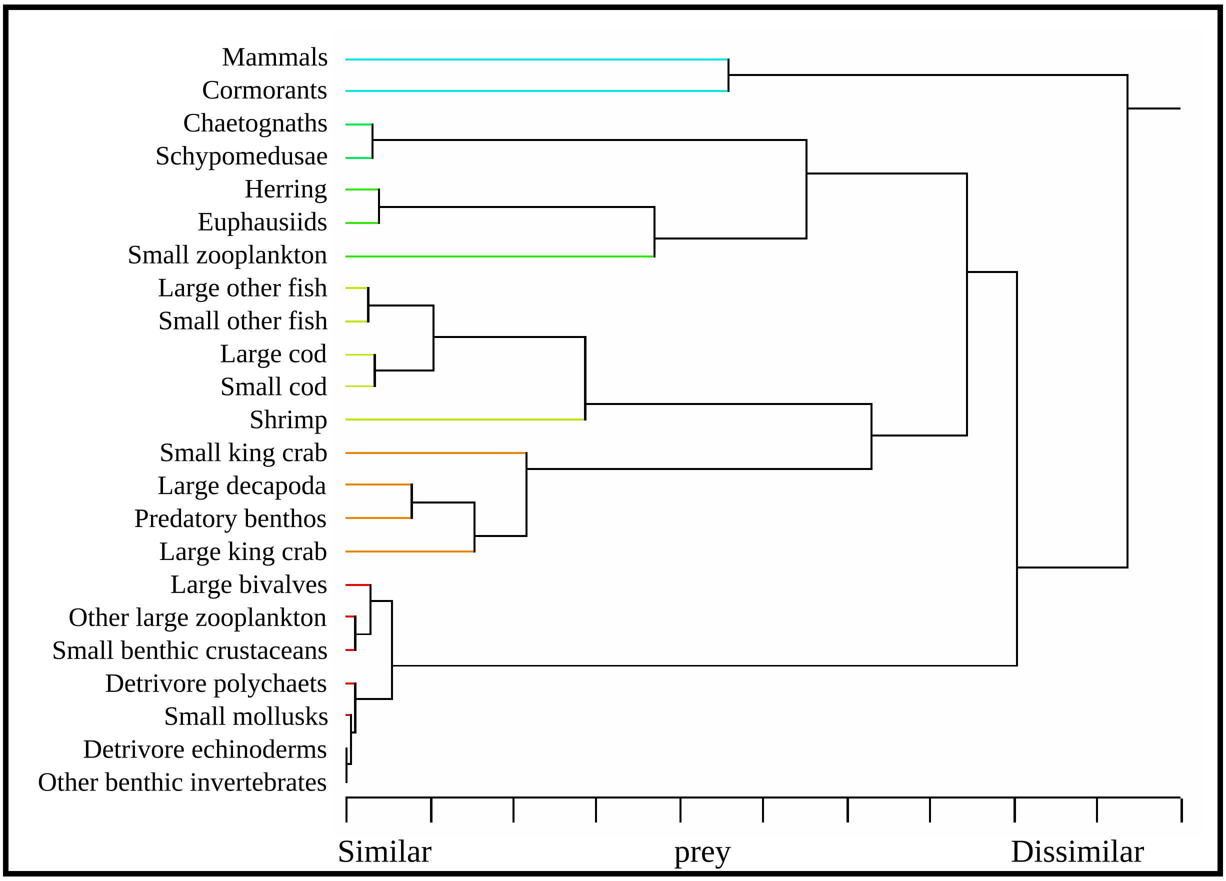

Figure 7. Cladogram of prey overlap for Sørfjord model II.

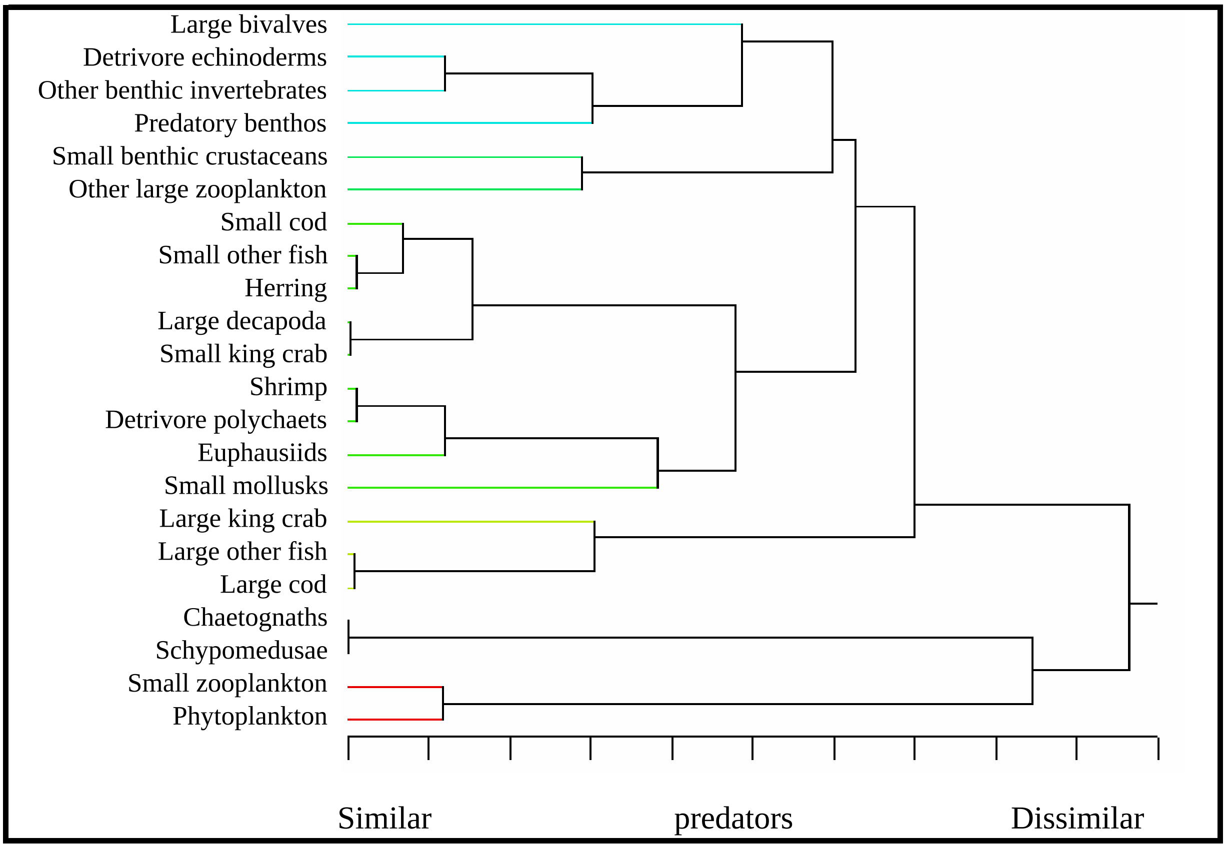

Figure 8. Cladogram of predator overlap for Sørfjord model II.

3.1.1 Mixed trophic impact analysis

The mixed trophic impact analysis of Model II is shown in Appendix E. The major groups impacted will be listed in decreasing order. Generally it can be seen that the pelagic groups will have the most impact on other pelagic groups and the benthic groups the most impact on other benthic groups.

An increase in large king crab biomass has a positive impact on the biomass of mammals, while they have little and no impact on their other predators large other fish and large cod. They have a negative impact on themselves and large bivalves and a small negative impact on large decapods, predatory benthos, small king crab and detrivore echinoderms. The direct negative impact on prey is outweighed by the indirect positive impact large king crabs have on small benthic crustaceans, small molluscs and other benthic invertebrates.

Small king crabs have a negative impact on themselves, detrivore echinoderms, large decapods and detrivore polychaetes.

Mammals have the largest negative impact on large king crab. Large cod and large other fish have a negative impact on the biomass of mammals. Large other fish and large cod, euphausiids and small king crabs have minor negative impacts on large king crab. Large bivalves have a positive impact on large king crab. Groups having negative impacts on small king crab include themselves, large cod, euphausiids, small other fish and large king crab, while detrivore echinoderms, mammals and detrivore polychaetes have a positive impact on small king crab.

3.1.2 Sensitivity analysis

The sensitivity analysis calculates the impact a ±50% change in input parameters will have on the estimated parameters of the other groups in the system. The output of the sensitivity analysis for Model II is shown in Appendix F. In general the model is quite insensitive to changes in input parameters and a change in a group’s input parameter is mainly reflected in output of the same group. EE of large king crab is the most sensitive to large king crab biomass followed by the EE of large bivalves (Figure 9). Large bivalves are the most sensitive to variations in king crab consume per biomass input (Figure 10).

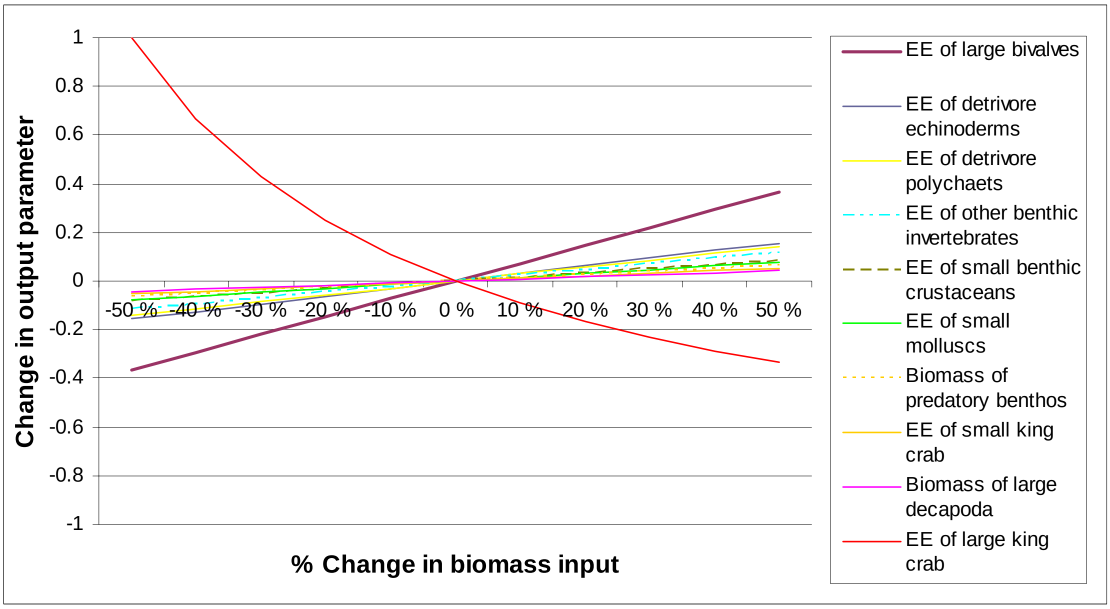

Figure 9. Sensitivity of ecotrophic efficiency (EE) and biomass output to large king crab biomass input shown as percentage change of biomass input.

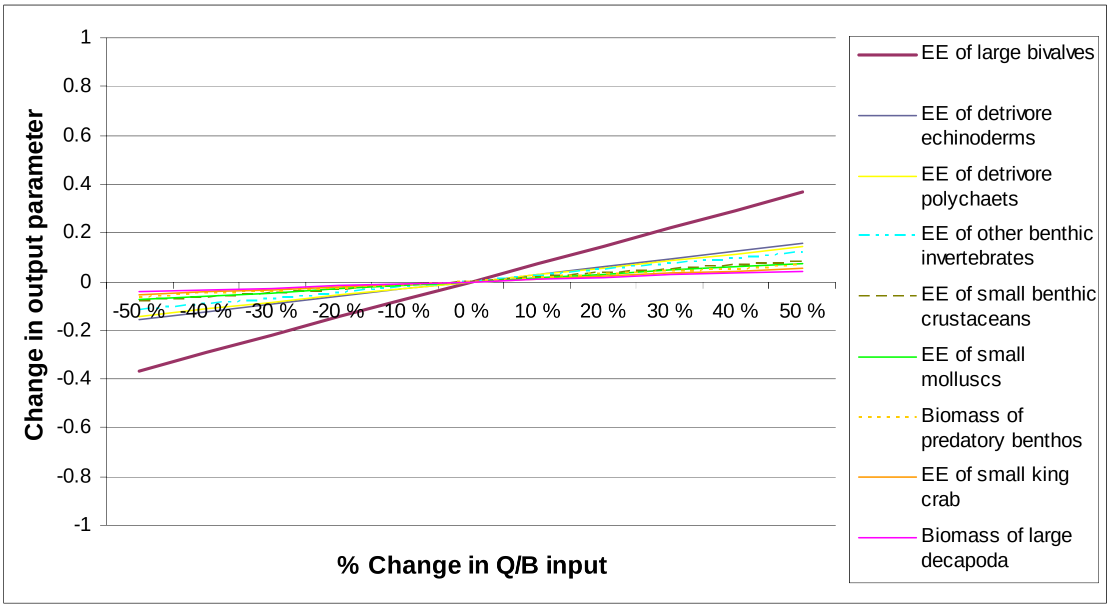

Figure 10. Sensitivity of ecotrophic efficiency (EE) and biomass output to large king crab consume per biomass (Q/B) input shown as percentage change of Q/B input.

Small king crab EE is sensitive their own biomass input. The other benthic groups are insensitive to small king crab biomass input (Figure 11). None of the groups are sensitive to consume per biomass input of small king crab (Figure 12).

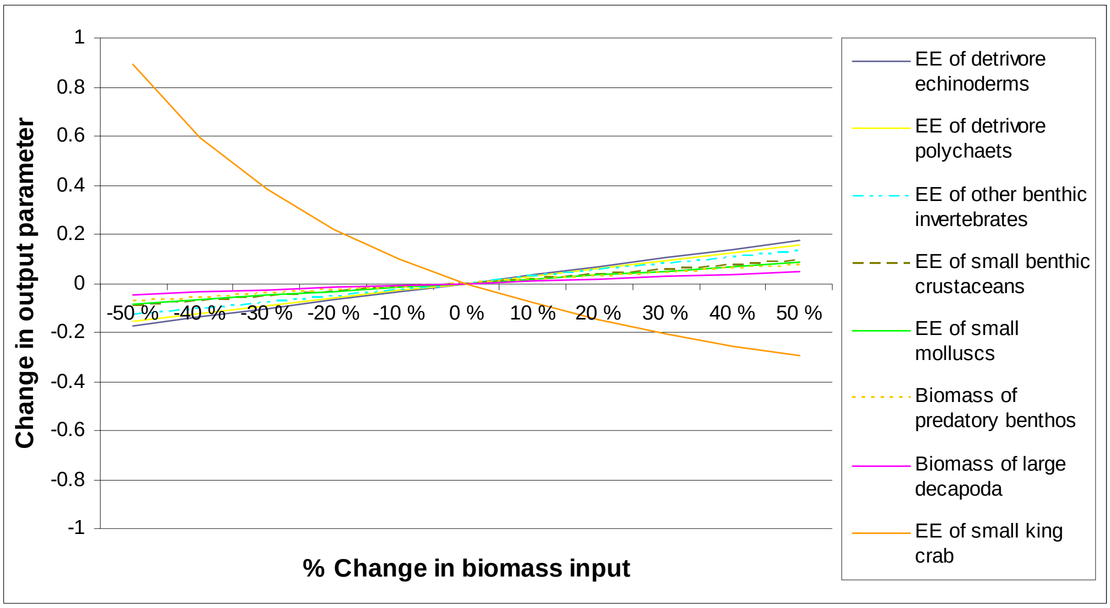

Figure 11. Sensitivity of ecotrophic efficiency (EE) and biomass (Biom) to small king crab biomass input shown as percentage change of biomass input.

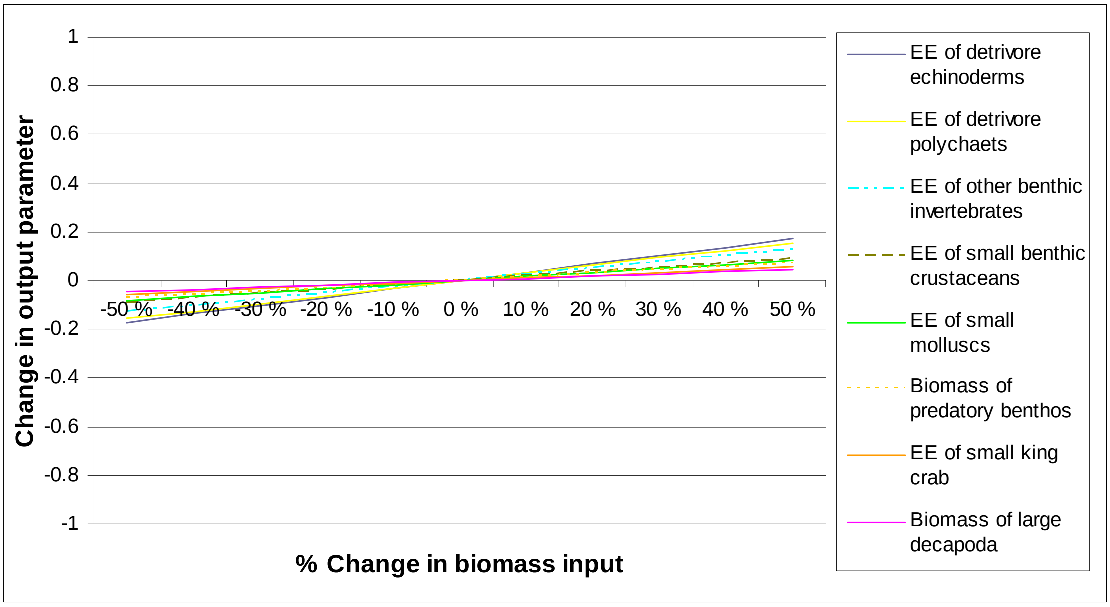

Figure 12. Sensitivity of ecotrophic efficiency (EE) and biomass (Biom) to small king crab consume per biomass (Q/B) input shown as percentage change of Q/B input.

A ±50% change in biomass and Q/B input of mammals gives a sensitivity of ±0.213 of EE output of large king crab. Large cod biomass and Q/B input gives a sensitivity of ±0.188 and ±0.305 for ±50% change in EE output for large and small king crab respectively. Small cod inputs do not have large impacts on small king crab EE outputs. Large king crab is not sensitive to biomass and Q/B inputs of large other fish. A ±50% change in P/B or EE inputs of small other fish has an effect on small king crab EE of ±0.159. Q/B of small other fish has little impact on the EE output of small king crab (Appendix F).

