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Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea–a review

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Abstract

> Falk-Petersen, J., Renaud, P., and Anisimova, N. 2011. Establishment and ecosystem effects of the alien invasive red king crab (*Paralithodes camtschaticus*) in the Barents Sea – a review. – ICES Journal of Marine Science, 68: .

Since its introduction to the Barents Sea from the North Pacific in the 1960s, the red king crab (*Paralithodes camtschaticus*) has become invasive. The crab represents an important source of income, but also a potential threat to the highly productive fisheries in the region through its ecosystem impacts. A literature review was conducted, identifying factors contributing to the success of the crab as well as its interactions with native biota. Characteristics of the Barents Sea and the crab itself that may explain its success include suitable habitat for settlement and growth of the larvae; the wide range of habitats occupied throughout its life history, high mobility, generalist prey choice, low fishing pressure during establishment, and the lack of parasites. Being a large, bottom-feeding omnivore of great mobility, the king crab can significantly impact the

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non-commercial fish species, through egg predation or indirect interactions, are difficult to detect and predict.

Keywords: alien invasive species, biological interactions, ecosystem impact, management

Introduction

Introduced species have been identified as major agents of global change and one of the main threats to marine systems because of their direct and indirect impacts on native ecosystems. Their effect on biodiversity, habitat structure, and economically important fisheries is a major source of concern (Mack *et al.*, 2000; Bax *et al.*, 2001; Courtenay *et al.*, 2009). The red king crab (*Paralithodes camtschaticus*; hereafter king crab) is one of a few large, higher-trophic-level marine organisms, which has established itself in a new geographic area (Jamieson *et al.*, 1998). It was introduced to the Barents Sea from the northern Pacific in the 1960s to establish a new commercial fishery. Since then, it has spread from the original area of introduction, the Kola fjord, Russia, west along the Norwegian coast and northeast of the Kola Peninsula (Figure 1; Anon., 2007). The crab is a highly valued delicacy on the international market and currently makes a significant contribution to the income from fisheries in the region (Wessel, 2004). There is a real concern, however, that the crab represents a threat to the other highly productive fisheries through its impact on the ecosystem (Anon., 2007).

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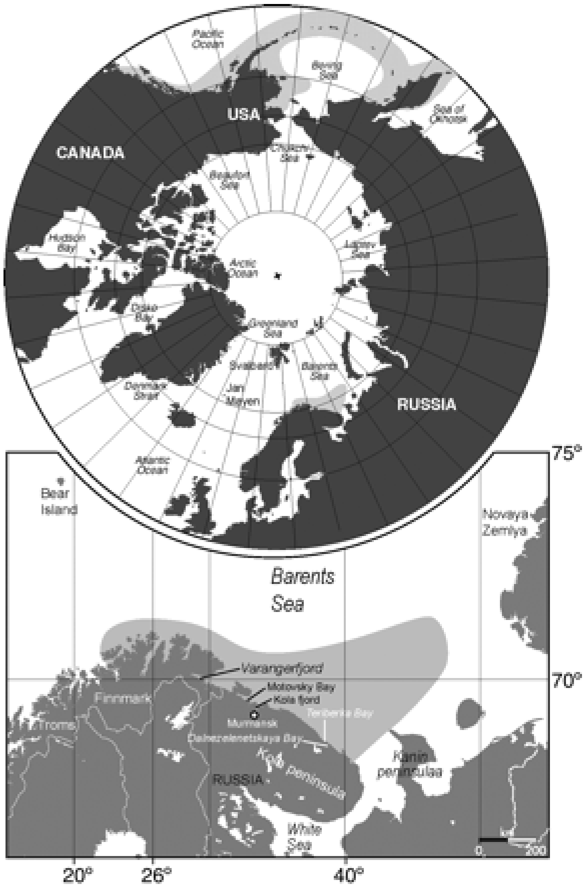

Figure 1. Distribution of red king crab in the Pacific and the Barents Sea (light grey), showing the locations of places mentioned in text.