3.2 ECOSIM ANALYSIS

3.2.1 Run II A

When king crab fishing effort was increased heavily in run II A the biomasses of large and small king crab as well as mammals declined. There is an increase in other fish, cormorants and the benthic groups except from detrivore polychaetes (Figure 13 and 14). Large cod declines initially, but stabilises on a slightly higher biomass level, while small cod remains fairly stable. The herring group drops before fishery manipulations starts in all simulations .

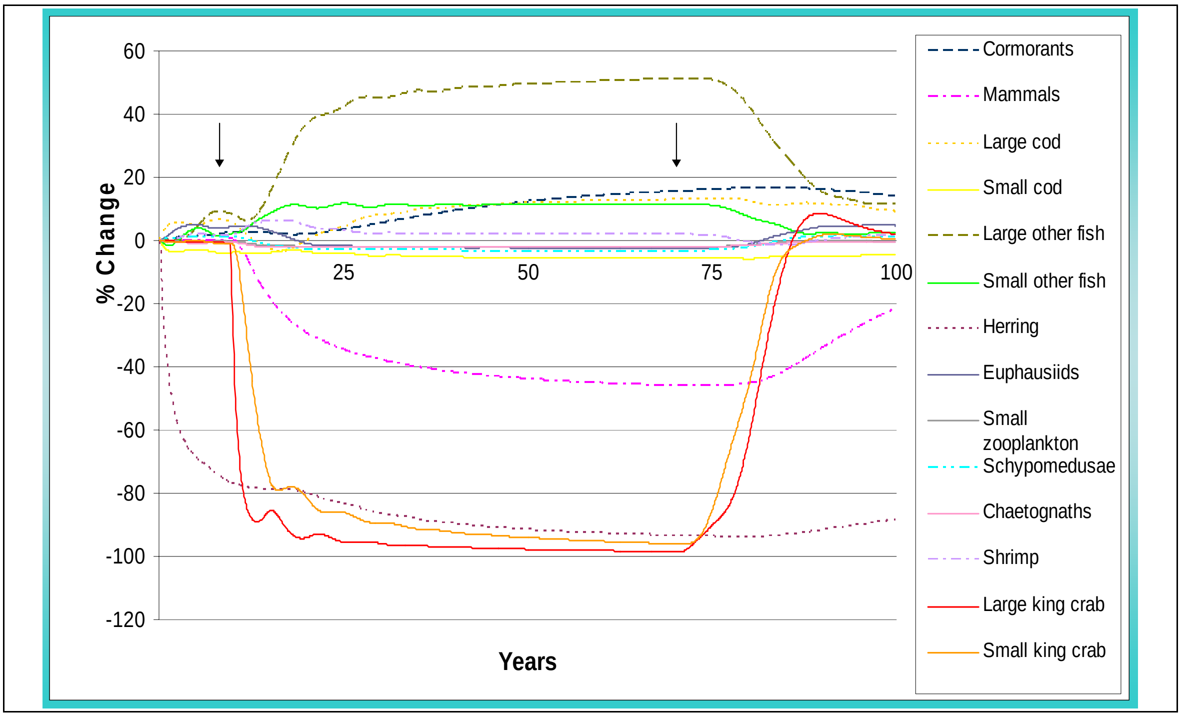

Figure 13. Run II A. Relative change in percentage of original biomass with an increase in fishing mortality rate of large king crab from 0.0004 yr^{-1} to 1.2 yr^{-1}. Start and stop of king crab fishery is marked with arrows.

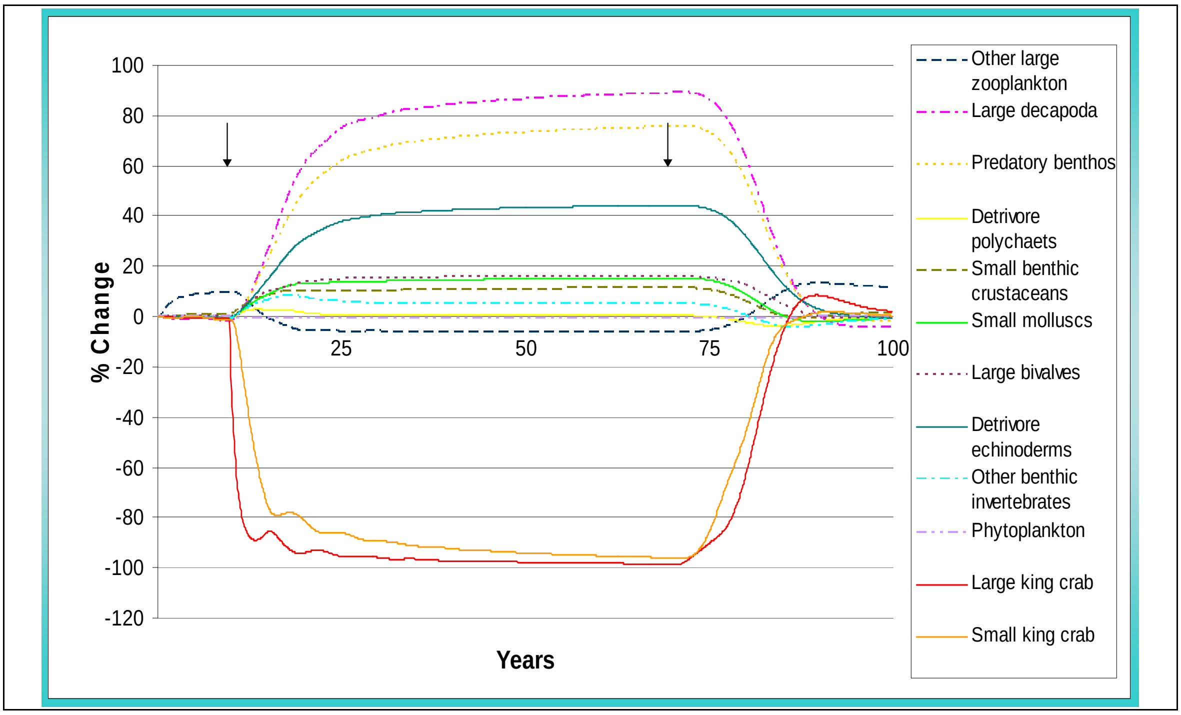

Figure 14. Run II A. Relative change in percentage of original biomass with an increase in fishing mortality rate of large king crab from 0.0004 yr^{-1} to 1.2 yr^{-1}. Start and stop of king crab fishery is marked with arrows.

3.2.2 Run II B

Increasing fishing effort of cod in simulation II B caused initial fluctuations of the biomasses in the system that levelled out over time. The biomasses of target groups for the fishery, large cod and large other fish, decreases but stabilise rapidly (Figure 15). Large king crab biomass increases by up to 15% over the time period of increased cod fishery, while small king crab only shows a small biomass increase. Mammal and cormorant biomasses decline significantly with increased cod fishery (Figure 15). There is a slight decline in the biomasses of predatory benthos, detrivore echinoderms and large decapoda (Figure 16).

Simulation II Ba excluding mammals as bycatch caused an increase in mammal biomass. Decreased cod abundance caused mammals to switch to large king crab whose biomass remained relatively unchanged.

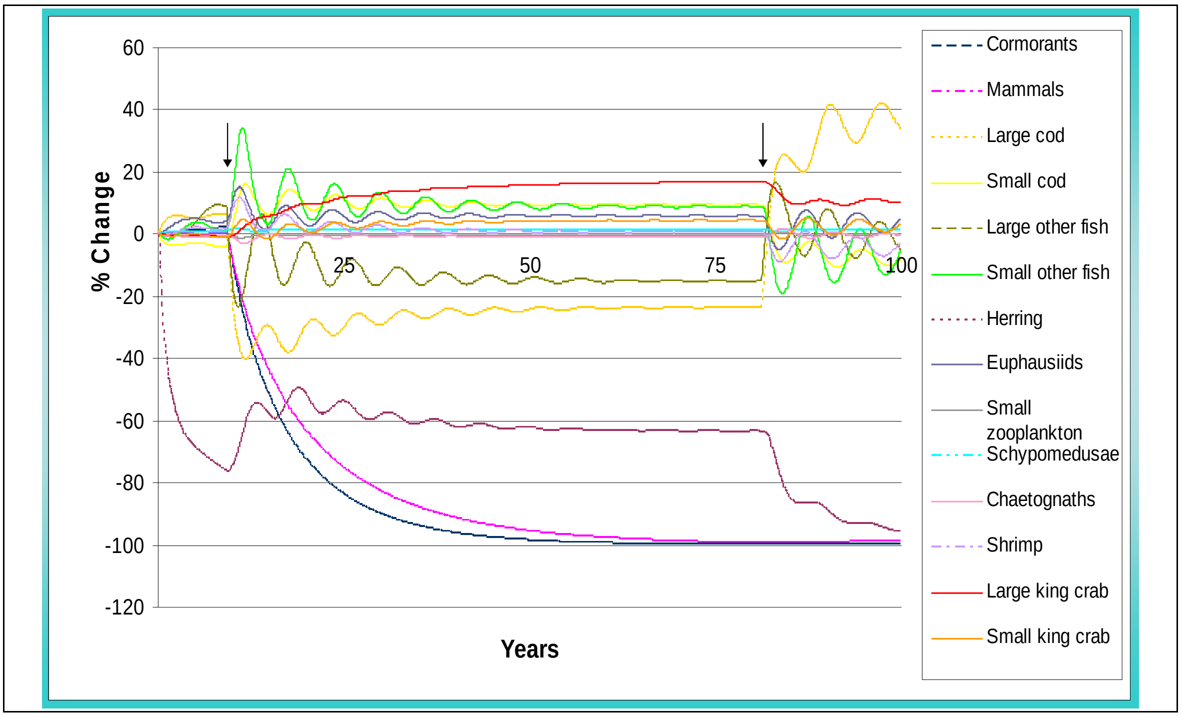

Figure 15. Run II B. Relative change in percentage of original biomass with increased fishing mortality rate of cod from 0.204 yr^{-1} to 0.612 yr^{-1} and large other fish from 0.192 yr^{-1} to 0.576 yr^{-1}. Start and stop of cod fishery is marked with arrows.

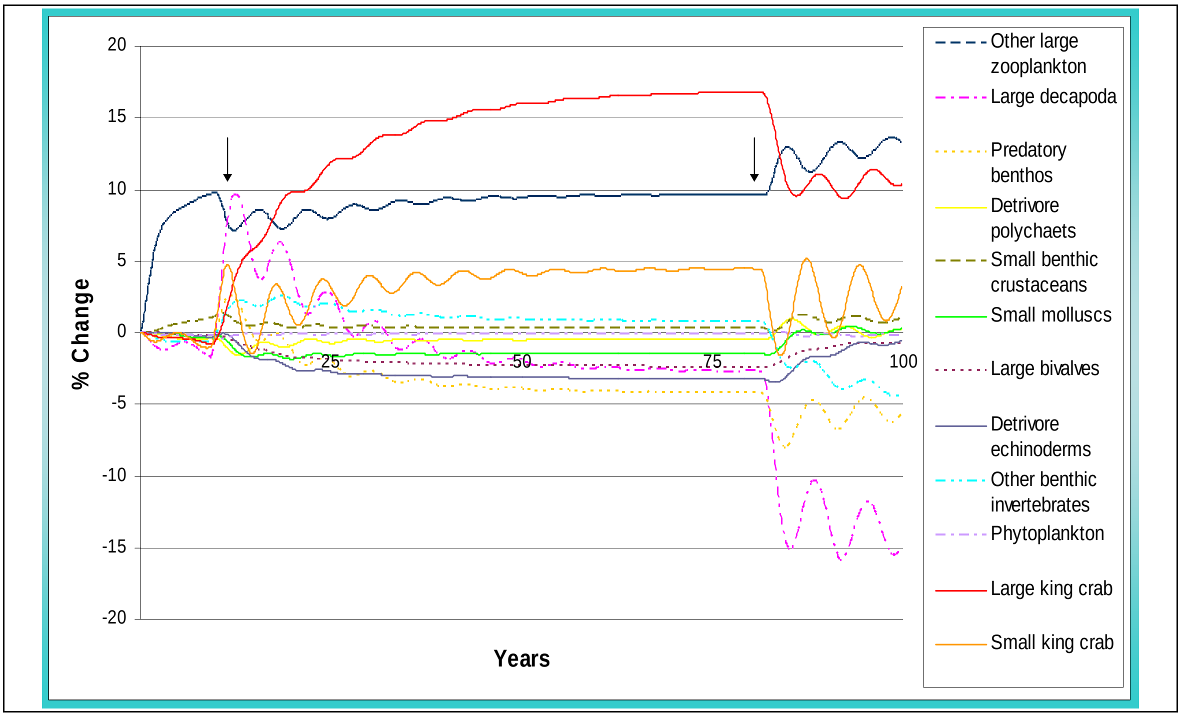

Figure 16. Run II B. Relative change in percentage of original biomass with increased fishing mortality rate of cod from 0.204 yr^{-1} to 0.612 yr^{-1} and large other fish from 0.192 yr^{-1} to 0.576 yr^{-1}. Start and stop of cod fishery is marked with arrows.

3.2.3 Run II C

Scenario II C had an initial high fishing mortality of small and large king crab. The complete stop in the king crab fishery allowed for their biomasses to increase rapidly over a period of 10 years. Large king crab biomass increases 120% and starts declining slowly after about 10 years of growth. After an initial fast growth the small king crab biomass drops quickly and remains below initial biomass levels. The mammal biomass increases following the growth of king crab. Except from a drop in herring biomass, the other pelagic groups show small changes in abundance (Figure 17). The benthic biomasses drop over a period of about 5 years and stabilize or increase slightly as king crab biomass drops. The organisms showing a decline in biomass are large decapods, predatory benthos, detrivore echinoderms, large bivalves and to lesser degree small molluscs. As the large king crab biomass declines, large decapods recover slightly (Figure 18). Generally the biomass changes in run II C is the opposite of those in run II A. Run II A, however, shows a large increase in large other fish, while this group remains fairly unchanged in run II C.

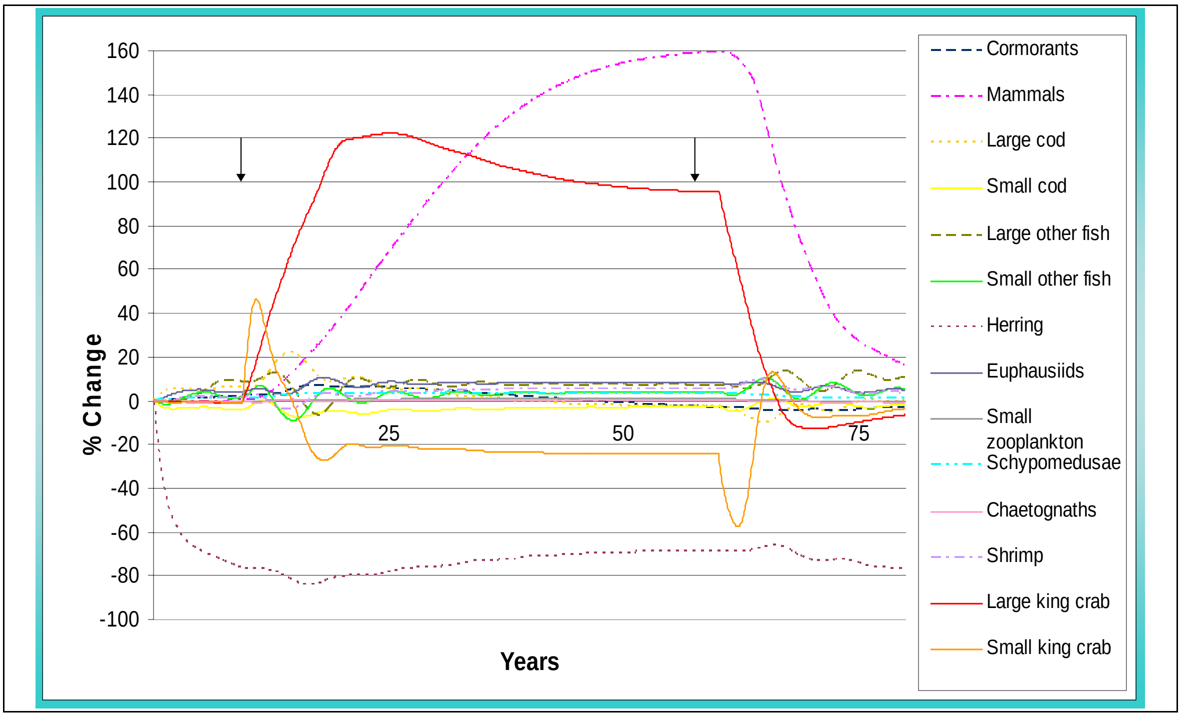

Figure 17. Run II C. Relative change in percentage of original biomass with an initial fishing mortality rate of small king crab of 0.5 yr^{-1} and large king crab of 0.1 yr^{-1} followed by a complete stop in king crab fishery from year 10 to 60. Stop and start of king crab fishery is marked with arrows.

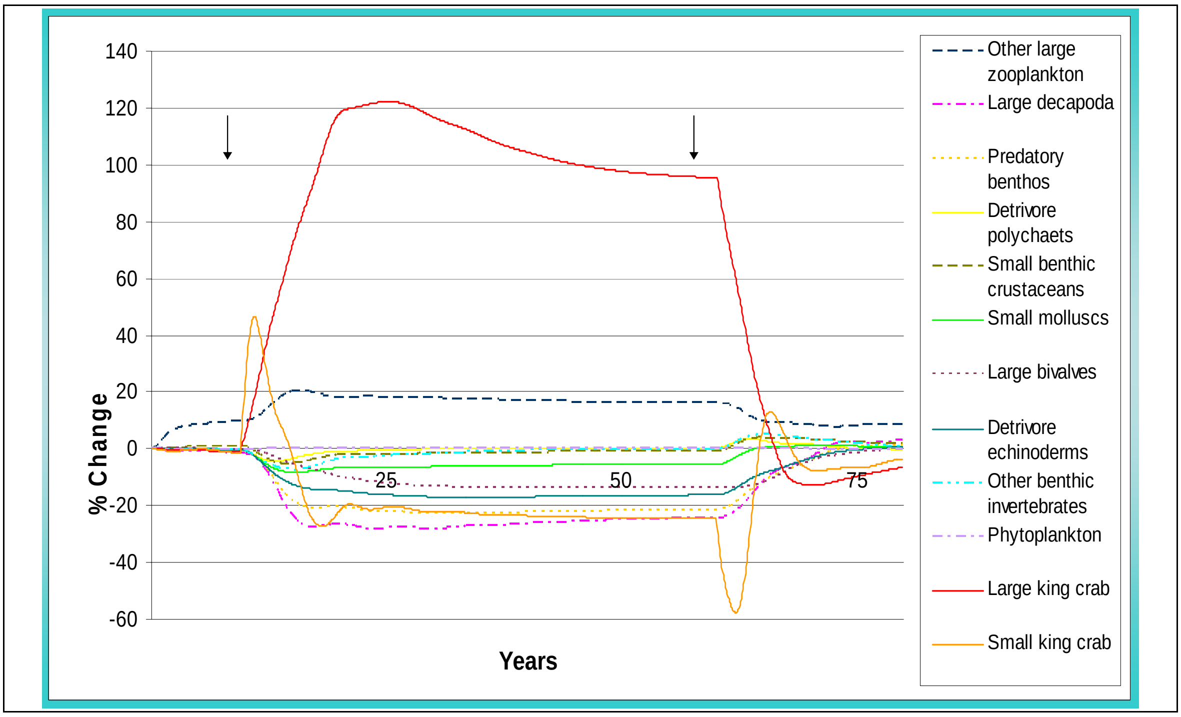

Figure 18. Run II C. Relative change in percentage of original biomass with an initial fishing mortality rate of small king crab of 0.5 yr^{-1} and large king crab of 0.1 yr^{-1} followed by a complete stop in king crab fishery from year 10 to 60. Stop and start of king crab fishery is marked with arrows.

Initially predation mortality constitutes a small part of annual mortality of large king crab and about half of the mortality rate of small king crabs (Table 6).

Table 6: Initial biomass (t $km^{-2}y^{-1}$), annual total mortality rate, relative feeding time, consume per biomass (Q/B) and annual predation mortality rate of small and large king crab.

	Biomass	Total mortality	Feeding time	Q/B	Predation mortality
Small king crab	1.2	1.0	1.0	5.0	0.425
Large king crab	2.8	0.2	1.0	3.0	0.099

When king crab biomass is allowed to increase the small king crab biomass and total mortality rate increase sharply and subsequently drop, fluctuate and stabilise at a lower level than at high king crab fishery. Increased feeding time is followed by increased predation mortality rate. Predation mortality of the group increases initially and stabilises at a rate over 30% higher than before stop in king crab fishery, while total mortality stabilises at a lower rate (Figure 19). Consume per biomass increases initially and levels out after about 20 years. Consume per biomass, feeding time and predation mortality level out at a higher level than at high king crab fishery (Figure 19).

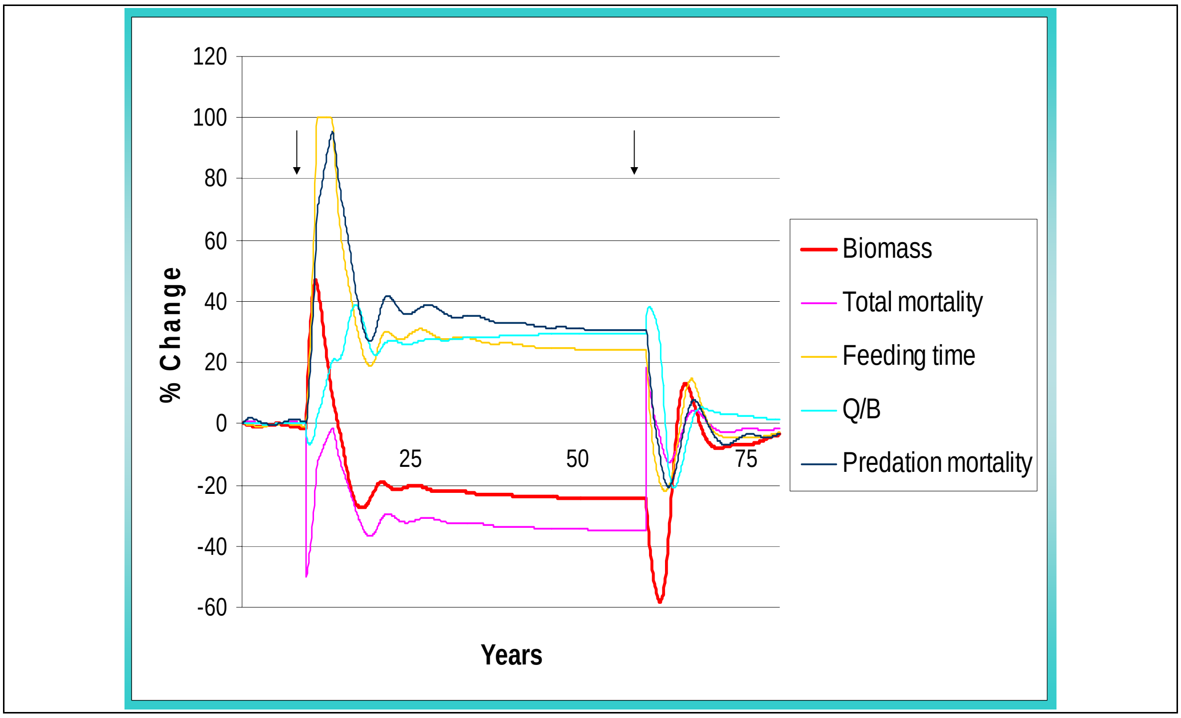

Figure 19. Relative change in biomass, annual total mortality rate, relative feeding time, consume per biomass (Q/B) and annual predation mortality rate of small king crab in scenario II C. Stop and start of king crab fishery is marked with arrows.

Large cod is the most important predator of small king crab. The groups increasing the most in importance as predators of small king crab are large king crab and small king crab. Predation pressure from large decapoda increases initially, but drops as large decapoda biomass drops (Figure 20). Large decapoda, detrivore echinoderms and predatory benthos, who all experience a drop in biomass with increasing king crab biomass, show a decline in proportion contribution to small king crab diet. The proportion of detrivore polyhaetes, other benthic invertebrates and small benthic crustaceans increases slightly in small king crab diet. The initial increase in small king crab biomass causes a large relative increase in small king crab in diet. The proportion of small king crab in diet stabilises at a higher level than initially despite reduced small king crab abundance (Figure 21).

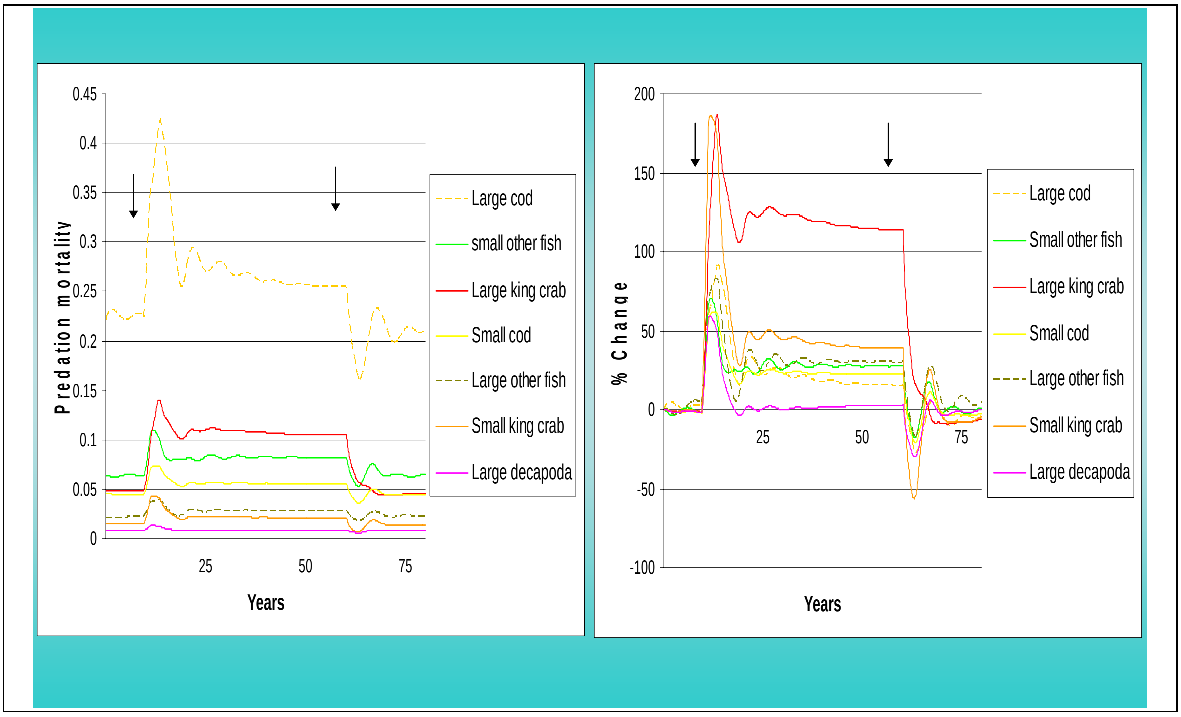

Figure 20. Predation mortality (left) and relative change in predation mortality (right) by small king crab predators in scenario II C. Stop and start of king crab fishery is marked with arrows.

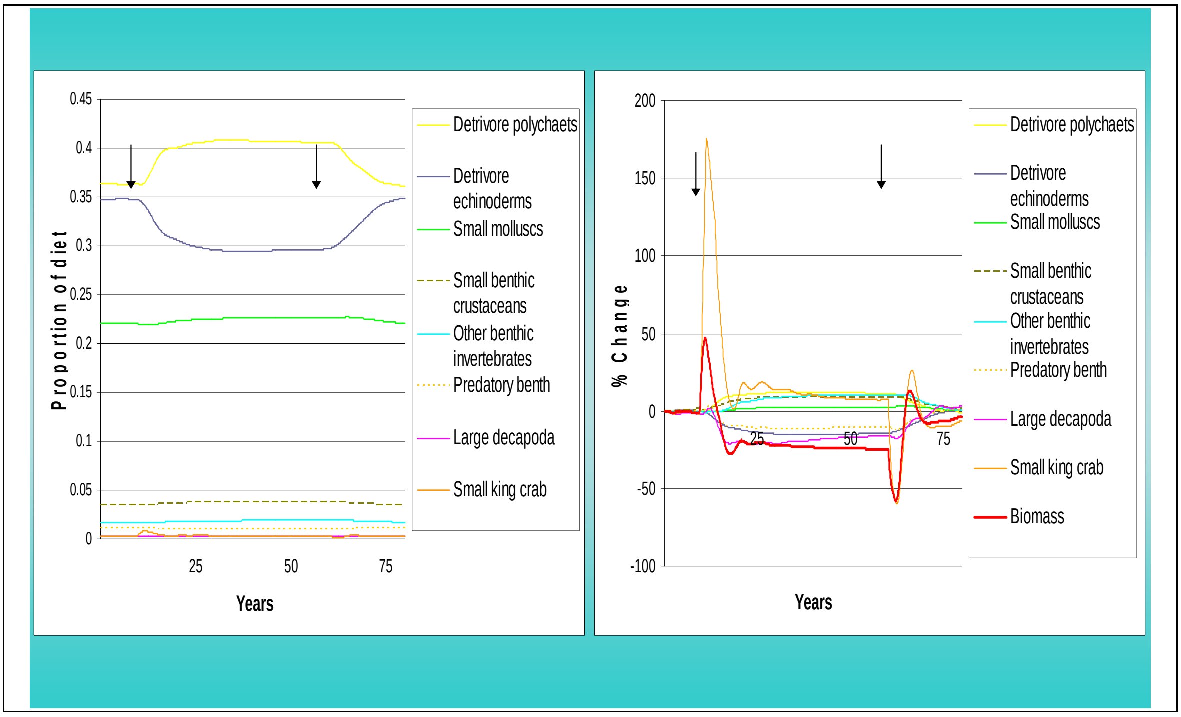

Figure 21. Proportion of prey group in diet (left) and relative change in proportion of prey group in diet (right) of small king crab prey in scenario II C. Stop and start of king crab fishery is marked with arrows.

When fishing of king crab stops, large king crab biomass increases significantly over 10 years before it levels off and starts declining slowly. Feeding time doubles over a period of 5 years and when it levels out consume per biomass drops rapidly (Figure 22). Increased feeding time is followed by increased predation mortality. Large king crab mortality rate drops as fishery stops, but increases steadily afterwards parallel with predation mortality rate (Figure 22). Predation mortality rate increases and shows an initial peak after stop in king crab fishery that could be caused by predation of large cod and large other fish (Figure 23). Thereafter mammals become the most important predator of large king crab. Predation mortality due to mammals shows a steady increase during the period of no king crab fishery. Predation pressure of large cod and large other fish seem to follow the biomass changes of large king crab (Figure 23).

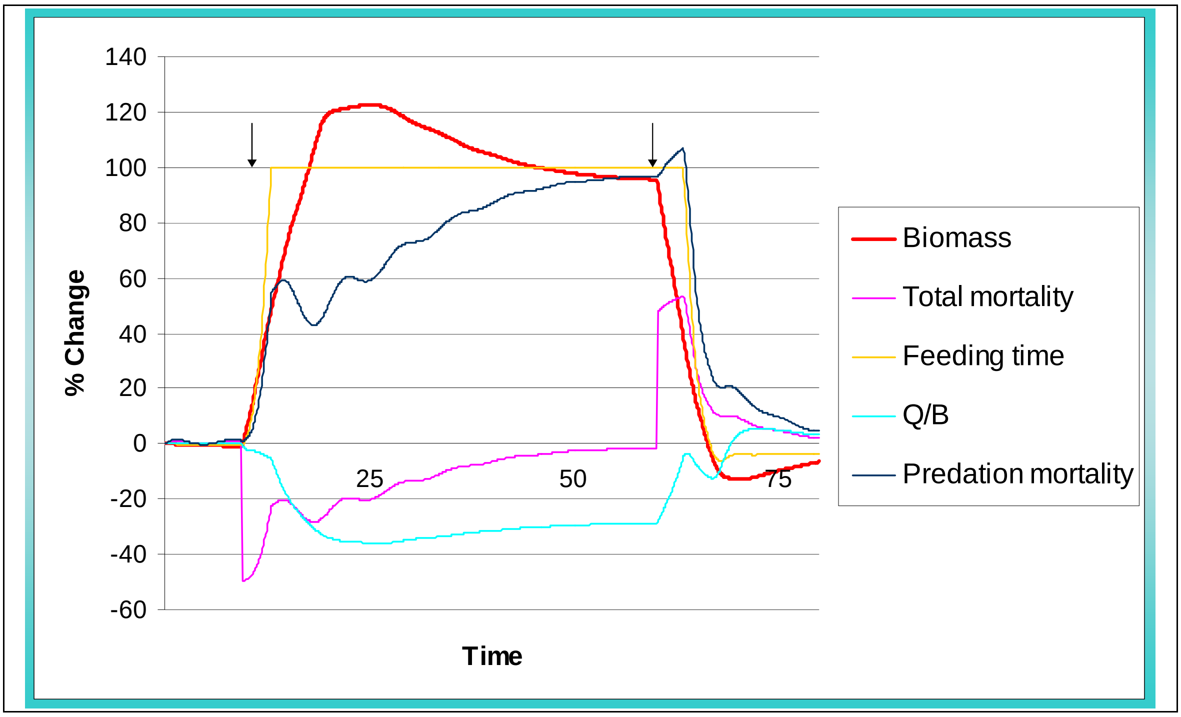

Figure 22. Relative change biomass, annual total mortality rate, relative feeding time, consume per biomass (Q/B) and annual predation mortality rate of large king crab in scenario II C. Stop and start of king crab fishery is marked with arrows.

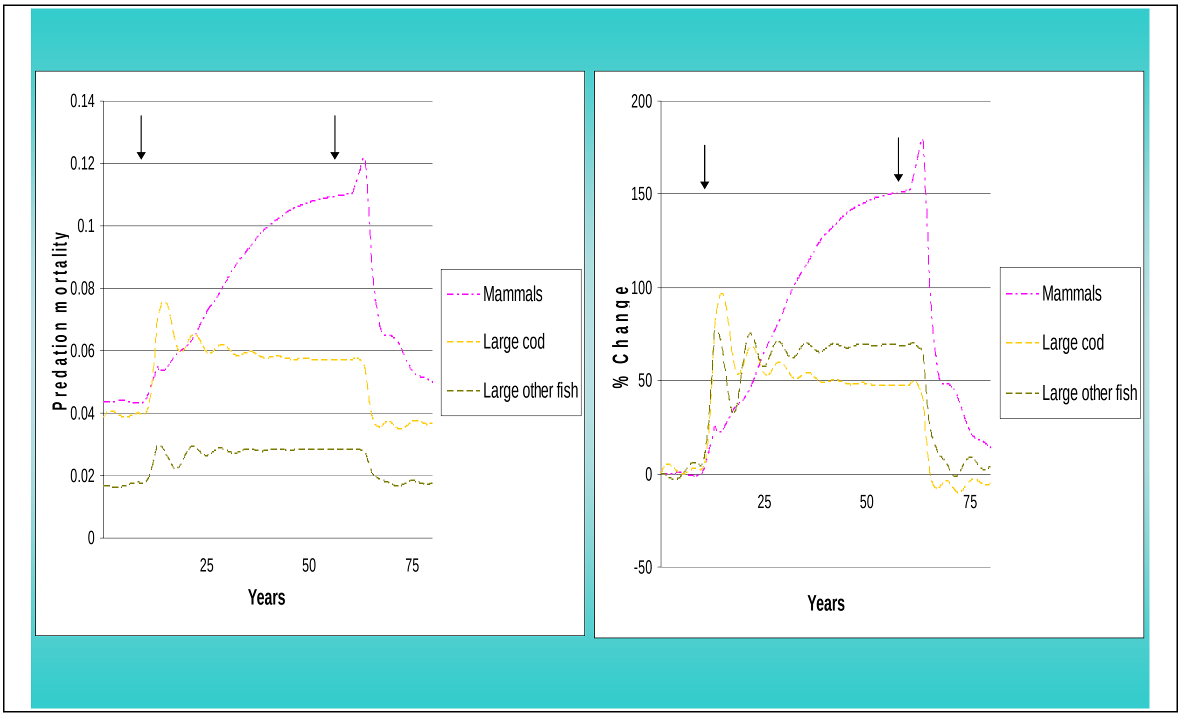

Figure 23. Predation mortality (left) and relative change in predation mortality (right) by large king crab predators in scenario II C. Stop and start of king crab fishery is marked with arrows.