Alien invasive species are rarely eradicated once established (Mack *et al.*, 2000), and the king crab has clearly come to stay in the Barents Sea. Understanding the factors determining their success is crucial if control efforts are to be established (Sakai *et al.*, 2001). Management institutions also stress the need for gaining a better understanding of what role the crab will play in the ecosystem (Anon., 2007). Being a large, bottom-feeding mobile omnivore, the king crab is likely to have a significant impact on the ecosystem through predation and competition. Predation on the Icelandic scallop (*Chlamys islandica*) and eggs of commercial fish (capelin *Mallotus villosus*, and lumpsucker *Cyclopteropsis macalpini*) has been documented in the Barents Sea (Anisimova *et al.*, 2005; Jørgensen, 2005; Anon., 2007). Dietary studies have also identified many non-commercial benthic

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Rzhavsky *et al.*, 2004; Anisimova *et al.*, 2005; Britaev *et al.*, 2006), population- and ecosystem-level effects are largely unknown.

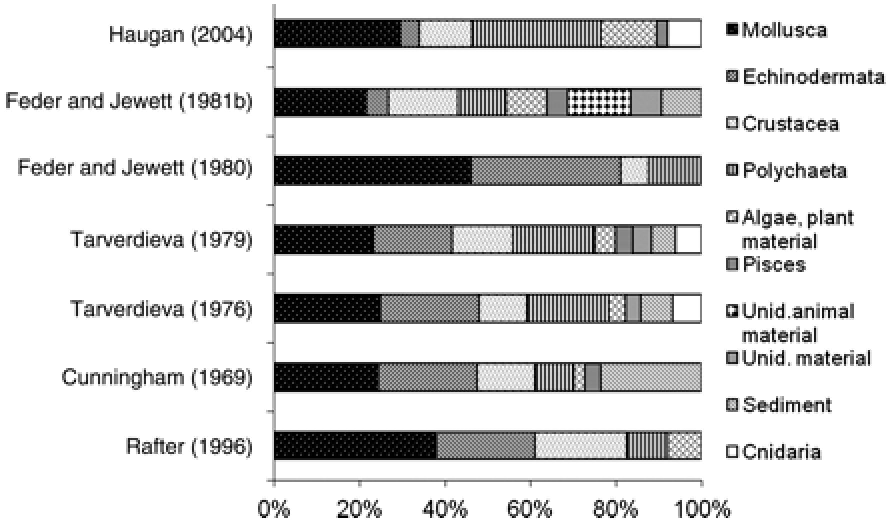

Figure 2. Frequency of occurrence of prey in the stomachs of king crab in comparable dietary studies. A selection of comparable studies is presented, because variability in reporting and study design made cross-comparison between all studies impossible (see Supplementary material for detailed information).

The focus of this paper is the potential role of the red king crab as an introduced species to the Barents Sea ecosystem. We review the biology of the crab, identifying factors contributing to its success. A literature study on the king crab's main prey and predators, as well as impact studies in the Barents Sea, summarizes what is known about their interactions with native biota. The data are synthesized for each of the main life stages of the king crab (larva, post-larva, and juvenile/adult) to provide an overview of (i) the factors determining its success, including competitors, vulnerability to predators, and habitat limitations, and (ii) the potential impact to the ecosystem, i.e. the impact the crab may have on the ecosystem through predation and competition.

Invasion and life history of the red king crab in the

consequence of a lack of predators, competitors, parasites, or diseases, all of which tend to limit their populations in their native areas (Mack *et al.*, 2000). Several factors can contribute to explaining the king crab's successful invasion of the Barents Sea. The environmental and biological conditions in the Barents Sea are similar to those in their native area, including the availability of suitable benthic prey. Temperature is believed to be the main factor limiting the distribution of the crab both in its native and introduced area. It is a boreal species that thrives best in water temperatures of 2–8°C (Orlov and Karpevich, 1978; Nakanishi, 1985; Hansen, 2002), although its tolerance has been recorded from −1.6 to 18°C, depending on life stage (Orlov and Karpevich, 1978). The species is believed to be able to grow and reproduce in the coastal areas of northern Norway, and in the shallower areas of Bear Island, Jan Mayen, and Svalbard. Cold temperatures at depths greater than 50 m could allow the crab to spread to large parts of western Europe (Nilssen, 2003; Pedersen *et al.*, 2006). Colder temperatures are expected to limit their eastward expansion to the southern part of Novaya Zemlya (Orlov and Karpevich, 1978). The biology of the king crab in the Barents Sea has been summarized by Kuzmin and Gudimova (2002) and Berenboim *et al.* (2003).

The crab's success can also be attributed to the wide range of habitats it occupies throughout its life history. Larvae are pelagic, allowing for long-range transport within current systems, and settle in nearshore habitats where physical and biological structures provide food and protection from predators (Powell and Nickerson, 1965; Loher and Armstrong, 2000). In the coastal areas of the Barents Sea, shallow, rocky, and complex seabeds, including scallop beds (Zolotarev, 2009), provide suitable habitats for the settlement and growth of juvenile crabs (Pedersen *et al.*, 2006). Post-settlement crabs have been found at depths ranging from intertidal and shallow rocky habitats of ~4 to ~510 m in water of salinity 28–30 psu or even higher (Rodin, 1989; Klitin and Nizyayev, 1999). Juveniles seek refuge in the if solitary (Dew, 1990). At an age of 5 years, the crabs reach sexual maturity (66–105 mm CL; Otto *et al.*, 1989; Rafter, 1996) and sexual segregation takes place. After maturity, their habitat is determined by a mating–moulting and feeding migratory pattern. In late winter/early spring, the adults migrate towards the shore to reproduce, and in winter, they move out to deeper water to feed. Individual crabs have been recorded to move more than 10 km in a single day (Marukawa, 1933; Stone *et al.*, 1992; Loher *et al.*, 1998). Whereas parasites have been hypothesized to have had an effect on recruitment to the Alaskan king crab fishery (Kuris *et al.*, 1991), these have not been found yet in the Barents Sea population (Haugen, 1999).

Biological interactions of the red king crab

Larvae

Control factors

Year-class strength has been a focus of research for understanding variations in the Bering Sea biomass of king crab. Temperature, storm conditions, duration of the ice period in shallow inlets, river discharge dynamics determining food supply, moulting mortality, prey availability, and species composition have been identified as factors affecting the mortality of the larvae in their native area (Kurata, 1959; Paul *et al.*, 1979, 1990; Shirley and Shirley, 1989; Gabaev, 2007).

Predation by planktivorous fish has been proposed as a factor determining larval supply (Fukuhara, 1985; Blau, 1986; Loher *et al.*, 1998). Declines in Pacific king crab have been found to coincide with increased abundance of flatfish, primarily yellowfin sole (*Pleuronectes asper*), which prey on crab larvae and juveniles (Haflinger and McRoy,

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as likely key predators of the larvae. These relationships are, however, disputed.

Several authors have concluded that the collapse of Pacific stocks of king crab appears to be a large-scale phenomenon, suggesting that climate forcing of recruitment is strong (e.g. Orensanz *et al.*, 1998; Zheng and Kruse, 2000; Gabaev, 2007). The connection between recruitment and climate regimes, however, remains a subject of speculation owing to a lack of information on time and spatial scales relevant to specific populations (Orensanz *et al.*, 1998).

Stock–recruitment relationships are poorly understood for most commercially important species of crabs and lobsters (Wahle, 2003). The Barents Sea king crab population is no exception. Pedersen *et al.* (2006) suggested that successful recruitment of juveniles is determined by whether the larvae reach favourable habitats along the coast. In the Barents Sea, larvae are subject to predation by salmon (*Salmo salar*), saithe (*Pollachius virens*), and flatfish, including halibut (*Hippoglossus hippoglossus*) and flounder (including *Hippoglossoides platessoides*, *Microstomus kitt*, *Glyptocephalus cynoglossus*). Determining the importance of predation on larvae for the Barents Sea crab population would require sampling the stomachs of many potential predators, estimates of the relative abundance of larvae and the predator species, and mapping the spatial overlap of larvae and planktivorous fish.