The benthic groups whose biomasses drop when large king crab biomass increases become less important as prey of large king crab. The proportions of detrivore polychaetes, other benthic invertebrates, and small benthic crustaceans in large king crab diet increases. Increased biomass of small king crab just after the stop in the fishery, results in a higher proportion of small king crab in the diet of large king crab. Despite the following decline in biomass of small king crab their proportion in the diet of large king crab is about 20% higher than initially (Figure 24).

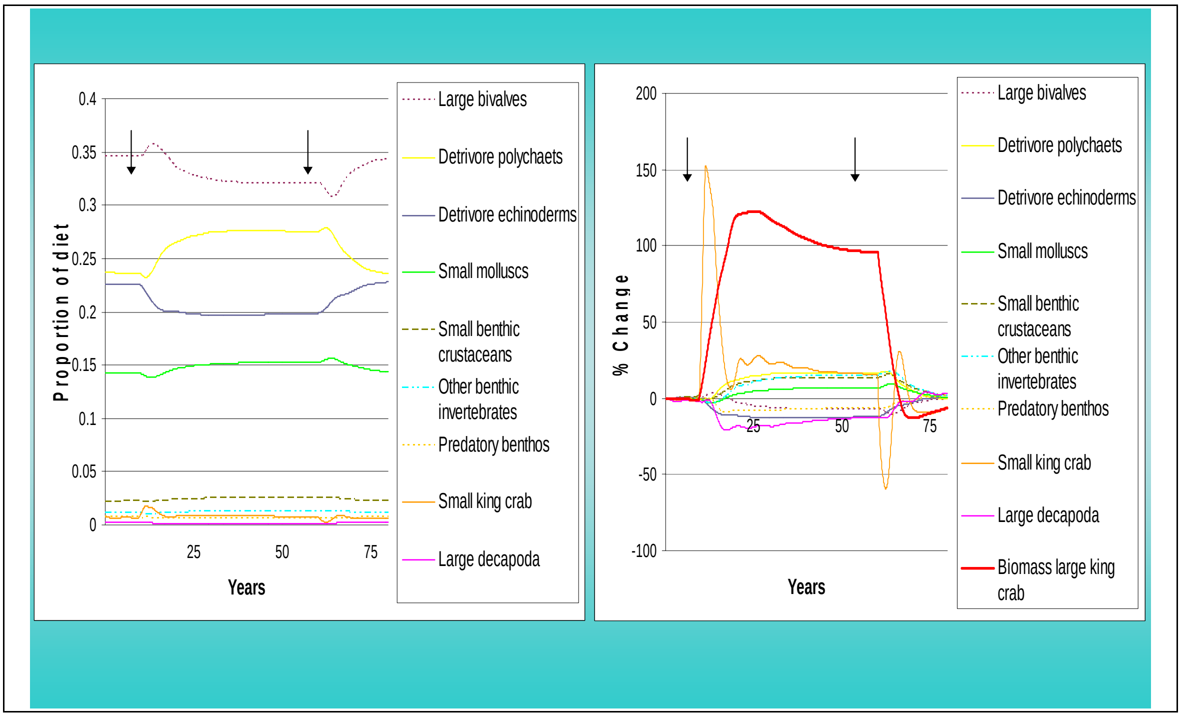

Figure 24. Proportion of prey group in diet (left) and relative change in proportion of prey group in diet (right) of large king crab prey in scenario II C. Stop and start of king crab fishery is marked with arrows.

3.2.4 Run II D

Running Model II C with increased vulnerability parameter for the less mobile groups (Model II D) resulted in a larger drop in biomass of prey groups with increasing king crab abundance. Given a vulnerability parameter of 1 the large bivalves, predatory benthos and detrivore echinoderms experienced the largest relative drop in biomasses. Due to software problems figures could not be made.

4. DISCUSSION

4.1 UNCERTAINTIES OF INPUT VALUES

To emphasize the potential effects of king crab their biomass was set high in the Ecopath model (Table 4). In Model II the annual benthic production can sustain a biomass of 1.2 t km^{-2} small and 2.8 t km^{-2} large king crabs. Gerasimova (1997) proposed that the carrying capacity of king crabs larger than 80 mm carapace width in the Barents Sea is 2.37 t km^{-2}. While keeping in mind all the uncertainties related to the estimates and possible consequences of the invasion, these estimates could give some indications of what biomass levels of king crab the benthic production could sustain. In Varanger fjord (Northern Norway) the current mean density estimate of adult king crab is 600 adult crabs km^{-2} (Hjelseth, A.M. Institute of Marine Research, personal communication). Assuming an average weight of 0.002 t, the biomass of adult crab is 1.2 t km^{-2} in Varanger fjord. There are no estimates of densities of juvenile king crabs. There is limited knowledge on the benthic production in other Norwegian fjords (Nilsen 2001) making it difficult to say whether Sørfjord may be representative for coastal areas in the king crab domain.

The proportion of small to large king crab may be important for the outcome of the model as consume per biomass (Q/B) and production per biomass (P/B) for small king crab are higher than that of larger crabs. As outlined in chapter 2.2 there are variations in Q/B and P/B reported for king crab and knowledge of juvenile crabs is limited. Except for large bivalves, however, the sensitivity analysis shows that the groups in the model are generally fairly insensitive to a ±50% change in Q/B and biomass input of king crab.

When balancing the model it was found to be very sensitive to diet input. An accuracy of 0.01 in diet studies will rarely be achieved. The diet data collected will not only be approximate due to the collection procedure, but also due to natural variations in food items consumed. In the model the predators and prey of king crab feed or are fed upon according to abundance. King crab contributes to about 1/3 of the diet of mammals in Model II. In comparison the highest contribution of large crustaceans to mammals in Morisette (2001) is 0.0004 for harbour seals (*Phoca vitulina*). It is difficult to determine how important king crab could be in the diets of mammals and fish in Sørfjord and whether predation by these could be an important factor controlling the king crab population.

In Ecopath models from the North Pacific that include large crustaceans, the diet proportion of large crustaceans in fish varies from 0.001 to 0.2 (Bundy et al. 2000, Morisette 2001, Aydin et al 2002). In comparison the diet proportion of king crab in fish diets in Model II ranged from 0.011 to 0.065 (Appendix B). While this model assumes that king crab does not feed on shrimps and fish, these groups make up parts of the diet of large crustaceans in Bundy et al. (2000) and shrimps are a part of king crab diet in Aydin et al. (2002). Comparing diet proportions of the models mentioned above is difficult due to differences in functional groups, but the diet proportions of the large crustacean groups are generally variable. The species compositions differ between the North Pacific and Barents Sea thereby making intersystem comparisons a poor guide for validating the Sørfjord model. Testing sensitivity of Ecopath model output to changes in diet, however, could give an indication of how prey preferences could influence the vulnerability of groups to king crab invasion.

The Sørfjord model used as a basis for the investigation represented the period 1993-96, which was a period of high abundance of euphausiids in the fjord. The proportion of euphausiids was high in the diet of fish groups in this period, while during 1990-92 benthic groups were more important (Pedersen, T., Nilsen, M., Nilssen, E.M. and Berg, E. *unpubl.*). This could influence the strength of the links between the benthic and pelagic groups in the model.

Through lumping different species into functional groups, important information may be lost. Within the respective functional groups organisms could differ substantially in their feeding interactions with king crab. The other fish groups in the Sørfjord model, for example, consist of both benthivore and more planktivore fish species. The benthivores may therefore have larger diet overlap with king crab. When looking at possible effects of king crab it may be preferable to build the model up according to predator-prey interactions with king crab.

4.2 LIMITATIONS OF MODEL

The model does not account for the egg and larval stage of the functional groups. Recruitment to the large groups of the model is therefore dependent on the sizes of the respective small groups, while the biomasses of the small groups are determined by the biomasses of the large groups. The success of king crab larvae has been a focus of research trying to explain the variations in king crab biomass in the Bering Sea and is also an important area of research related to its invasion success. Survival of king crab larvae does not seem to be related to synchrony with phytoplankton bloom (Shirley and Shirley 1989). Predation by planktivorous fish has been proposed as an important factor determining larval supply (Fukuhara 1985, Loher et al. 1998) as has changes in large scale climate and physical oceanography (Zheng and Kruse 2000). Mapping overlap between king crab larvae and potential predators of these in time and space could give an indication of how important this factor could be in the Barents Sea. Biogenic assemblages are important for successful settlement of larvae (Loher and Armstrong 2000). It could be hypothesized that king crab through grazing could reduce abundance of benthic organisms that again can have a negative impact on settlement of their larva. This modelling exercise, however, has focused on biological factors potentially controlling king crab abundance after settlement.

Putting ecotrophic efficiency (EE) constant for large decapods and predatory benthos gives the impression that these groups will experience a higher predation mortality rate when king crab is introduced to Model I. In order to compensate for the new predator Ecopath estimates higher biomasses for these two groups. This further result in increased predation mortality rates of prey of large decapods and predatory benthos. This is an unwanted artefact of the model when looking at ecosystem changes with species introductions. Being the main indicator of use in the system it is preferable that EE is not put constant. Alternative run putting biomass constant gave EEs of large decapods and predator benthos that exceeded unity. Christensen et al. (2002) also warn against using Ecopath to estimate biomass as the empirical basis for EE is generally weak. The reduced biomasses of small other fish, euphausiids, shrimp and other large zooplankton after introducing king crab to Model I could also be attributed to the model parameterisation when EE is set constant.

Ecopath with Ecosim (EwE) does not account for spatial issues such as overlap of potential predators and prey, a factor a third component of the software, Ecospace, can account for (Christensen et al. 2000). Availability of refuge can to some degree be taken into account through the vulnerability parameter. Subjective ranking of species according to ability to seek refuge and structural defence, could give better indications of which groups are most vulnerable to king crab invasion. Changing the vulnerability parameter for a group could also highlight groups sensitive to a food preference of king crab. The diet study showed that plant material can be an important component of king crab diet. The Sørfjord model does not include macroalgae that may have important functions both in terms of trophic dynamics and structure (Power 1992). King crab utilize detritus and can thus function as a converter of energy into commercially exploitable species directly (king crab itself) or indirectly (commercial predators of king crab). The effect of king crab on nutrient cycling is an interesting issue outside the scope of this thesis.

The EwE analysis aimed at identifying factors determining king crab abundance as well as groups vulnerable to king crab invasion. As the different groups are linked through feeding interactions the model should indicate to what degree king crab will affect its predators (bottom-up control) and prey (top-down control) and vice versa. The Ecopath analysis points out groups that are instantly vulnerable to king crab invasion. When assessing long term impacts, however, the potential biomass changes of the different groups as well as changes in predator and prey availability should be considered. Ecosim is considered a more appropriate tool for making long-term predictions as it allows for changes in diet composition with changes in abundance (Christensen et al. 2000). Ecosystems are characterised by fluctuations. The changes predicted by the simulations should therefore be regarded merely as an indication of the direction of change. Ecosystems are of great complexity and identifying important factors for their structuring is difficult. By narrowing the focus of research important information can be lost. Parameters of both Ecopath and Ecosim analyses will therefore be discussed as they all contain useful information that could contribute to a better understanding of the processes of interest to the invasion issue. Potentially important factors not accounted for in the model will also be pointed out.

4.3 WHAT FACTORS COULD CONTROL KING CRAB ABUNDANCE?

The king crab has succeeded in establishing a self-sustaining population in the Barents Sea. A number of factors have contributed to this success including the suitable physical conditions it has met in its new environment. Table 7 summarises potential factors determining king crab abundance in the Sørfjord model as identified through Ecopath and Ecosim analysis. The groups identified through Ecosim analysis are rated according to relative change in biomass.

Table 7: Potential factors determining small and large king crab abundance as identified through Ecopath and Ecosim analyses.

Indicator	Functional groups/ factors				
Ecotrophic efficiency	Availability of prey of king crab		Low utilization of king crab		
Prey overlap	Large decapods	Predatory benthos	Fish groups		
Mixed trophic impact					
Small king crab	Small king crab	Large cod	Euphausiids	Small other fish	Large king crab
Large king crab	Mammals	Large king crab	Large fish groups	Euphausiids	Small king crab
Sensitivity analysis					
Small king crab	Large cod				
Large king crab	Mammals	Large cod			
Ecosim					
Run II A	High fishing mortality of large king crab				
Run II B					
Small king crab	Large cod				
Large king crab	Mammals				
Run II C					
Small king crab	Large cod	Large king crab	Small king crab	Prey availability	
Large king crab	Mammals	Large fish groups	Large king crab	Recruitment	Prey availability

4.3.1 Availability of resources

A biomass of 1.2 t km^{-2} small and 2.8 t km^{-2} large king crabs could be introduced to Model I without any of the prey groups experiencing a higher annual mortality than productivity rate (Table 4). This could suggest that there is “unused” production, or niches, in the system that could support the king crab biomass. The idea of vacant niches has been widely debated in the literature as has the assertion that their existence has been demonstrated by the fact that many introduced species have no effect on the native community. The concept of empty niches has also been used to justify introductions (eg. Herbold and Moyle 1986, Cizek et al. 2003).

Invasion success could be investigated in terms of species taking advantage of niche opportunities (Shea and Chesson 2002). One such niche opportunity can be availability of resources. A resource opportunity arises when the resources a species needs are abundant due to high supply of the resource, that resident species have not reduced resource densities or interfered with access to the resource. From this one can hypothesize that by underutilizing benthic production and/or being inferior competitors of the king crab the resident species of the Sørfjord could contribute to the crab's invasion success.

The initial growth in biomass and increased consumption rate for small king crab in run II C suggests that it is able to take advantage of a resource opportunity in the system. The subsequent levelling out of Q/B could indicate that a reduction of prey biomass with time is one limiting factor of small king crab biomass growth. A large increase in large king crab biomass relative to drop in consumption rate could also suggest that there is production available in Sørfjord.

Due to their long life cycle Gerasimova (1997) proposed that the king crab abundance will overshoot and then stabilize at a level of the carrying capacity of the environment after a series of dampening fluctuations. Such a overshooting is indicated in the small king crab in run II C. The impact of king crab on other species in the ecosystem is expected to be more significant at the peaks of high abundance. Gerasimova suggests that this effect can be eliminated by an appropriate fishing pressure of the stock.

Following an increase in king crab biomass, the king crab groups will increase the proportion of detrivore polychaetes, small benthic crustaceans, other benthic invertebrates and small king crab in their diet (run II C). Generally these groups have relatively high production rates and low initial ecotrophic efficiency (EE) compared to the other benthic groups in the system. This finding is in accordance with the niche opportunity theory that predicts invasions to be facilitated by high supply and low utilization in the system (Shea and Chesson 2002).

Predatory benthos and large decapods have the highest prey overlap with king crab, followed by cod and other fish. The low EE of the benthic prey of these groups in the model, however, limits their significance as food competitors of king crab. Specialized species may reduce resources more effectively than a generalist (Sea and Chesson 2002). A lack of specialist benthic feeders in Sørfjord could therefore contribute to the abundance of benthos. A lack of natural enemies, competitors and parasites may contribute to the success of the king crab. In the Bering Sea tanner crabs (*Chionoecetes bairdi* and *C. opilio*), sea stars (*Asterias amurensis*), Pacific cod (*Gadus macrocephalus*), yellowfin sole (*Limanda aspera*), Alaska plaice (*Pleuronectes quadrituberculatus*), rock sole (*Lepidopsetta bilineata*), flathead sole (*Hippoglossoides elassodon*) and rex sole (*Glyptocephalus zachirus*) are considered important competitors of king crab. These are similar species to those found in the Barents Sea. While it has been hypothesised that their abundance can impact the growth of the king crab stock in the Bering Sea, supporting data is lacking (Feder and Jewett 1981, Fukuhara 1985, Zheng and Kruse 2000). A study comparing the presence of these factors in its native and invaded area may be useful to understand the success of the king crab in the Barents Sea.

It can be argued that the apparent availability of a resource is an illusion caused by limited understanding of the functions and interactions of the numerous components of an ecosystem. A contributing factor to this illusion in the Sørfjord system could be a lack of knowledge on the interactions within the benthic system and the function of micro-organisms. The biomasses of large decapoda and predatory benthos were estimated from predation from their predators, mostly cod. Internal consumption within these groups is uncertain contributing to the biomass estimates of these groups to be uncertain. If these groups were better represented in the model the EEs of the benthic groups could be expected to increase. It is difficult to determine if invasion success of the king crab could be explained by resident species underutilization of resources or inferior competitive ability.

4.3.2 Fishing

Run II A indicated that a heavy fishery of large king crab can control the abundance of the king crab and allow for recovery of benthic organisms (Figure 14). Overharvesting has been blamed for the collapse of the Bering Sea king crab stock in the early 1980s. It is hypothesized that large reductions in the number of mature males through fishing in the Bering Sea has resulted in a sex ratio of males to females lower than what can realize the breeding potential of females (Loher et al. 1998). Focusing fishery on the commercially valuable males could therefore lead to overall reduction in king crab abundance.

The model predicts recovery of the benthic community when king crab abundance is reduced through fishery. Disturbance of the ecosystem could, however, cause irreversible changes. Stability has been used to measure a system’s response to stress and describes the ability a system has to return to equilibrium state after a temporary disturbance (Holling 1973). Ecopath allows for quantification of many of the attributes related to ecosystem stability (Christensen 1995b, Christensen and Walters *in press*). Characteristics of stable, or healthy, ecosystems include the maintenance of a certain balance between the different components as well as adequate diversity of taxa or complexity of functioning (Ulanowicz 1997). It could be hypothesised that effects of king crab invasion could reduce the stability of the Sørfjord ecosystem. Ecopath with Ecosim could be used to explore this hypothesis as well as identifying groups important for maintaining ecosystem health.

4.3.3 Predation and cannibalism

Due to higher vulnerability to predation the ecotrophic efficiency (EE) of small king crab could be expected to be higher than that of large king crab. In Ecopath Model II the large king crab is subject to a fishery contributing to their comparatively higher EE. EE of king crab is relatively low compared to other models (0.95 for snow crab and American lobster in Morisette (2001) and Bundy et al. (2000), 0.936 in for king crab in Aydin et al. (2002), 0.9 for large decapods in Pedersen, T., Nilsen, M., Nilssen, E.M. and Berg, E. (*unpubl.*)). In a new environment many alien species experience released predation pressure as they come to areas where they have not co-evolved with their predators (Elton 1958). The degree to which king crab experience decreased predation pressure in their new environment is an open question. One might expect lower predation pressure of small king crabs compared to large decapods as the king crab is very spiny. Gregarious behaviour is a trait of successful invaders (Ehrlich 1989) and could be a factor making the king crabs a less preferred prey.