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Dietary studies of king crab larvae are based primarily on rearing results. In laboratory cultures, larvae fed on diatoms, nauplii, and copepods (Kurata, 1960; Bright, 1967; Paul *et al.*, 1979, 1990). Fragments of small hydroids (*Sertularia* spp.) and barnacle (*Balanus arcticus*) and horse crab (*Telmessus cheiragonus*) larvae have been found in third- and fourth-stage zoea (Bright, 1967). Kurata (1959) successfully fed the zoea trochophores of *Chone teres* (Polychaeta)

Post-larvae

Control factors

The post-larval stage in this paper is defined as being from the time of settlement and metamorphosis to the juvenile stage, when the crabs start to show podding behaviour at 17–18 mm CL as 1-year olds (Dew, 1990). However, Dew (1990) regards the post-larval stage to include the podding stage from 1 to 2 years of age. Larvae of king crab depend on there being suitable substratum for settlement, food, and shelter (Powell and Nickerson, 1965; Loher and Armstrong, 2000). Predators of new recruits are believed to be smaller fish species, including yellowfin sole, flathead sole (*Hippoglossoides elassodon*), Alaska plaice (*Pleuronectes quadrituberculatus*), skates (Rajidae), sculpins (Cottidae), and snailfish (Liparidae), as well as sea stars (Loher and Armstrong, 2000). Fukuhara (1985) believed that predation at this stage could be significant, whereas Livingston *et al.* (1999) concluded that it was of minor importance to the population dynamics of the species. Ecologically similar species exist in the Barents Sea (Table 1), but the importance of their predation on crab post-larvae has not been studied.

Cannibalism has been documented in laboratory experiments and related to cohort density and cover (Rounds *et al.*, 1989; Stevens and Swiney, 2005), along with the availability of alternative food (Brodersen *et al.*, 1989). Habitat availability is believed to influence the population dynamics of king crab (Loher and Armstrong, 2000; Stevens and Swiney, 2005; Gabaev, 2007), and cannibalism on small individuals may be particularly important in the Barents Sea, where the crab is abundant (Haugan, 2004).

Table 1.

Potential competitors and predators of the red king crab in the Bering and Barents

Tanner crab (*C. bairdi*), snow crab (*C. opilio*), sea stars		Troll crab (*L. maja*), snow crab, sea stars	
Pacific cod (*G. macrocephalus*)	Pacific cod, walleye pollock (*T. chalcogramma*)	Atlantic cod (*G. morhua*), Norwegian pollock (*Theragra finnmarchica*), haddock (*Melanogrammus aeglefinus*)	Atlantic cod, Norwegian pollock, saithe (*P. virens*)
Rock sole (*Lepidopsetta* spp.), flathead sole (*H. elassodon*), rex sole (*E. zachirus*), yellowfin sole (*Limanda aspera*), Alaska plaice (*P. quadrituberculatus*)	Rock sole, flathead sole, rex sole, Dover sole (*Microstomus pacificus*), arrowtooth flounder (*Atheresthes stomias*)	Lemon sole (*M. kitt)*, common sole (*Solea solea*), plaice (*P. platessa*)	Lemon sole, common sole, flounders (e.g. *H. platessoides*, *M. kitt*, *G. cynoglossus*)
	Elasmobranchs, halibut, sculpins, Greenland turbot (*Reinhardtius hippoglossoides*), Pacific salmon, Pacific herring (*Clupea pallasii*)		Elasmobranchs, Greenland halibut (*Reinhardtius hippoglossoides*), sculpins, turbot (*Psetta maxima*), Atlantic salmon (*S. salar*), Norwegian spring-spawning herring (*Clupea harengus*)
	Sea otter (*Enhydra lutris*), seals		Otter (*Lutra lutra*), seals

sediment and associated organisms, including diatoms that had settled to the seabed, sponge spicules, algae, and bryozoans, suggest that foraging in the sediment is a common method of feeding (Feder *et al.*, 1980). Although the utilization of detritus and bacteria is important to the nutrition of some crustaceans (Rieper, 1978), it still remains to be investigated for king crab post-larvae (Feder *et al.*, 1980). Crabs settle on complex substrata that represent important habitat for a number of species. To elucidate the impact that post-larval king crabs may have on such communities, there is a need for increased understanding of Barents Sea nearshore ecology.