The mixed trophic impact analysis suggests that changes in the trophic structure of the pelagic community generally have little impact on the benthic community and vice versa. Pelagic groups the mixed trophic impact analysis predicts will negatively impact king crab are mammals, large cod and the other fish groups. The negative impact of euphasiids on king crab, as suggested by the mixed trophic impact analysis, could be due to their importance in the diet of groups that have a negative impact on king crabs. Ecosim analysis II C showed that large cod is the major predator of small king crab. The weak recovery of small king crab with increased fishing mortality (run II B) could suggest that large cod could influence the biomass of small king crab. The drop in total mortality of small king crab is not completely compensated by increased predation pressure in run II C, resulting in a lower total mortality rate after stop in king crab fishery (Figure 19). It is difficult to explain why small king crab biomass is lower after king crab fishery stopped, despite lower total mortality rate.

Large king crab is mainly predated upon by mammals, followed by large cod and large other fish. An increased fishery of large cod and large other fish (run II B) resulted in increased large king crab abundance. The alternative simulation (run II Ba) where mammals were excluded as bycatch showed that the increase in large king crab biomass was largely due to reduced mammal predation, not reduced predation by large cod and large other fish. Ecosim assumes density dependent predation. Allowing king crab biomass to increase in run II C therefore caused an increase in their predation mortality rate. After 60 years the predation mortality rate contributes almost as much to total mortality rate as the king crab fishery did.

As outlined in chapter 2.2, king crab is potentially subject to a number of predators. It is debated whether predation of king crab by cod and yellowfin sole, as well as other non-commercial species, can explain declines in king crab abundance in the Bering Sea (Fukuhura 1985, Livingston 1989, Loher et al. 1998, Zheng and Kruse 2000).

The Ecosim analyses II C suggest that when king crab biomass is allowed to grow their abundance will increase rapidly. Cannibalism within the small king crab group increases, while biomass declines suggesting that increased cannibalism is due to reduced prey abundance. As large king crab biomass grows, so do their importance as predators of small king crab (Figure 20). Initially this could be a response to an increase in small king crab biomass, but as their abundance decreases it could be caused by the reduction in other prey groups (Figure 18). Reduced prey availability is confirmed by the large increase in feeding time and drop in consume per biomass of large king crab. The other predators of small king crab (cod, other fish and large decapoda) switch to small king crab as their respective benthic prey biomasses are reduced. In addition reduced prey availability causes small king crab to spend more time feeding, which exposes the group to predation. The total increase in predation pressure by their predator groups could explain some of the drop in small king crab biomass.

In laboratory experiments cannibalism was the major source of mortality for 1 and 2 year old juvenile king crab. Cannibalism was related to cohort density and cover, particularly in the younger crabs (Rounds et al. 1989). The king crab changes habitat after reaching maturity, which reduces the spatial overlap of large and small king crab (Marukawa 1933, Stone et al. 1992). No documentation of cannibalism by adult on juvenile king crab was found in the king crab literature. Intraspecific competition and predation by large king crabs upon small king crabs may therefore be less than indicated by the model. Cannibalism has been documented in snow crabs (*Chionoecetes opilio)* and was found to be more frequent when alternative prey was scarce or competing conspecifics abundant. To some extent cannibalism is believed to regulate population size structure and recruitment of snow crabs (Lovrich and Saint-Marie 1997). In a relatively shallow fjord with limited migration opportunities and thus separation of small and large king crabs, cannibalism could be expected to be more frequent than in an area with easy access to open ocean. Juvenile king crabs have been found in the stomachs of large king crab in Varangerfjord (Northern Norway) (Haugan, T.A. Norwegian College of Fishery Science, personal communication). This observation triggers questions such as if this is a phenomenon solely in the invaded area and if cannibalism is due to prey scarcity. How important the large king crabs could be as a regulating mechanism of small king crab is also an interesting topic for further research.

When large king crab biomass increases in run II C their feeding time levels out due to the default assumption used that feeding time can at the most double. At this stage an increase in biomass will not be compensated by increased feeding time. This could cause the drop in consume per biomass. Feeding time is limited due to empirical evidence that there is a limit to how great predation risk an organism will take (Ecopath with Ecosim version 5 help menu). Since large king crab has few predators their time spent feeding could be expected to keep increasing as prey biomass is reduced. Except from during periods of molting large king crabs are not known to seek shelter (Powell and Nickerson 1965a).

The decline in large king crab biomass in run II C after 25 years could be due to low recruitment from the small king crab group. A reduction in large king crab biomass is followed by a weak recovery of large decapoda, while large king crab consumption rate increases. This could suggest poor recruitment, not competition, as an important factor regulating large king crab abundance. Also small king crabs recover slightly with reduced large king crab abundance indicating that large king crab is their major food competitor and/or predator.

In summary the Ecosim analysis suggests that a heavy fishery of large king crab will reduce king crab biomass to a low level. Increasing fishing of large cod and large other fish will not facilitate growth in king crab abundance. When king crab abundance is allowed to grow, the small king crab biomass is regulated mainly through predation, including cannibalism, and prey availability. Large king crab biomass seems to be limited by recruitment from the small king crab population as well as predation by mammals.

4.4 WHAT EFFECTS WILL THE KING CRAB HAVE ON THE SØRFJORD ECOSYSTEM AS PREDICTED BY ECOPATH WITH ECOSIM?

Table 8 gives a summary of what groups are the most vulnerable to king crab invasion as identified through the Ecopath with Ecosim analysis. The groups identified through Ecosim analysis are ranged according to relative change in biomass.

Table 8: Functional groups vulnerable to king crab invasion as identified through Ecopath and Ecosim analysis.

Indicator	Functional groups					
Ecotrophic efficiency	Large bivalves	Detrivore echinoderms	Detrivore polychaets	Other benthic invertebrates		
Mortality rates	Large bivalves	Detrivore echinoderms	Detrivore polychaets	Other benthic invertebrates		
Prey overlap						
Large king crab	Large decapoda/ Predatory benthos	Small king crab	Fish groups			
Small king crab	Large king crab	Large decapoda/ Predatory benthos	Fish groups			
Mixed trophic impact						
Large king crab	Large king crab	Large bivalves	Large decapoda	Predatory benthos	Small king crab	Detrivore echinoderms
Small king crab	Small king crab	Detrivore echinoderms	Large decapoda	Detrivore polychaets	Other benthic invertebrates	Predatory benthos
Sensitivity analysis						
Large king crab biomass	Large king crab	Large bivalves				
Small king crab biomass	Small king crab					
Ecosim						
Run II A	Large decapoda	Predatory benthos	Large other fish	Detrivore echinoderms	Large bivalves	Small molluscs
Run II B	Predatory benthos	Detrivore echinoderms	Large decapoda			
Run II C	Large decapoda	Small king crab	Predatory benthos	Detrivore echinoderms	Large bivalves	Small molluscs
Run II D	Large bivalves	Detrivore echinoderms	Predatory benthos	Large decapoda	Small king crab	

4.4.1 The positioning of king crab in the food web

The king crab operates on a medium trophic level (3.03 for large and 3.04 for small king crab) similar to that estimated in the Ecopath analysis of the Bering Sea (Aydin et al. 2002). It is prevented from climbing to a higher trophic level in the model by the assumption that fish are of too high mobility for the crabs to feed upon them.

4.4.2 Effect of king crab on benthic groups

Most of the effects caused by king crab on benthos in the mixed trophic impact analysis are negative indicating that king crab will play an important role structuring the benthic community.

Introduction of king crab resulted in a large increase in the predation mortality rate and ecotrophic efficiency (EE) of the major benthic groups whose EE were calculated by the model (Figure 4 and 5). Large bivalves, detrivore echinoderms and detrivore polychaetes experience the largest relative increase in predation mortality rate (Figure 5). The high proportion of mortality rate due to king crab predation suggests that their impact on benthic groups will to a large extent be through direct predation.

Through the mixed trophic impact and sensitivity analysis large bivalves was highlighted as the most sensitive group to an increase in king crab biomass. Ecosim analyses II A and II C, however, suggest that large decapods and predatory benthos will experience the highest relative biomass losses when king crab is introduced to the system. In addition to being subject to king crab predation, large decapods and predatory benthos have the highest prey overlap with king crab.

Run II D illustrated that the impact of an increase in king crab biomass on the benthic groups is dependent on the vulnerability parameter of the functional groups. When vulnerability is equal in all prey groups large decapoda stands out as the most vulnerable to king crab invasion. It is reasonable to assume that large bivalves, detrivore echinoderms and predatory benthos will be more vulnerable to king crab predation due to their low mobility. In the Bering Sea reduced number of clams and sea stars has been found in areas of high king crab abundance (Feder and Jewett 1981). Intensive predation by large crab populations and bottom feeding fishes has been suggested as an explanation of the low biomass of benthos in the south-eastern compared to the north-eastern Bering Sea shelf (Feder and Jewett 1981).

The model assumes density dependent predator-prey switching. Models with prey switching are known to stabilize prey populations in a multiple-prey system. In systems where this mechanism is in place no prey population is drastically reduced or become very abundant. If, on the other hand, the predator has a strong preference for a prey, the prey abundance will not stabilize (Murdoch 1969, Pelletier 2000). Factors that may influence prey switching of king crab include the ability of the prey to escape, hide or defend themselves. Distribution and size of prey may influence prey preference of king crab. It can be hypothesized that king crab will prefer clustered over scattered prey, while prey size is dependent on the size of the crab. Large king crabs are known to show a preference for large prey (Nilssen, E. Norwegian College of Fishery Science, personal communication). Thus the stabilization of prey biomasses over time as suggested by Ecosim, could be due to the assumption that king crab show density dependent prey switching behaviour. In a system with strong prey preference of predators the prey biomasses could be expected not to stabilize. Getting a better understanding of mechanisms of prey switching of king crab is important when identifying groups vulnerable to king crab invasion.

4.4.3 Effects of king crab on benthopelagic and pelagic groups

The mixed trophic impact analysis suggests that the pelagic and benthic communities are relatively independent of each other in determining the respective community structures. King crab could, however, have some impact up the food chain due to their role as competitors of benthic production as well as prey of cod, other fish and mammals.

Herring experiences a drop in biomass over time since their predation mortality rate calculated by the model is higher than production rate. All the parameters of herring were put constant in the Ecopath input matrix. The output resulted in negative biomass accumulation, which was carried through to the Ecosim analysis.

Reduced ecotrophic efficiency (EE) and predation pressure of large other fish and the cod groups (Figure 4 and 5) is largely due to reduced predation pressure by mammals. This is a result of the diet proportion of mammals in Ecopath Model I being distributed over more groups with inclusion of king crabs. In the mixed trophic impact analysis mammals are positively impacted by an increase in king crab biomass. The positive effect of king crab as prey of large cod and large other fish is outweighed. This could be through competition or the positive impact of king crab on mammals causing increased predation pressure on the fish groups. The increase in large other fish and large cod has a negative impact on mammals. This suggests that the large fish groups are important king crab predators. Simulation II A illustrates how the importance of king crab in the diet of mammals leads to a decline in mammal biomass when king crab biomass is reduced. The reduced mammal biomass could further allow for large other fish biomass to increase through released predation pressure. In run II C large other fish remains relatively unchanged despite increasing mammal biomass. This could be because mammals switch to large king crab as large king crab become more abundant. In the process of constructing the model with king crab the diet proportions were changed causing a bias in the output. The interaction between these groups may be overrated in the model due to the importance given to large king crab in mammal diets. Although the modelling exercise can suggest how predation pressure will be distributed its predictive power is dubious. It could on the other hand be an issue that should be investigated further.

A major increase in king crab biomass in run II C caused small changes in the abundance of pelagic fish groups. This could indicate that the pelagic and benthic communities are relatively independent of each other, as suggested by the mixed trophic impact analysis. The number of trophic links connecting the pelagic and benthic communities could be higher than indicated by the model due to limited knowledge or the coarsity of the model. Exchange between the benthos and overlying water body is recognised as important both for the pelagic and the benthic compartments. The benthic community contributes to nutrient cycling and many pelagic groups depend on the benthic environment for part of their life (Raffaelli et al. 2003). Organisms that lay eggs at the sea bottom could be vulnerable to king crab predation. Gastropod eggs and fish roe have been found in king crab stomachs (Feder and Paul 1980, Rafter 1996, Gerasimova 1997). Capelin is a key species transporting energy up the food web in the Barents Sea ecosystem. Their main spawning area is along the coast of Northern Norway and Kola area in Russia, which are areas of king crab distribution. Capelin eggs are demersal and hatch after 25 to 60 days (Gjøsæter 1998, Gjøsæter and Bogstad 1998). It could be hypothesised that predation of capelin eggs by king crab could cause recruitment failure of capelin. Since spawning is followed by mass mortality by the females (Pethon 1985) the abundance of dead capelin could be expected to be preferred food preventing predation of eggs.

4.5 WHAT ARE THE IMPLICATIONS FOR MANAGEMENT?

There seem to be resource opportunities in form of benthic production in Sørfjord allowing for rapid growth of king crab. It is not known if the resource opportunity is due to underutilization of benthic production or inferior competition from resident species or merely an illusion due to limited knowledge. To prevent biomass loss of native benthic groups in Sørfjord the model suggests that total biomass of king crab should not exceed 1.2 t km^{-2} small and 2.8 t km^{-2} large king crabs. The outcome of the model is sensitive to diet preferences of king crab. Management should account for this uncertainty. Due to the limited knowledge of the potential effects of king crab invasion, the abundance should therefore be kept lower.

Fish predation could have an impact on small king crab biomass, while predation by mammals could affect large king crab biomass. The commercially exploited fish groups in Sørfjord are expected to have minor effects on king crab biomass. Changing the fishing mortality of large cod and large other fish will therefore have little effect on king crab abundance.

King crab will mainly affect the benthic community through direct predation. The groups expected to experience the highest biomass losses due to the invasion are large bivalves, detrivore echinoderms, predatory benthos and large decapods. King crab is not expected to have an effect on the abundance of commercial fish. If king crab abundance is not kept down they could overshoot the carrying capacity of the benthic environment. The model suggests that once established, the king crab abundance could increase rapidly and reduce resident benthic biomass significantly. Management efforts should therefore be in place within a couple of years after king crab invasion. King crab biomass can be kept low through intensive fishing of the large crabs. Increased fishing of king crab could, however, have a negative impact on the market causing prices to drop. Current policies, however, aim at limiting availability of king crab on the market in order to keep the prices high. It must be recognized that management of king crab is not independent of social and economical factors. Neither should potential biological consequences be ignored due to the potential socio-economic consequences.

4.6 WHAT FACTORS HAVE THE MODELLING EXERCISE IDENTIFIED THAT WE NEED TO LOOK FURTHER INTO?

There is a lack of knowledge on the biology and abundance of the small king crabs as well as the population structure of the king crab. Food preference of king crab should be studied as it is an important factor identifying vulnerable groups. The numbers and composition of functional groups could change the conclusions of the model. Building up the model according to predator-prey interactions of king crab could improve the model's ability to detect groups that should receive more attention.

Transport routes and overlap in time and space with potential predators of the planktonic stages of king crab should be mapped. This can give an indication of pattern of colonization and whether any native species have the potential to regulate larval supply. The occurrence and potential significance of cannibalism regulating king crab abundance should be investigated further. Preference of potential predators of king crab should also be studied as it could give an indication of the predation pressure they could exert on king crab.

The effect of potential structural changes of the seabed following king crab invasion should be investigated. Ecospace could be a useful tool for identifying important factors ignored through Ecosim analysis (Christensen et al. 2000). Ecopath with Ecosim could be used to explore how king crab invasion could change the stability of the invaded system as well as identifying groups whose function should receive more attention.

Knowledge on the benthic interactions is limited giving the impression that king crab will not have a significant impact on the native community unless their biomass exceeds 1.2 t km^{-2} small and 2.8 t km^{-2} large king crabs. Production of and interaction between benthic organisms as well as their importance for the pelagic community, both as prey and habitat, should therefore receive more attention. Good understanding of what determines the structure of the current benthic community can provide a reference for comparison if king crabs invade the area. Long time series data could give insight to the relative importance of trophic interactions and physical factors for ecosystem structure. It could also test whether invasion of the king crab will cause the changes as predicted through this analysis.

4.7 CONCLUDING REMARKS

Working and attempting to apply ecosystem theories to management is like walking around in a mine field. It is impossible not to step on anyone’s toes. Every theory is controversial, the empirical evidence often lacking, dodgy or the relationships difficult to prove. This ecosystem approach to consequences of king crab invasion has focused on major trophic relationships and thereby ignored other important factors structuring the ecosystem.

However, this modelling exercise has shown that a resource opportunity, in the form of benthic production, could allow for king crab biomass growth in the Sørfjord. Mammals could have a negative impact on king crab biomass, while fish predation is expected to have minor effects on king crab abundance. King crabs are expected to have a negative effect on the benthic community trough direct predation, but no significant impact on the pelagic community. To avoid negative impacts on native benthic groups in Sørfjord, king crab biomass should not exceed 1.2 t km^{-2} small and 2.8 t km^{-2} large king crabs. King crab abundance could be controlled through a fishery on large king crab, while a change in fishing of other commercial fish species is not expected to influence their abundance. Factors identified that should receive further attention include population structure, biology and food preference of king crab, as well as production and interactions within the native benthic community.

Ecosystems are complex and our ability to understand, predict and control them limited. The solution to the king crab invasion may, however, require that we look further than understanding the ecological impacts of the introductions. The key to managing the king crab is on land and determined by socio-economic factors.

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APPENDIXES

APPENDIX A: Diet matrix for Model I.

APPENDIX B: Diet matrix for Model II.

APPENDIX C: Calculation of relative biomass of small and large king crab.

APPENDIX D: Predation mortality rate in Model I.

Predation mortlity rate in Model II.

APPENDIX E: Mixed trophic impact analysis of Model II.

APPENDIX F: Sensitivity analysis of Model II.

APPENDIX A

Diet matrix for Model I (Pedersen, T., Nilsen, M., Nilssen, E.M. and Berg, E. (*unpubl*.).

	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	Cormorants																						
2	Mammals																						
3	Large cod	0.430	0.500																				
4	Small cod	0.420	0.050	0.011																			
5	Large other fish	0.070	0.250	0.001																			
6	Small other fish	0.080	0.150	0.128	0.094	0.003	0.011																
7	Herring		0.050	0.054	0.084																		
8	Euphausiids			0.53	0.477	0.612	0.625	0.500	0.020		0.070												
9	Small zooplankton							0.400	0.080	0.050	0.800	1.000	0.150										
10	Schypomedusae										0.050												
11	Chaetognaths										0.030												
12	Shrimp			0.028	0.064	0.001	0.036																
13	Other large zooplankton			0.009	0.052			0.100			0.010		0.100					0.050					
14	Large decapoda			0.018	0.026	0.004	0.008								0.003								
15	Predatory benthos			0.035	0.040	0.001	0.031								0.013	0.050							
16	Detrivore polychaets			0.035	0.037	0.059	0.098						0.200		0.348	0.300		0.030					
17	Small benthic crustaceans			0.020	0.100	0.001	0.006						0.040		0.016	0.030		0.030					
18	Small molluscs			0.034	0.001	0.099	0.093						0.080		0.210	0.070			0.070				
19	Large bivalves														0.127	0.200							
20	Detrivore echinoderms			0.072	0.021	0.220	0.092								0.166	0.170		0.010					
21	Other benthic invertebrates			0.025	0.004										0.016	0.020							
22	Phytoplankton								0.600	0.850			0.200	0.200			0.100	0.100		0.300			
23	Detritus								0.300	0.100	0.040		0.230	0.800	0.101	0.160	0.900	0.780	0.930	0.700	1.000	1.000	

APPENDIX B

Diet matrix for Model II.

	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	Cormorants																							
2	Mammals																							
3	Large cod	0.430	0.328																					
4	Small cod	0.420	0.032	0.010																				
5	Large other fis	0.070	0.164	0.001																				
6	Small other fis	0.080	0.098	0.119	0.088	0.003	0.011																	
7	Herring		0.032	0.051	0.079																			
8	Euphausiids			0.489	0.443	0.594	0.606	0.500	0.020		0.070													
9	Small zooplankt							0.400	0.080	0.050	0.800	1.000	0.150											
10	Schypomedusae										0.050													
11	Chaetognaths										0.030													
12	Shrimp			0.026	0.060	0.001	0.036																	
13	Other large zooplankton			0.008	0.049			0.100			0.010		0.100					0.050						
14	Large decapoda			0.018	0.025	0.004	0.008								0.003								0.002	0.003
15	Predatory benth			0.034	0.038	0.001	0.031								0.013	0.050							0.007	0.011
16	Detrivore polychaets			0.034	0.036	0.056	0.097						0.200		0.345	0.300		0.030					0.237	0.362
17	Small benthic crustaceans			0.019	0.093	0.001	0.006						0.040		0.016	0.030		0.030					0.022	0.034
18	Small mollusks			0.033	0.001	0.094	0.092						0.080		0.209	0.070			0.070				0.143	0.219
19	Large bivalves														0.126	0.200							0.346	
20	Detrivore echinoderms			0.068	0.020	0.215	0.091								0.165	0.170		0.010					0.226	0.345
21	Other benthic invertebrates			0.024	0.004										0.016	0.020							0.011	0.017
22	Large king crab		0.346	0.020		0.020																		
23	Small king crab			0.049	0.065	0.011	0.022								0.007								0.007	0.010
24	Phytoplankton								0.600	0.850			0.200	0.200			0.100	0.100		0.300				
25	Detritus								0.300	0.100	0.040		0.230	0.800	0.101	0.160	0.900	0.780	0.930	0.700	1.000	1.000		

APPENDIX C

Calculation of relative biomass of small and large king crab.

Population structure of the king crab population as well as relative biomass of large and small crabs were estimated. Growth of king crab was based on unpublished mark-recapture data from Varanger fjord (Northern Norway) and literature study (Nilssen and Sundet *in prep.*). Parameters of the von Bertalannfy growth equation and values used to convert CL to wet weight are shown in Table C1.

Table C1. Parameters of the von Bertalannfy growth equation used to calculate growth of king crab: L∞ (maximum carapace length in mm), K and t_0 (left). Equation and parameters used for converting CL to wet weight (right).

Lt=Loo*(1-exp(-k*(t- t_0)))		Wet weight=a*CL^b	
L∞	230.000	**a**	0.001
K	0.133	**b**	2.942
to	-0.100		

Mortality rate was assumed to decrease from 0.7 at age at settlement to year 8 when mortality was put constant at 0.3. Number of king crabs at t_0 was set to 1000. The number of crabs in each cohort was timed by weight of individual crabs to give total biomass (Table C2). Proportion of small to large crabs was found to be about 30:70.

Table C2. Carapace length (CL) in millimetres, wet weight (g), mortality rate and relative abundance in numbers and biomass for different age classes of king crab.

Age (t)	CL	Wet weight	Mortality rate	Numbers	Biomass
0	3.039	0.026		1000.000	26.308
1	31.303	25.120	-0.700	496.585	12474.464
2	56.048	139.400	-0.600	272.532	37991.059
3	77.711	364.587	-0.600	149.569	54530.791
4	96.676	693.127	-0.600	82.085	56895.317
5	113.280	1104.885	-0.500	49.787	55008.973
6	127.816	1576.048	-0.500	30.197	47592.525
7	140.541	2083.711	-0.400	20.242	42178.290
8	151.682	2607.995	-0.300	14.996	39108.389
9	161.435	3132.786	-0.300	11.109	34802.114
10	169.974	3645.731	-0.300	8.230	30003.444
11	177.449	4137.864	-0.300	6.097	25227.509
12	183.994	4603.095	-0.300	4.517	20790.253
13	189.723	5037.666	-0.300	3.346	16855.855
14	194.739	5439.640	-0.300	2.479	13483.518
15	199.130	5808.463	-0.300	1.836	10666.109
16	202.975	6144.593	-0.300	1.360	8358.907
17	206.340	6449.193	-0.300	1.008	6499.403
18	209.287	6723.903	-0.300	0.747	5019.971
19	211.866	6970.650	-0.300	0.553	3855.357
20	214.124	7191.512	-0.300	0.410	2946.614

APPENDIX D

Table D1. Predation mortality rate in Model I. Parameters discussed in text are marked in bold.

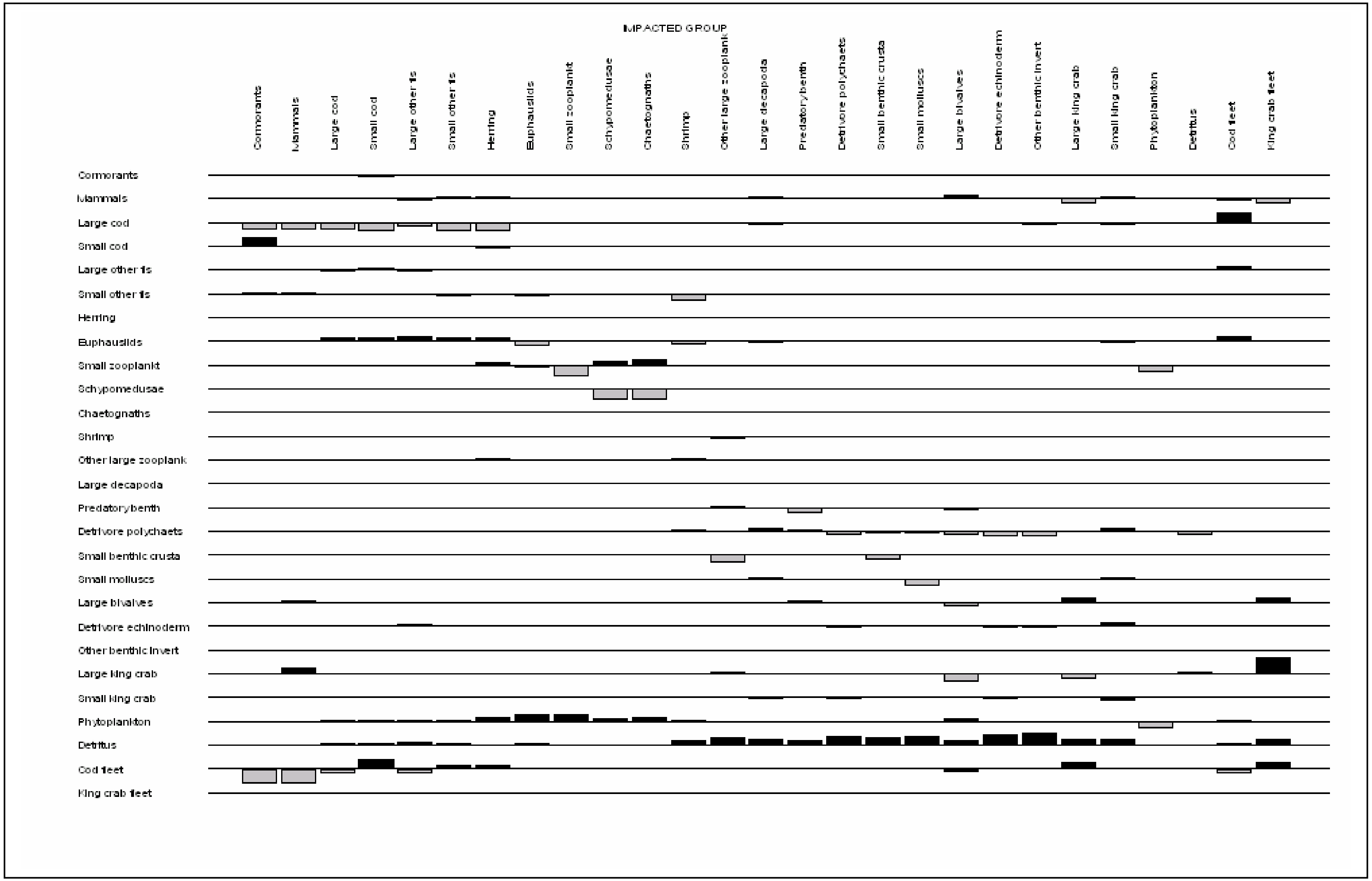
Group number	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	Cormorants	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Mammals	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Large cod	0,008	**0,098**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Small cod	0,100	**0,126**	**0,427**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Large other fis	0,003	**0,113**	**0,007**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Small other fis	0,005	**0,092**	**1,210**	0,137	0,012	0,074	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Herring	-	**0,080**	**1,333**	0,321	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Euphausiids	-	-	**0,637**	0,089	0,317	0,533	0,146	0,334	-	0,193	-	-	-	-	-	-	-	-	-	-	-	-
9	Small zooplankt	-	-	-	-	-	-	0,026	0,302	1,300	0,499	0,190	0,019	-	-	-	-	-	-	-	-	-	-
10	Schypomedusae	-	-	-	-	-	-	-	-	-	0,867	-	-	-	-	-	-	-	-	-	-	-	-
11	Chaetognaths	-	-	-	-	-	-	-	-	-	1,872	-	-	-	-	-	-	-	-	-	-	-	-
12	Shrimp	-	-	**0,789**	0,279	0,012	0,719	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	Other large zooplankton	-	-	**0,069**	0,062	-	-	0,187	-	-	0,177	-	0,363	-	-	-	-	0,943	-	-	-	-	-
14	Large decapoda	-	-	**0,269**	0,060	0,026	0,085	-	-	-	-	-	-	-	**0,010**	-	-	-	-	-	-	-	-
15	Predatory benth	-	-	**0,149**	0,026	0,002	0,094	-	-	-	-	-	-	-	**0,012**	**0,167**	-	-	-	-	-	-	-
16	Detrivore polychaets	-	-	**0,004**	0,001	0,003	0,009	-	-	-	-	-	0,012	-	**0,010**	**0,030**	-	0,009	-	-	-	-	-
17	Small benthic crustaceans	-	-	**0,027**	0,021	0,001	0,006	-	-	-	-	-	0,026	-	**0,005**	**0,032**	-	0,100	-	-	-	-	-
18	Small molluscs	-	-	**0,007**	0,000	0,009	0,014	-	-	-	-	-	0,008	-	**0,010**	**0,011**	-	-	0,163	-	-	-	-
19	Large bivalves	-	-	-	-	-	-	-	-	-	-	-	-	-	**0,002**	**0,013**	-	-	-	-	-	-	-
20	Detrivore echinoderms	-	-	**0,010**	0,000	0,013	0,009	-	-	-	-	-	-	-	**0,005**	**0,018**	-	0,003	-	-	-	-	-
21	Other benthic invertebrates	-	-	**0,068**	0,002	-	-	-	-	-	-	-	-	-	**0,010**	**0,042**	-	-	-	-	-	-	-
22	Phytoplankton	-	-	-	-	-	-	-	2,262	22,100	-	-	0,026	0,094	-	-	1,060	0,067	-	1,991	-	-	-

Table D2. Predation mortality rate in Model II. Parameters discussed in text are marked in bold.

Group number	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1	Cormorants	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	Mammals	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Large cod	0,008	**0,064**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Small cod	0,100	**0,080**	**0,385**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Large other fis	0,003	**0,074**	**0,007**	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Small other fis	0,005	**0,066**	**1,232**	0,141	0,013	0,074	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Herring	-	**0,051**	**1,250**	0,301	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Euphausiids	-	-	**0,629**	0,088	0,330	0,505	0,157	0,334	-	0,207	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Small zooplankt	-	-	-	-	-	-	0,026	0,282	1,300	0,499	0,190	0,018	-	-	-	-	-	-	-	-	-	-	-	-
10	Schypomedusae	-	-	-	-	-	-	-	-	-	0,867	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	Chaetognaths	-	-	-	-	-	-	-	-	-	1,872	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	Shrimp	-	-	**0,789**	0,283	0,013	0,714	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	Other large zooplankton	-	-	**0,062**	0,060	-	-	0,191	-	-	0,181	-	0,342	-	-	-	-	0,965	-	-	-	-	-	-	-
14	Large decapoda	-	-	**0,224**	0,049	0,021	0,065	-	-	-	-	-	-	-	**0,010**	-	-	-	-	-	-	-	0,039	0,042	-
15	Predatory benth	-	-	**0,111**	0,019	0,001	0,066	-	-	-	-	-	-	-	**0,011**	**0,167**	-	-	-	-	-	-	0,035	0,040	-
16	Detrivore polychaets	-	-	**0,004**	0,001	0,003	0,008	-	-	-	-	-	0,011	-	**0,012**	**0,039**	-	0,009	-	-	-	-	0,046	0,050	-
17	Small benthic crustaceans	-	-	**0,026**	0,020	0,001	0,005	-	-	-	-	-	0,024	-	**0,006**	**0,041**	-	0,100	-	-	-	-	0,046	0,051	-
18	Small molluscs	-	-	**0,007**	0,000	0,008	0,012	-	-	-	-	-	0,007	-	**0,012**	**0,015**	-	-	0,163	-	-	-	0,046	0,050	-
19	Large bivalves	-	-	-	-	-	-	-	-	-	-	-	-	-	**0,003**	**0,018**	-	-	-	-	-	-	0,046	-	-
20	Detrivore echinoderms	-	-	**0,009**	0,000	0,012	0,008	-	-	-	-	-	-	-	**0,006**	**0,023**	-	0,003	-	-	-	-	0,046	0,050	-
21	Other benthic invertebrates	-	-	**0,065**	0,002	-	-	-	-	-	-	-	-	-	**0,012**	**0,055**	-	-	-	-	-	-	0,046	0,051	-
22	Large king crab	-	0,044	0,039	-	0,017	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23	Small king crab	-	-	0,220	0,045	0,021	0,065	-	-	-	-	-	-	-	0,008	-	-	-	-	-	-	-	0,049	0,050	-
24	Phytoplankton	-	-	-	-	-	-	-	2,113	22,100	-	-	0,024	0,092	-	-	1,060	0,067	-	1,991	-	-	-	-	-

APPENDIX E

Mixed trophic impact analysis of Model II. The figure shows positive (above line) and negative (below line) impacts. Impacted groups are shown along the horizontal axis and impacting groups along the vertical axis.



APPENDIX F

Sensitivity analysis of Model II showing the impact of a ±50% variation of input parameters on estimated parameter. Parameters discussed in text are marked in bold.