Juveniles and adults

Control factors

As crabs increase in size, the number of potential predators decreases. King crabs 3 years old and more (~40 mm CL) are too large for most fish to feed on (Jewett and Powell, 1981). They remain vulnerable during moulting (Blau, 1986; Livingston *et al.*, 1993; Loher *et al.*, 1998), however, and Pacific cod (*Gadus macrocephalus*) have been identified as important predators of soft-shelled female king crabs (Orlov and Karpevich, 1978; Fukuhara, 1985; Blau, 1986). Increased abundance of Pacific cod, and the groundfish community as a whole, has been suggested as an explanation for the decline in southeastern Bering Sea king crab (Fukuhara, 1985; Blau, 1986; Otto, 1986). Several have questioned the link between fish predation and king crab abundance, however (Feder and Jewett, 1981a; Fukuhara, 1985; Livingston, 1989; Zheng and Kruse, 2000). Overfishing of top predatory groundfish in the Northwest Atlantic is believed to have led to increases in populations of another large crustacean, the American lobster (*Homarus americanus*; Steneck, 2006).

In the eastern Bering Sea, the king crab competes for food with a number of mobile bottom-dwelling organisms including sea stars,

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interactions were not revealed between Tanner (*Chionoecetes bairdi*), snow (*Chionoecetes opilio*), and king crabs (Zheng and Kruse, 2000).

The Barents Sea king crab is expected to be subject to predators and competitors similar to those found in their native area of distribution (Table 1). Although Orlov and Karpevich (1978) suggested that predators would play less of a role in the Barents Sea than in the Pacific, saithe have been reported to consume larvae and juveniles of red crab, and up to half the content of saithe stomachs has consisted of juvenile crabs (Dolgov, 2002; Matyushkin, 2003). Haddock has been identified as a potentially important competitor in the Barents Sea because of its extensively overlapping diet with crab (Orlov and Karpevich, 1978), as has the troll crab (*Lithodes maja*) because of its overlapping diet and biology (Hufthammer, 1996). Observations, however, indicate that it is the king crab that is having a negative impact on the native *L. maja* (Haugan, 2004; Rzhavsky *et al.*, 2004). The reappearance of *L. maja* in Dalnezelenetskaya Bay (Russia), as well as pre-invasion recordings, suggests that climate changes could explain the population variations observed (Propp, 1971; Britaev *et al.*, 2007).

Although natural cycles in species abundance and environmental factors can partly explain the population fluctuations observed, intense fishing pressure has contributed to the collapse of Pacific king crab stocks (Zheng *et al.*, 1995; Orensanz *et al.*, 1998; Livingston *et al.*, 1999; Zheng and Kruse, 2000, 2003; Gabaev, 2007). Reductions in spawning-stock biomass (SSB) may limit recruitment directly (Zheng *et al.*, 1995; Zheng and Kruse, 2003), and a weak depensatory effect on recruitment under low effective SSB has been identified (Zheng *et al.*, 1995). Low fishing pressure during establishment of the king crab population could have facilitated its success as an invasive species in the Barents Sea. Although the population is considered to have been established in the late 1970s, it was not until 1994 that a limited fishery for research was opened. In 2002, commercial harvesting started with the management objective of exploiting the

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regulate the crab population size, it may not be sufficient to stop the invasion of king crab.

Impact

The diet of juvenile and adult red king crabs includes a range of benthic organisms (Figure 2, Supplementary Table S1). The crabs attack the prey, then tear apart larger animals, and collect and filter small invertebrates from the substratum (Cunningham, 1969). These varied strategies suggest that the crab will influence local benthic communities in the Barents Sea through foraging. The vulnerability of prey organisms will be determined by feeding preferences of the crab and the biology of the prey. Indirect ecosystem impacts may also affect native populations through mechanisms such as competition, alteration of foodwebs, restriction of native organisms to less favourable habitats, and habitat modification. Predicting the magnitude of these impacts and the consequences for other commercial species is a major challenge.

It is generally believed that the king crab is an opportunistic feeder that forages on the most available sessile or slow-moving benthos (Takeuchi, 1959; Bright, 1967; Cunningham, 1969; Feder and Jewett, 1981a; Sundet *et al.*, 2000; Haugan, 2004). A review of 23 dietary field studies of juvenile and adult crabs confirms that the king crab is a generalist feeder (Figure 2, Supplementary Table S1). Generalist crab species have significant impacts on benthic community structure (Virnstein, 1977; Grosholz *et al.*, 2000). Their gregarious behaviour concentrates feeding activity in limited areas where benthos is abundant, and because many of their prey items are slow-moving or sessile, heavy predation by king crab could cause considerable damage to benthic community structure (Cunningham, 1969).