Group	Input parameter	Group	Estimated parameter	-50 %	-40 %	-30 %	-20 %	-10 %	0 %	10 %	20 %	30 %	40 %	50 %
Cormorants	Biomass	Cormorants	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Cormorants	Biomass	Small cod	EE	-0,089	-0,071	-0,053	-0,035	-0,018	0	0,018	0,035	0,053	0,071	0,089
Cormorants	P/B	Cormorants	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Cormorants	Q/B	Small cod	EE	-0,089	-0,071	-0,053	-0,035	-0,018	0	0,018	0,035	0,053	0,071	0,089
Mammals	Biomass	Mammals	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Mammals	Biomass	Large cod	EE	-0,096	-0,077	-0,058	-0,039	-0,019	0	0,019	0,039	0,058	0,077	0,096
Mammals	Biomass	Small cod	EE	-0,071	-0,057	-0,043	-0,028	-0,014	0	0,014	0,028	0,043	0,057	0,071
Mammals	Biomass	Large other fish	EE	-0,134	-0,108	-0,081	-0,054	-0,027	0	0,027	0,054	0,081	0,108	0,134
Mammals	Biomass	Large king crab	EE	-0,213	-0,171	-0,128	-0,085	-0,043	0	0,043	0,085	0,128	0,171	0,213
Mammals	P/B	Mammals	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Mammals	Q/B	Large cod	EE	-0,096	-0,077	-0,058	-0,039	-0,019	0	0,019	0,039	0,058	0,077	0,096
Mammals	Q/B	Small cod	EE	-0,071	-0,057	-0,043	-0,028	-0,014	0	0,014	0,028	0,043	0,057	0,071
Mammals	Q/B	Large other fish	EE	-0,134	-0,108	-0,081	-0,054	-0,027	0	0,027	0,054	0,081	0,108	0,134
Mammals	**Q/B**	**Large king crab**	**EE**	**-0,213**	**-0,171**	**-0,128**	**-0,085**	**-0,043**	**0**	**0,043**	**0,085**	**0,128**	**0,171**	**0,213**
Large cod	Biomass	Large cod	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Large cod	Biomass	Small cod	EE	-0,34	-0,272	-0,204	-0,136	-0,068	0	0,068	0,136	0,204	0,272	0,34
Large cod	Biomass	Small other fish	Biomass	-0,423	-0,338	-0,254	-0,169	-0,085	0	0,085	0,169	0,254	0,338	0,423
Large cod	Biomass	Euphausiids	Biomass	-0,276	-0,221	-0,165	-0,11	-0,055	0	0,055	0,11	0,165	0,221	0,276
Large cod	Biomass	Small zooplanktion	EE	-0,037	-0,029	-0,022	-0,015	-0,007	0	0,007	0,015	0,022	0,029	0,037
Large cod	Biomass	Shrimp	Biomass	-0,387	-0,31	-0,232	-0,155	-0,077	0	0,077	0,155	0,232	0,31	0,387
Large cod	Biomass	Other large zooplankton	Biomass	-0,091	-0,073	-0,055	-0,036	-0,018	0	0,018	0,036	0,055	0,073	0,091
Large cod	Biomass	Large decapoda	Biomass	-0,318	-0,254	-0,191	-0,127	-0,064	0	0,064	0,127	0,191	0,254	0,318
Large cod	Biomass	Predatory benthos	Biomass	-0,306	-0,245	-0,184	-0,122	-0,061	0	0,061	0,122	0,184	0,245	0,306
Large cod	Biomass	Detrivore polychaets	EE	-0,138	-0,11	-0,083	-0,055	-0,028	0	0,028	0,055	0,083	0,11	0,138
Large cod	Biomass	Small benthic crustaceans	EE	-0,121	-0,097	-0,073	-0,049	-0,024	0	0,024	0,049	0,073	0,097	0,121
Large cod	Biomass	Small mollusks	EE	-0,061	-0,049	-0,037	-0,025	-0,012	0	0,012	0,025	0,037	0,049	0,061
Large cod	Biomass	Large bivalves	EE	-0,094	-0,076	-0,057	-0,038	-0,019	0	0,019	0,038	0,057	0,076	0,094
Large cod	Biomass	Detrivore echinoderms	EE	-0,105	-0,084	-0,063	-0,042	-0,021	0	0,021	0,042	0,063	0,084	0,105
Large cod	Biomass	Other benthic invertebrates	EE	-0,23	-0,184	-0,138	-0,092	-0,046	0	0,046	0,092	0,138	0,184	0,23
Large cod	**Biomass**	**Large king crab**	**EE**	**-0,188**	**-0,151**	**-0,113**	**-0,075**	**-0,038**	**0**	**0,038**	**0,075**	**0,113**	**0,151**	**0,188**
Large cod	**Biomass**	**Small king crab**	**EE**	**-0,305**	**-0,244**	**-0,183**	**-0,122**	**-0,061**	**0**	**0,061**	**0,122**	**0,183**	**0,244**	**0,305**
Large cod	P/B	Large cod	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Large cod	Q/B	Small cod	EE	-0,34	-0,272	-0,204	-0,136	-0,068	0	0,068	0,136	0,204	0,272	0,34
Large cod	Q/B	Small other fish	Biomass	-0,423	-0,338	-0,254	-0,169	-0,085	0	0,085	0,169	0,254	0,338	0,423
Large cod	Q/B	Euphausiids	Biomass	-0,276	-0,221	-0,165	-0,11	-0,055	0	0,055	0,11	0,165	0,221	0,276
Large cod	Q/B	Small zooplanktion	EE	-0,037	-0,029	-0,022	-0,015	-0,007	0	0,007	0,015	0,022	0,029	0,037
Large cod	Q/B	Shrimp	Biomass	-0,387	-0,31	-0,232	-0,155	-0,077	0	0,077	0,155	0,232	0,31	0,387
Large cod	Q/B	Other large zooplankton	Biomass	-0,091	-0,073	-0,055	-0,036	-0,018	0	0,018	0,036	0,055	0,073	0,091
Large cod	Q/B	Large decapoda	Biomass	-0,318	-0,254	-0,191	-0,127	-0,064	0	0,064	0,127	0,191	0,254	0,318
Large cod	Q/B	Predatory benthos	Biomass	-0,306	-0,245	-0,184	-0,122	-0,061	0	0,061	0,122	0,184	0,245	0,306

Sensitivity analysis of Model II (continue).

Group	Input parameter	Group	Estimated parameter	-50 %	-40 %	-30 %	-20 %	-10 %	0 %	10 %	20 %	30 %	40 %	50 %
Large cod	Q/B	Detrivore polychaets	EE	-0,138	-0,11	-0,083	-0,055	-0,028	0	0,028	0,055	0,083	0,11	0,138
Large cod	Q/B	Small benthic crustaceans	EE	-0,121	-0,097	-0,073	-0,049	-0,024	0	0,024	0,049	0,073	0,097	0,121
Large cod	Q/B	Small mollusks	EE	-0,061	-0,049	-0,037	-0,025	-0,012	0	0,012	0,025	0,037	0,049	0,061
Large cod	Q/B	Large bivalves	EE	-0,094	-0,076	-0,057	-0,038	-0,019	0	0,019	0,038	0,057	0,076	0,094
Large cod	Q/B	Detrivore echinoderms	EE	-0,105	-0,084	-0,063	-0,042	-0,021	0	0,021	0,042	0,063	0,084	0,105
Large cod	Q/B	Other benthic invertebrates	EE	-0,23	-0,184	-0,138	-0,092	-0,046	0	0,046	0,092	0,138	0,184	0,23
Large cod	Q/B	Large king crab	EE	-0,188	-0,151	-0,113	-0,075	-0,038	0	0,038	0,075	0,113	0,151	0,188
Large cod	Q/B	Small king crab	EE	-0,305	-0,244	-0,183	-0,122	-0,061	0	0,061	0,122	0,183	0,244	0,305
Small cod	Biomass	Small cod	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Small cod	Biomass	Small other fish	Biomass	-0,048	-0,039	-0,029	-0,019	-0,01	0	0,01	0,019	0,029	0,039	0,048
Small cod	Biomass	Euphausiids	Biomass	-0,036	-0,029	-0,021	-0,014	-0,007	0	0,007	0,014	0,021	0,029	0,036
Small cod	Biomass	Shrimp	Biomass	-0,098	-0,078	-0,059	-0,039	-0,02	0	0,02	0,039	0,059	0,078	0,098
Small cod	Biomass	Other large zooplankton	Biomass	-0,035	-0,028	-0,021	-0,014	-0,007	0	0,007	0,014	0,021	0,028	0,035
Small cod	Biomass	Large decapoda	Biomass	-0,062	-0,05	-0,037	-0,025	-0,012	0	0,012	0,025	0,037	0,05	0,062
Small cod	Biomass	Predatory benthos	Biomass	-0,048	-0,038	-0,029	-0,019	-0,01	0	0,01	0,019	0,029	0,038	0,048
Small cod	Biomass	Small benthic crustaceans	EE	-0,046	-0,037	-0,028	-0,018	-0,009	0	0,009	0,018	0,028	0,037	0,046
Small cod	**Biomass**	**Small king crab**	**EE**	**-0,057**	**-0,046**	**-0,034**	**-0,023**	**-0,011**	**0**	**0,011**	**0,023**	**0,034**	**0,046**	**0,057**
Small cod	P/B	Small cod	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Small cod	Q/B	Small other fish	Biomass	-0,048	-0,039	-0,029	-0,019	-0,01	0	0,01	0,019	0,029	0,039	0,048
Small cod	Q/B	Euphausiids	Biomass	-0,036	-0,029	-0,021	-0,014	-0,007	0	0,007	0,014	0,021	0,029	0,036
Small cod	Q/B	Shrimp	Biomass	-0,098	-0,078	-0,059	-0,039	-0,02	0	0,02	0,039	0,059	0,078	0,098
Small cod	Q/B	Other large zooplankton	Biomass	-0,035	-0,028	-0,021	-0,014	-0,007	0	0,007	0,014	0,021	0,028	0,035
Small cod	Q/B	Large decapoda	Biomass	-0,062	-0,05	-0,037	-0,025	-0,012	0	0,012	0,025	0,037	0,05	0,062
Small cod	Q/B	Predatory benthos	Biomass	-0,048	-0,038	-0,029	-0,019	-0,01	0	0,01	0,019	0,029	0,038	0,048
Small cod	Q/B	Small benthic crustaceans	EE	-0,046	-0,037	-0,028	-0,018	-0,009	0	0,009	0,018	0,028	0,037	0,046
Small cod	Q/B	Small king crab	EE	-0,057	-0,046	-0,034	-0,023	-0,011	0	0,011	0,023	0,034	0,046	0,057
Large other fish	Biomass	Large other fish	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Large other fish	Biomass	Euphausiids	Biomass	-0,087	-0,07	-0,052	-0,035	-0,017	0	0,017	0,035	0,052	0,07	0,087
Large other fish	Biomass	Detrivore echinoderms	EE	-0,041	-0,032	-0,024	-0,016	-0,008	0	0,008	0,016	0,024	0,032	0,041
Large other fish	**Biomass**	**Large king crab**	**EE**	**-0,081**	**-0,065**	**-0,049**	**-0,032**	**-0,016**	**0**	**0,016**	**0,032**	**0,049**	**0,065**	**0,081**
Large other fish	P/B	Large other fish	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Large other fish	Q/B	Euphausiids	Biomass	-0,087	-0,07	-0,052	-0,035	-0,017	0	0,017	0,035	0,052	0,07	0,087
Large other fish	Q/B	Detrivore echinoderms	EE	-0,041	-0,032	-0,024	-0,016	-0,008	0	0,008	0,016	0,024	0,032	0,041
Large other fish	**Q/B**	**Large king crab**	**EE**	**-0,081**	**-0,065**	**-0,049**	**-0,032**	**-0,016**	**0**	**0,016**	**0,032**	**0,049**	**0,065**	**0,081**
Small other fish	P/B	Small other fish	Biomass	1,107	0,725	0,46	0,266	0,117	0	-0,095	-0,174	-0,24	-0,296	-0,344
Small other fish	P/B	Euphausiids	Biomass	0,292	0,191	0,121	0,07	0,031	0	-0,025	-0,046	-0,063	-0,078	-0,091
Small other fish	P/B	Shrimp	Biomass	0,439	0,288	0,183	0,106	0,047	0	-0,038	-0,069	-0,095	-0,117	-0,137
Small other fish	P/B	Other large zooplankton	Biomass	0,083	0,055	0,035	0,02	0,009	0	-0,007	-0,013	-0,018	-0,022	-0,026
Small other fish	P/B	Large decapoda	Biomass	0,164	0,107	0,068	0,039	0,017	0	-0,014	-0,026	-0,036	-0,044	-0,051
Small other fish	P/B	Predatory benthos	Biomass	0,264	0,173	0,11	0,063	0,028	0	-0,023	-0,041	-0,057	-0,07	-0,082
Small other fish	P/B	Detrivore polychaets	EE	0,14	0,092	0,058	0,034	0,015	0	-0,012	-0,022	-0,03	-0,037	-0,044

Sensitivity analysis of Model II (continue).

Group	Input parameter	Group	Estimated parameter	-50 %	-40 %	-30 %	-20 %	-10 %	0 %	10 %	20 %	30 %	40 %	50 %
Small other fish	P/B	Small benthic crustaceans	EE	0,088	0,058	0,037	0,021	0,009	0	-0,008	-0,014	-0,019	-0,024	-0,027
Small other fish	P/B	Small mollusks	EE	0,071	0,046	0,03	0,017	0,008	0	-0,006	-0,011	-0,015	-0,019	-0,022
Small other fish	P/B	Large bivalves	EE	0,077	0,05	0,032	0,018	0,008	0	-0,007	-0,012	-0,017	-0,02	-0,024
Small other fish	P/B	Detrivore echinoderms	EE	0,099	0,065	0,041	0,024	0,01	0	-0,009	-0,016	-0,021	-0,026	-0,031
Small other fish	P/B	Other benthic invertebrates	EE	0,071	0,047	0,03	0,017	0,008	0	-0,006	-0,011	-0,015	-0,019	-0,022
Small other fish	**P/B**	**Small king crab**	**EE**	**0,159**	**0,104**	**0,066**	**0,038**	**0,017**	**0**	**-0,014**	**-0,025**	**-0,034**	**-0,042**	**-0,049**
Small other fish	Q/B	Euphausiids	Biomass	-0,135	-0,109	-0,082	-0,055	-0,028	0	0,028	0,056	0,084	0,113	0,142
Small other fish	Q/B	Shrimp	Biomass	-0,203	-0,163	-0,123	-0,083	-0,041	0	0,042	0,084	0,127	0,17	0,214
Small other fish	Q/B	Other large zooplankton	Biomass	-0,039	-0,031	-0,023	-0,016	-0,008	0	0,008	0,016	0,024	0,032	0,041
Small other fish	Q/B	Large decapoda	Biomass	-0,076	-0,061	-0,046	-0,031	-0,015	0	0,016	0,031	0,047	0,064	0,08
Small other fish	Q/B	Predatory benthos	Biomass	-0,122	-0,098	-0,074	-0,05	-0,025	0	0,025	0,051	0,076	0,102	0,128
Small other fish	Q/B	Detrivore polychaets	EE	-0,065	-0,052	-0,039	-0,026	-0,013	0	0,013	0,027	0,041	0,054	0,068
Small other fish	Q/B	Small benthic crustaceans	EE	-0,041	-0,033	-0,025	-0,017	-0,008	0	0,008	0,017	0,025	0,034	0,043
Small other fish	Q/B	Small mollusks	EE	-0,033	-0,026	-0,02	-0,013	-0,007	0	0,007	0,014	0,021	0,028	0,035
Small other fish	Q/B	Large bivalves	EE	-0,035	-0,029	-0,021	-0,014	-0,007	0	0,007	0,015	0,022	0,03	0,037
Small other fish	Q/B	Detrivore echinoderms	EE	-0,046	-0,037	-0,028	-0,019	-0,009	0	0,009	0,019	0,029	0,038	0,048
Small other fish	Q/B	Other benthic invertebrates	EE	-0,033	-0,027	-0,02	-0,013	-0,007	0	0,007	0,014	0,021	0,028	0,035
Small other fish	Q/B	Small king crab	EE	-0,074	-0,059	-0,045	-0,03	-0,015	0	0,015	0,03	0,046	0,062	0,077
Small other fish	EE	Small other fish	Biomass	1,107	0,725	0,46	0,266	0,117	0	-0,095	-0,174	-0,24	-0,296	-0,344
Small other fish	EE	Euphausiids	Biomass	0,292	0,191	0,121	0,07	0,031	0	-0,025	-0,046	-0,063	-0,078	-0,091
Small other fish	EE	Shrimp	Biomass	0,439	0,288	0,183	0,106	0,047	0	-0,038	-0,069	-0,095	-0,117	-0,137
Small other fish	EE	Other large zooplankton	Biomass	0,083	0,055	0,035	0,02	0,009	0	-0,007	-0,013	-0,018	-0,022	-0,026
Small other fish	EE	Large decapoda	Biomass	0,164	0,107	0,068	0,039	0,017	0	-0,014	-0,026	-0,036	-0,044	-0,051
Small other fish	EE	Predatory benthos	Biomass	0,264	0,173	0,11	0,063	0,028	0	-0,023	-0,041	-0,057	-0,07	-0,082
Small other fish	EE	Detrivore polychaets	EE	0,14	0,092	0,058	0,034	0,015	0	-0,012	-0,022	-0,03	-0,037	-0,044
Small other fish	EE	Small benthic crustaceans	EE	0,088	0,058	0,037	0,021	0,009	0	-0,008	-0,014	-0,019	-0,024	-0,027
Small other fish	EE	Small mollusks	EE	0,071	0,046	0,03	0,017	0,008	0	-0,006	-0,011	-0,015	-0,019	-0,022
Small other fish	EE	Large bivalves	EE	0,077	0,05	0,032	0,018	0,008	0	-0,007	-0,012	-0,017	-0,02	-0,024
Small other fish	EE	Detrivore echinoderms	EE	0,099	0,065	0,041	0,024	0,01	0	-0,009	-0,016	-0,021	-0,026	-0,031
Small other fish	EE	Other benthic invertebrates	EE	0,071	0,047	0,03	0,017	0,008	0	-0,006	-0,011	-0,015	-0,019	-0,022
Small other fish	**EE**	**Small king crab**	**EE**	**0,159**	**0,104**	**0,066**	**0,038**	**0,017**	**0**	**-0,014**	**-0,025**	**-0,034**	**-0,042**	**-0,049**
Herring	Biomass	Euphausiids	Biomass	-0,041	-0,033	-0,025	-0,016	-0,008	0	0,008	0,016	0,025	0,033	0,041
Herring	Biomass	Other large zooplankton	Biomass	-0,053	-0,042	-0,032	-0,021	-0,011	0	0,011	0,021	0,032	0,042	0,053
Herring	Q/B	Euphausiids	Biomass	-0,041	-0,033	-0,025	-0,016	-0,008	0	0,008	0,016	0,025	0,033	0,041
Herring	Q/B	Other large zooplankton	Biomass	-0,053	-0,042	-0,032	-0,021	-0,011	0	0,011	0,021	0,032	0,042	0,053
Euphausiids	P/B	Euphausiids	Biomass	1,422	0,886	0,544	0,307	0,133	0	-0,105	-0,19	-0,261	-0,32	-0,37
Euphausiids	P/B	Small zooplanktion	EE	0,173	0,108	0,066	0,037	0,016	0	-0,013	-0,023	-0,032	-0,039	-0,045
Euphausiids	P/B	Pytoplankton	Q/B	0,109	0,068	0,042	0,024	0,01	0	-0,008	-0,015	-0,02	-0,025	-0,028
Euphausiids	Q/B	Euphausiids	Biomass	-0,08	-0,065	-0,05	-0,034	-0,017	0	0,018	0,036	0,055	0,075	0,095
Euphausiids	Q/B	Small zooplanktion	EE	-0,066	-0,053	-0,041	-0,028	-0,014	0	0,015	0,03	0,045	0,061	0,078
Euphausiids	Q/B	Pytoplankton	Q/B	-0,042	-0,034	-0,026	-0,017	-0,009	0	0,009	0,019	0,029	0,039	0,05

Sensitivity analysis of Model II (continue).

Group	Input parameter	Group	Estimated parameter	-50 %	-40 %	-30 %	-20 %	-10 %	0 %	10 %	20 %	30 %	40 %	50 %
Euphausiids	EE	Euphausiids	Biomass	1,422	0,886	0,544	0,307	0,133	0	-0,105	-0,19	-0,261	-0,32	-0,37
Euphausiids	EE	Small zooplanktion	EE	0,173	0,108	0,066	0,037	0,016	0	-0,013	-0,023	-0,032	-0,039	-0,045
Euphausiids	EE	Pytoplankton	Q/B	0,109	0,068	0,042	0,024	0,01	0	-0,008	-0,015	-0,02	-0,025	-0,028
Small zooplankton	Biomass	Small zooplanktion	EE	0,438	0,292	0,188	0,11	0,049	0	-0,04	-0,073	-0,101	-0,125	-0,146
Small zooplankton	Biomass	Pytoplankton	Q/B	-0,403	-0,322	-0,242	-0,161	-0,081	0	0,081	0,161	0,242	0,322	0,403
Small zooplankton	P/B	Small zooplanktion	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Small zooplankton	Q/B	Small zooplanktion	EE	-0,281	-0,225	-0,168	-0,112	-0,056	0	0,056	0,112	0,168	0,225	0,281
Small zooplankton	Q/B	Pytoplankton	Q/B	-0,403	-0,322	-0,242	-0,161	-0,081	0	0,081	0,161	0,242	0,322	0,403
Schypomedusae	Biomass	Euphausiids	Biomass	-0,054	-0,043	-0,032	-0,022	-0,011	0	0,011	0,022	0,032	0,043	0,054
Schypomedusae	Biomass	Small zooplanktion	EE	-0,114	-0,092	-0,069	-0,046	-0,023	0	0,023	0,046	0,069	0,092	0,114
Schypomedusae	Biomass	Chaetognaths	EE	-0,5	-0,4	-0,3	-0,2	-0,1	0	0,1	0,2	0,3	0,4	0,5
Schypomedusae	Biomass	Other large zooplankton	Biomass	-0,05	-0,04	-0,03	-0,02	-0,01	0	0,01	0,02	0,03	0,04	0,05
Schypomedusae	P/B	Schypomedusae	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Schypomedusae	Q/B	Euphausiids	Biomass	-0,054	-0,043	-0,032	-0,022	-0,011	0	0,011	0,022	0,032	0,043	0,054
Schypomedusae	Q/B	Small zooplanktion	EE	-0,114	-0,092	-0,069	-0,046	-0,023	0	0,023	0,046	0,069	0,092	0,114
Schypomedusae	Q/B	Schypomedusae	EE	-0,5	-0,4	-0,3	-0,2	-0,1	0	0,1	0,2	0,3	0,4	0,5
Schypomedusae	Q/B	Chaetognaths	EE	-0,5	-0,4	-0,3	-0,2	-0,1	0	0,1	0,2	0,3	0,4	0,5
Schypomedusae	Q/B	Other large zooplankton	Biomass	-0,05	-0,04	-0,03	-0,02	-0,01	0	0,01	0,02	0,03	0,04	0,05
Chaetognaths	Biomass	Small zooplanktion	EE	-0,041	-0,033	-0,025	-0,016	-0,008	0	0,008	0,016	0,025	0,033	0,041
Chaetognaths	Biomass	Chaetognaths	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Chaetognaths	P/B	Chaetognaths	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Chaetognaths	Q/B	Small zooplanktion	EE	-0,041	-0,033	-0,025	-0,016	-0,008	0	0,008	0,016	0,025	0,033	0,041
Shrimp	P/B	Shrimp	Biomass	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Shrimp	P/B	Other large zooplankton	Biomass	0,19	0,127	0,081	0,047	0,021	0	-0,017	-0,032	-0,044	-0,054	-0,063
Shrimp	P/B	Detrivore polychaets	EE	0,06	0,04	0,026	0,015	0,007	0	-0,005	-0,01	-0,014	-0,017	-0,02
Shrimp	P/B	Small benthic crustaceans	EE	0,074	0,049	0,032	0,019	0,008	0	-0,007	-0,012	-0,017	-0,021	-0,025
Shrimp	Q/B	Other large zooplankton	Biomass	-0,095	-0,076	-0,057	-0,038	-0,019	0	0,019	0,038	0,057	0,076	0,095
Shrimp	Q/B	Small benthic crustaceans	EE	-0,037	-0,03	-0,022	-0,015	-0,007	0	0,007	0,015	0,022	0,03	0,037
Shrimp	EE	Shrimp	Biomass	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Shrimp	EE	Other large zooplankton	Biomass	0,19	0,127	0,081	0,047	0,021	0	-0,017	-0,032	-0,044	-0,054	-0,063
Shrimp	EE	Detrivore polychaets	EE	0,06	0,04	0,026	0,015	0,007	0	-0,005	-0,01	-0,014	-0,017	-0,02
Shrimp	EE	Small benthic crustaceans	EE	0,074	0,049	0,032	0,019	0,008	0	-0,007	-0,012	-0,017	-0,021	-0,025
Other large zooplankton	P/B	Other large zooplankton	Biomass	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Other large zooplankton	EE	Other large zooplankton	Biomass	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Large decapoda	P/B	Large decapoda	Biomass	1,046	0,692	0,443	0,257	0,114	0	-0,093	-0,17	-0,235	-0,29	-0,338
Large decapoda	P/B	Detrivore polychaets	EE	0,075	0,049	0,032	0,018	0,008	0	-0,007	-0,012	-0,017	-0,021	-0,024
Large decapoda	P/B	Other benthic invertebrates	EE	0,062	0,041	0,026	0,015	0,007	0	-0,006	-0,01	-0,014	-0,017	-0,02
Large decapoda	Q/B	Detrivore polychaets	EE	-0,036	-0,029	-0,022	-0,015	-0,007	0	0,007	0,015	0,022	0,029	0,037
Large decapoda	EE	Large decapoda	Biomass	1,046	0,692	0,443	0,257	0,114	0	-0,093	-0,17	-0,235	-0,29	-0,338
Large decapoda	EE	Detrivore polychaets	EE	0,075	0,049	0,032	0,018	0,008	0	-0,007	-0,012	-0,017	-0,021	-0,024
Large decapoda	EE	Other benthic invertebrates	EE	0,062	0,041	0,026	0,015	0,007	0	-0,006	-0,01	-0,014	-0,017	-0,02

Sensitivity analysis of Model II (continue).

Group	Input parameter	Group	Estimated parameter	-50 %	-40 %	-30 %	-20 %	-10 %	0 %	10 %	20 %	30 %	40 %	50 %
Predatory benthos	P/B	Predatory benthos	Biomass	3,846	1,739	0,909	0,465	0,189	0	-0,137	-0,241	-0,323	-0,388	-0,442
Predatory benthos	P/B	Detrivore polychaets	EE	0,809	0,366	0,191	0,098	0,04	0	-0,029	-0,051	-0,068	-0,082	-0,093
Predatory benthos	P/B	Small benthic crustaceans	EE	0,5	0,226	0,118	0,06	0,025	0	-0,018	-0,031	-0,042	-0,05	-0,057
Predatory benthos	P/B	Small mollusks	EE	0,178	0,08	0,042	0,022	0,009	0	-0,006	-0,011	-0,015	-0,018	-0,02
Predatory benthos	P/B	Large bivalves	EE	1,014	0,459	0,24	0,123	0,05	0	-0,036	-0,064	-0,085	-0,102	-0,117
Predatory benthos	P/B	Detrivore echinoderms	EE	0,557	0,252	0,132	0,067	0,027	0	-0,02	-0,035	-0,047	-0,056	-0,064
Predatory benthos	P/B	Other benthic invertebrates	EE	0,923	0,417	0,218	0,112	0,045	0	-0,033	-0,058	-0,077	-0,093	-0,106
Predatory benthos	Q/B	Predatory benthos	Biomass	-0,227	-0,19	-0,15	-0,105	-0,055	0	0,062	0,133	0,214	0,307	0,416
Predatory benthos	Q/B	Detrivore polychaets	EE	-0,129	-0,108	-0,085	-0,06	-0,032	0	0,035	0,076	0,122	0,175	0,236
Predatory benthos	Q/B	Small benthic crustaceans	EE	-0,08	-0,067	-0,053	-0,037	-0,019	0	0,022	0,047	0,075	0,108	0,146
Predatory benthos	Q/B	Small mollusks	EE	-0,028	-0,024	-0,019	-0,013	-0,007	0	0,008	0,017	0,027	0,038	0,052
Predatory benthos	Q/B	Large bivalves	EE	-0,162	-0,136	-0,107	-0,075	-0,04	0	0,044	0,095	0,152	0,219	0,296
Predatory benthos	Q/B	Detrivore echinoderms	EE	-0,089	-0,074	-0,059	-0,041	-0,022	0	0,024	0,052	0,084	0,12	0,163
Predatory benthos	Q/B	Other benthic invertebrates	EE	-0,147	-0,123	-0,097	-0,068	-0,036	0	0,04	0,086	0,139	0,199	0,27
Predatory benthos	EE	Predatory benthos	Biomass	3,846	1,739	0,909	0,465	0,189	0	-0,137	-0,241	-0,323	-0,388	-0,442
Predatory benthos	EE	Detrivore polychaets	EE	0,809	0,366	0,191	0,098	0,04	0	-0,029	-0,051	-0,068	-0,082	-0,093
Predatory benthos	EE	Small benthic crustaceans	EE	0,5	0,226	0,118	0,06	0,025	0	-0,018	-0,031	-0,042	-0,05	-0,057
Predatory benthos	EE	Small mollusks	EE	0,178	0,08	0,042	0,022	0,009	0	-0,006	-0,011	-0,015	-0,018	-0,02
Predatory benthos	EE	Large bivalves	EE	1,014	0,459	0,24	0,123	0,05	0	-0,036	-0,064	-0,085	-0,102	-0,117
Predatory benthos	EE	Detrivore echinoderms	EE	0,557	0,252	0,132	0,067	0,027	0	-0,02	-0,035	-0,047	-0,056	-0,064
Predatory benthos	EE	Other benthic invertebrates	EE	0,923	0,417	0,218	0,112	0,045	0	-0,033	-0,058	-0,077	-0,093	-0,106
Detrivore polychaets	Biomass	Detrivore polychaets	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Detrivore polychaets	P/B	Detrivore polychaets	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Small benthic crustaceans	Biomass	Other large zooplankton	Biomass	-0,268	-0,214	-0,161	-0,107	-0,054	0	0,054	0,107	0,161	0,214	0,268
Small benthic crustaceans	Biomass	Small benthic crustaceans	EE	0,686	0,458	0,294	0,172	0,076	0	-0,062	-0,114	-0,158	-0,196	-0,229
Small benthic crustaceans	P/B	Small benthic crustaceans	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Small benthic crustaceans	Q/B	Other large zooplankton	Biomass	-0,268	-0,214	-0,161	-0,107	-0,054	0	0,054	0,107	0,161	0,214	0,268
Small benthic crustaceans	Q/B	Small benthic crustaceans	EE	-0,157	-0,125	-0,094	-0,063	-0,031	0	0,031	0,063	0,094	0,125	0,157
Small molluscs	Biomass	Small mollusks	EE	0,492	0,328	0,211	0,123	0,055	0	-0,045	-0,082	-0,114	-0,141	-0,164
Small molluscs	P/B	Small mollusks	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Small molluscs	Q/B	Small mollusks	EE	-0,254	-0,203	-0,152	-0,102	-0,051	0	0,051	0,102	0,152	0,203	0,254
Large bivalves	Biomass	Large bivalves	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Large bivalves	Biomass	Pytoplankton	Q/B	-0,036	-0,029	-0,022	-0,015	-0,007	0	0,007	0,015	0,022	0,029	0,036
Large bivalves	P/B	Large bivalves	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Large bivalves	Q/B	Pytoplankton	Q/B	-0,036	-0,029	-0,022	-0,015	-0,007	0	0,007	0,015	0,022	0,029	0,036
Detrivore echinoderms	Biomass	Detrivore echinoderms	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Detrivore echinoderms	P/B	Detrivore echinoderms	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Other benthic invertebrates	Biomass	Other benthic invertebrates	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Other benthic invertebrates	P/B	Other benthic invertebrates	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Large king crab	Biomass	Large decapoda	Biomass	-0,044	-0,035	-0,026	-0,018	-0,009	0	0,009	0,018	0,026	0,035	0,044
Large king crab	Biomass	Predatory benthos	Biomass	-0,064	-0,051	-0,039	-0,026	-0,013	0	0,013	0,026	0,039	0,051	0,064

Sensitivity analysis of Model II (continue).

Group	Input parameter	Group	Estimated parameter	-50 %	-40 %	-30 %	-20 %	-10 %	0 %	10 %	20 %	30 %	40 %	50 %
Large king crab	Biomass	Detrivore polychaets	EE	-0,143	-0,114	-0,086	-0,057	-0,029	0	0,029	0,057	0,086	0,114	0,143
Large king crab	Biomass	Small benthic crustaceans	EE	-0,082	-0,065	-0,049	-0,033	-0,016	0	0,016	0,033	0,049	0,065	0,082
Large king crab	Biomass	Small mollusks	EE	-0,076	-0,061	-0,046	-0,031	-0,015	0	0,015	0,031	0,046	0,061	0,076
Large king crab	Biomass	Large bivalves	EE	-0,365	-0,292	-0,219	-0,146	-0,073	0	0,073	0,146	0,219	0,292	0,365
Large king crab	Biomass	Detrivore echinoderms	EE	-0,157	-0,126	-0,094	-0,063	-0,031	0	0,031	0,063	0,094	0,126	0,157
Large king crab	Biomass	Other benthic invertebrates	EE	-0,118	-0,094	-0,071	-0,047	-0,024	0	0,024	0,047	0,071	0,094	0,118
Large king crab	Biomass	Large king crab	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Large king crab	Biomass	Small king crab	EE	-0,054	-0,043	-0,032	-0,022	-0,011	0	0,011	0,022	0,032	0,043	0,054
Large king crab	P/B	Large king crab	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Large king crab	Q/B	Large decapoda	Biomass	-0,044	-0,035	-0,026	-0,018	-0,009	0	0,009	0,018	0,026	0,035	0,044
Large king crab	Q/B	Predatory benthos	Biomass	-0,064	-0,051	-0,039	-0,026	-0,013	0	0,013	0,026	0,039	0,051	0,064
Large king crab	Q/B	Detrivore polychaets	EE	-0,143	-0,114	-0,086	-0,057	-0,029	0	0,029	0,057	0,086	0,114	0,143
Large king crab	Q/B	Small benthic crustaceans	EE	-0,082	-0,065	-0,049	-0,033	-0,016	0	0,016	0,033	0,049	0,065	0,082
Large king crab	Q/B	Small mollusks	EE	-0,076	-0,061	-0,046	-0,031	-0,015	0	0,015	0,031	0,046	0,061	0,076
Large king crab	Q/B	Large bivalves	EE	-0,365	-0,292	-0,219	-0,146	-0,073	0	0,073	0,146	0,219	0,292	0,365
Large king crab	Q/B	Detrivore echinoderms	EE	-0,157	-0,126	-0,094	-0,063	-0,031	0	0,031	0,063	0,094	0,126	0,157
Large king crab	Q/B	Other benthic invertebrates	EE	-0,118	-0,094	-0,071	-0,047	-0,024	0	0,024	0,047	0,071	0,094	0,118
Large king crab	Q/B	Small king crab	EE	-0,054	-0,043	-0,032	-0,022	-0,011	0	0,011	0,022	0,032	0,043	0,054
Small king crab	Biomass	Large decapoda	Biomass	-0,047	-0,038	-0,028	-0,019	-0,009	0	0,009	0,019	0,028	0,038	0,047
Small king crab	Biomass	Predatory benthos	Biomass	-0,072	-0,058	-0,043	-0,029	-0,014	0	0,014	0,029	0,043	0,058	0,072
Small king crab	Biomass	Detrivore polychaets	EE	-0,156	-0,125	-0,094	-0,062	-0,031	0	0,031	0,062	0,094	0,125	0,156
Small king crab	Biomass	Small benthic crustaceans	EE	-0,09	-0,072	-0,054	-0,036	-0,018	0	0,018	0,036	0,054	0,072	0,09
Small king crab	Biomass	Small mollusks	EE	-0,084	-0,067	-0,05	-0,033	-0,017	0	0,017	0,033	0,05	0,067	0,084
Small king crab	Biomass	Detrivore echinoderms	EE	-0,172	-0,137	-0,103	-0,069	-0,034	0	0,034	0,069	0,103	0,137	0,172
Small king crab	Biomass	Other benthic invertebrates	EE	-0,13	-0,104	-0,078	-0,052	-0,026	0	0,026	0,052	0,078	0,104	0,13
Small king crab	Biomass	Small king crab	EE	0,889	0,593	0,381	0,222	0,099	0	-0,081	-0,148	-0,205	-0,254	-0,296
Small king crab	P/B	Small king crab	EE	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Small king crab	Q/B	Large decapoda	Biomass	-0,047	-0,038	-0,028	-0,019	-0,009	0	0,009	0,019	0,028	0,038	0,047
Small king crab	Q/B	Predatory benthos	Biomass	-0,072	-0,058	-0,043	-0,029	-0,014	0	0,014	0,029	0,043	0,058	0,072
Small king crab	Q/B	Detrivore polychaets	EE	-0,156	-0,125	-0,094	-0,062	-0,031	0	0,031	0,062	0,094	0,125	0,156
Small king crab	Q/B	Small benthic crustaceans	EE	-0,09	-0,072	-0,054	-0,036	-0,018	0	0,018	0,036	0,054	0,072	0,09
Small king crab	Q/B	Small mollusks	EE	-0,084	-0,067	-0,05	-0,033	-0,017	0	0,017	0,033	0,05	0,067	0,084
Small king crab	Q/B	Detrivore echinoderms	EE	-0,172	-0,137	-0,103	-0,069	-0,034	0	0,034	0,069	0,103	0,137	0,172
Small king crab	Q/B	Other benthic invertebrates	EE	-0,13	-0,104	-0,078	-0,052	-0,026	0	0,026	0,052	0,078	0,104	0,13
Small king crab	Q/B	Small king crab	EE	-0,055	-0,044	-0,033	-0,022	-0,011	0	0,011	0,022	0,033	0,044	0,055
Phytoplankton	Biomass	Pytoplankton	Q/B	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333
Phytoplankton	P/B	Pytoplankton	Q/B	1	0,667	0,429	0,25	0,111	0	-0,091	-0,167	-0,231	-0,286	-0,333