Large epibenthic organisms are believed to play an important role in the functioning of benthic systems (Piepenburg and Schmid, 1996). Many taxa, including molluscs, echinoderms, polychaetes, and

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fewer clams and sea stars have been observed in areas heavily populated by king crab in the Bering Sea (Feder and Jewett, 1981a). It has been suggested that, after moulting, crabs feed on young clams and barnacles to replace the calcium carbonate lost in the process (Feder and Jewett, 1981b). In areas invaded by the crab, reductions in large individuals of prey species have been reported (Haugan, 2004; Pavlova, 2004, 2008; Rzhavsky *et al.*, 2004; Anisimova *et al.*, 2005). In Varanger (Norway), large mussels and echinoderms have disappeared from areas where crabs are in high density, and the soft-bottom fauna is now dominated by small individuals (Haugan, 2004). Motovsky Bay (Russia) soft-bottom communities have experienced a reduction in the number of large individuals, including bivalves, polychaetes, sipunculids, and echinoderms, but although benthic community composition has changed, a complete loss of species or a reduction in total biomass was not documented (Anisimova *et al.*, 2005). Some of these changes could be attributed to bottom trawling (Anisimova *et al.*, 2005), but benthic time-series from Dalnezelenetskaya Bay (Russia) from the 1960s up to 2002 show changes in the benthic community structure that could be attributed to crab invasion, including decreases in sea urchins, bivalves, and sea cucumbers (Rzhavsky *et al.*, 2004). A reduction in the number of large individuals in a population could make it more vulnerable, because size influences an organism's success as a predator or a competitor, its vulnerability to other predators, and its reproductive output (Begon *et al.*, 1996). An experimental study suggests that the size composition of the king crab population, as well as benthic diversity, influences the vulnerability of its prey to predation (Jørgensen and Primicerio, 2007). A preference for small individuals could explain observed reductions in small, but not large, individuals of the sea urchin *Strongylocentrotus droebachiensis*. Predator-avoidance behaviour of small sea urchins has also been observed. Although previously found on open surfaces, they now move into crevices and between boulders providing shelter (Pavlova, 2004; Britaev *et al.*, 2007; Buyanovsky and Rzhavsky, 2007).

experience a more sustained impact because the crabs are present there year-round. Moreover, consumption in spring/summer, when the crabs have recently moulted, is greater than during autumn/winter (Takeuchi, 1959; Feder and Jewett, 1981b). Additionally, juvenile crabs have a higher consumption-to-biomass ratio than adults (Cunningham, 1969), enabling them to have a great impact, despite their smaller size. The juveniles feed on species that play a leading role in shallow, soft-bottom communities (Rzhavsky *et al.*, 2006). Kola Bay soft-bottom benthic biomass and diversity are negatively correlated with juvenile crab density. The greatest decrease was found for bivalves and polychaetes (Pavlova, 2008), preferred prey of the crab (Pavlova *et al.*, 2007). Depletion of food resources with increasing juvenile crab density has been reflected in the decreased dietary proportion of infaunal invertebrates over time, particularly with respect to bivalves, molluscs, and polychaetes (Pavlova, 2008). Britaev *et al.* (2006) found that consumption by juvenile and female crabs exceeded the benthic biomass production in soft-bottom communities, but that they consumed <5% of biomass production in hard-bottom communities in Dalnezelenetskaya Bay. Britaev *et al.* (2006) did not find any substantial changes to the structure of Dalnezelenetskaya Bay hard-bottom communities, but another study reported decreased abundance of prey populations and an altered size structure (Pavlova, 2004).

Juvenile king crabs are clearly important predators of, and competitors for, food and habitat with native organisms, but the vast majority of research on king crab has focused on the adults. Of the 23 dietary studies reviewed here, 13 were conducted exclusively on crabs >60 mm CL, and although four studies sampled both adults and juveniles, their diets were not reported separately (Supplementary Table S1). Four papers reported juvenile diet (Bright, 1967; Rzhavsky and Pereladov, 2003; Tarverdieva, 2003; Pavlova, 2004) and two looked at crab post-larvae (Feder *et al.*, 1980; Matyushkin, 2003; Supplementary Table S1). Although the juvenile portion of the

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population and its impact on nearshore communities is needed. Monitoring the size of the non-commercial part of a stock is also important for understanding its population dynamics (Steneck, 2006).

Estimates of benthic carrying capacity suggest that the Barents Sea can sustain a biomass of 1.2 t km^{-2} of small (<100 mm CL) and 2.8 t km^{-2} of large crabs (>100 mm CL; Falk-Petersen, 2004), or 2.74 t km^{-2} of crabs >80 mm CW (Gerasimova, 1997). Densities of juvenile king crabs exceeding five per 100 m^2 may deteriorate their own food resources, as well as those of fish, in benthic communities with a biomass <50 g m^{-2} (Pavlova, 2008). These estimates, however, only consider the capacity of the benthic community to produce biomass, and they do not take into account other issues such as maintaining biological and structural diversity.

Estimates of predation pressure on crab prey are often based on studies of diet, which may be biased. Digestion time differs depending on the type of prey consumed, and mastication of the food makes identification difficult. Additionally, parts of the prey may not be ingested or prey may be abandoned after they have been killed. Damage to prey populations can therefore be underestimated (Sundet *et al.*, 2000; Gudimov *et al.*, 2003; Haugan, 2004; Jørgensen, 2005; Pavlova *et al.*, 2007). Diet studies need therefore to be supplemented with long-term monitoring of benthic communities, preferably over time-series that start before the crab invasion to separate natural fluctuations from crab impact.

Invasive species that act as ecosystem engineers [organisms that change the environment through their own physical structures (autogenic engineers) and/or by transforming living or non-living materials from one physical state to another, via mechanical or other means (allogenic engineers; Jones *et al.*, 1994)] are regarded as high impact/risk species that can influence ecosystem properties and biodiversity (Bouma *et al.*, 2009). The reduction in large epibenthic

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communities. Biogenic structures influence the architecture on both soft-sediment and rocky substrata and represent important habitat, feeding areas, and nursery areas for a number of commercial and non-commercial species (Sjøtun *et al.*, 1995; Lekve *et al.*, 2005; Wallentinus and Nyberg, 2007; Bouma *et al.*, 2009). For example, structurally complex scallop beds support very diverse communities. In invaded areas, local divers have reported declines in the populations of Icelandic scallops (Jørgensen, 2005; Jørgensen and Primicerio, 2007). Crab feeding modifies soft-sediment habitats both physically and chemically though increased bioturbation and removal of sedimentary organisms. The crabs are also physical structures themselves and may thereby represent new habitats that could allow increased biodiversity. A consequence of the latter could be an increase in trypanosome infection in Atlantic cod (*Gadus morhua*), because the crab carapace is a favoured substratum for the leech *Johanssonia arctica*, a vector for this parasite (Hemmingsen *et al.*, 2005).

Estimates suggest that the king crab consumes 10–30% of the sea urchin stock annually in invaded areas of the Barents Sea (Gudimov *et al.*, 2003; Pavlova, 2009). Sea urchins play an important role in the formation of benthic community structure and the transformation of organic matter (Pavlova, 2009), but have also been associated with the decimation of kelp forests along the Norwegian coast (Sundet, 2008). Kelp forests are highly diverse, providing habitat, nursery ground, and food for a number of species (Steneck *et al.*, 2002). It has been hypothesized that the recovery of kelp beds is one of the keys to the recovery of the Norwegian coastal cod (*G. morhua*) population (Bjørge and Nilssen, 2009). If the Barents Sea king crab was to become an important predator on sea urchin, its predatory impact may help recover the kelp forest, but there is little evidence to suggest how likely this is. Sivertsen (2006) concluded that predation has a minor impact on Barents Sea populations of sea urchin. As kelp forests are an important habitat for newly settled crab larvae, kelp

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the sea urchin population in check, so the system switched to an alternative stable state where recovery of macroalgae resulted in increases in crab populations (Steneck *et al.*, 2002).

The king crab is not likely to have a direct negative impact on demersal and pelagic fish in the Barents Sea through predation. Although debated in the literature (McLaughlin and Hebard, 1961; Bright, 1967; Cunningham, 1969; Stone *et al.*, 1992; Zhou and Shirley, 1997), live fish and shrimps are unlikely to be important prey. Indirectly, however, those groups may be affected through mechanisms such as competition for food and habitat, as well as by predation on their eggs and predation by crab larvae.

Because of similarity in their diets, king crabs can act as a food competitor of benthic-feeding fish such as plaice (*Pleuronectes platessa*), haddock, wolffish (*Anarhichas lupus*), and Atlantic cod (Pavlova *et al.*, 2004). Stomach analysis of haddock, however, did not suggest that competition for prey with king crabs has had a negative effect on the haddock population (Anisimova *et al.*, 2005). Gastropod eggs and fish roe have been found in king crab stomachs (Feder and Paul, 1980; Rafter, 1996; Gerasimova, 1997). The Arctic lumpsucker (*C. macalpini*) is believed to be particularly vulnerable to egg predation by the king crab (N. Mikkelsen, University of Tromsø, pers. comm.). Capelin is a key species that transports energy up the Barents Sea foodweb, and their main spawning area along the coast of northern Norway and the Kola area of Russia coincides with areas where king crabs are currently distributed. A major concern is that crab predation on capelin eggs will negatively impact the fish population (Gjøsæter, 1998; Haugan, 2004). Anisimova *et al.* (2005) estimated that in 2001, a year of heavy consumption by the crabs on capelin eggs, the crab consumed just 0.03% of the eggs and concluded that egg predation did not represent a threat to the capelin population. In 2001, however, the mature capelin population was relatively large. In years of small capelin populations, the impact of egg predation could have population-level consequences if the

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Knowledge gaps and conclusions

Despite the important role that benthic communities are believed to play in the Barents Sea, relatively few long-term studies describe their structure and dynamics (Gerasimova, 1997; Wassmann *et al.*, 2006; but see Anisimova *et al.*, 2005, and Britaev *et al.*, 2006). A lack of benthic time-series and quantitative information on feeding interactions makes it difficult to develop sound predictions with regard to the effects of the king crab on the Barents Sea ecosystem. Important knowledge gaps include: Despite these limitations and the fact that predicting their impact is inherent to the problem of alien species (Lowe *et al.*, 2000; Pimm, 2002), current knowledge does allow for some preliminary conclusions that can be valuable in guiding management and research. The king crab clearly has the potential to reduce biodiversity and alter habitats. Loss of ecosystem function results in ecosystems becoming more vulnerable to disturbance and can be a clear consequence of biological invasion (Galil, 2007). Research needed to understand the ecosystem effects of the king crab includes studies on the multiple trophic levels the king crab feeds upon throughout its life history, and implementation of long-term monitoring.

i. a stock–recruitment relationship for king crabs, including the survival of juveniles;

ii. biological interactions at the larva and post-larva stages, including predation pressure on native plankton and benthic communities;

iii. knowledge of the extent to which the population of king crabs is predator-controlled;

iv. how to control the king crab invasion through fishing;

v. the impact of juvenile and adult king crabs on native communities, including their role as ecosystem engineers;

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vii. separate time-series of natural, human, and king crab impacts on the Barents Sea ecosystem.

i. The Barents Sea offers favourable physical and biological conditions for the king crab, helping to explain its success as an invasive species. Its ability to occupy a wide range of habitats throughout its life history, its mobility, generalist diet, lack of parasites, and low fishing pressure during establishment are all factors that have likely facilitated its invasion.

ii. Transportation to and availability of appropriate habitat at the larva stage, as well as fishing, are likely to be important controlling factors in the dynamics of the Barents Sea red king crab.

iii. Juvenile and adult king crabs can alter benthic community structure significantly. Large, epibenthic organisms are particularly vulnerable to predation, and reduced species diversity and biomass have been recorded following invasion by red king crabs. Through structural modifications of the environment, crab predation could be a threat to crucial habitats, including those provided by large epibenthos, such as scallop beds. Predation by king crabs on eggs laid on the seabed may have population-level consequences on some important fish species.

Supplementary material

Supplementary material is available at ICESJMS online. It contains a review (Table S1) of food items found in the stomachs of king crab.

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