The Invasive History, Impact and Management of the Red King Crab Paralithodes camtschaticus off the Coast of Norway

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Abstract The red king crab, *Paralithodes camtschaticus*, was intentionally transferred from Russian territorial waters in the Northern Pacific Ocean and introduced into the Barents Sea between 1961 and 1969 in order to create a new commercial fishery. A decade later a reproducing population was found to be well established in the latter region. The red king crab has since dispersed southwards along the coast of Northern Norway. Its ecological impacts on the native fauna have been investigated. From 2002 till 2007 the management of the commercial fishery has been undertaken jointly by Norway and Russia. Since then, management has continued within the countries respective fishery zones in the Barents Sea. In 2004 Norway was given free rein to apply all necessary management methods to limit the spread of the crab westwards of 26°E longitude.

1 Introduction

The red king crab *Paralithodes camtschaticus* (Tilesius, 1815) (Lithodidae Samouelle, 1819) (Fig. 1) is among the world's largest arthropods, reaching ~220 mm carapace length (CL), a weight over 10 kg (Powell and Nickerson 1965a, Powell and Nickerson 1965b), and living up to 20 years (Kurata 1961).

It is native to the Northern Pacific Ocean (Fig. 2) with reported range from the Korea and Japan, Kamchatka, the Aleutian Island chain, Alaska, and southeast to Vancouver Island, Canada (Rodin 1990).

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Fig. 1 Dorsal view of *Paralithodes camtschaticus* (photographer: Lis Lindal Jørgensen, Institute of Marine Research)

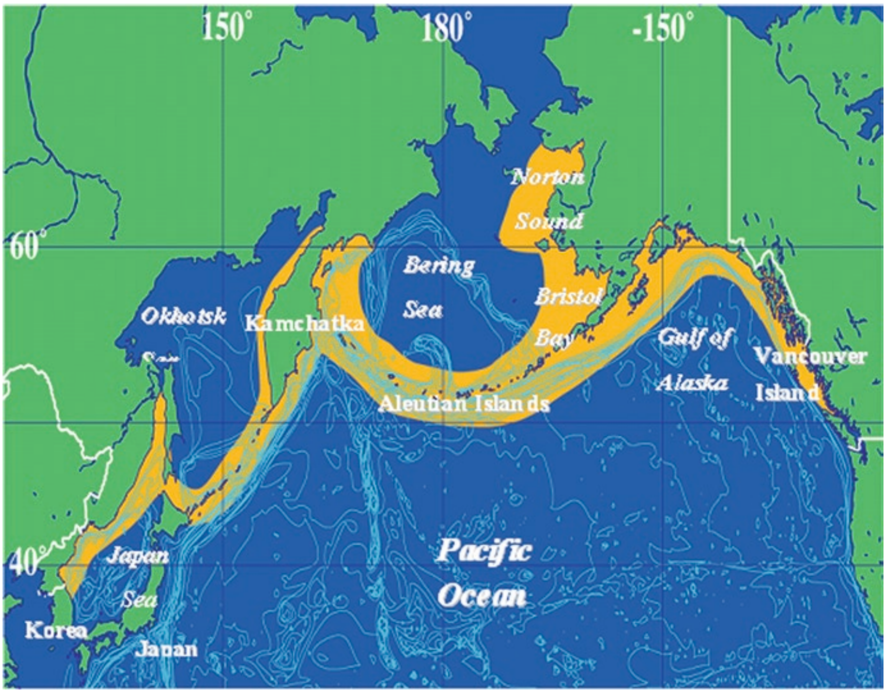

Fig. 2 The native distribution of the red king crab (*yellow colour*) along the coasts of Korea, Japan, Russia, Alaska, and Canada

The red king crab was collected by Russian scientists during the 1960s and 1970s from Peter the Great Bay, Okhotsk Sea, and introduced into the Barents Sea (Orlov and Karpevich 1965; Orlov and Ivanov 1978) (Fig. 3). Between 1961 and 1969, 1.5 million first stage zoeae, 10,000 1–3 year old juveniles (50% females and 50% males) and 2,609 5–15 year old adult (1,655 females and 954 males) crabs from West Kamchatka, were intentionally released into the Kolafjord, east Barents Sea, Russia, in order to create a commercial fishery (Orlov and Karpevich 1965; Orlov and Ivanov 1978). In the Russian part of the Barents Sea the highest densities were observed on both sides of the Rybachi Island (Fig. 4) during late 1980s and early 1990s. Later in the 1990s, the red king crabs became abundant along the eastern part of the Kola Peninsula and were reported from Cape Kanin and the entrance of the White Sea during 2002. Further northwards the crab was found on the Kanin Bank and at the Goose Bank (Zelina et al. 2008).

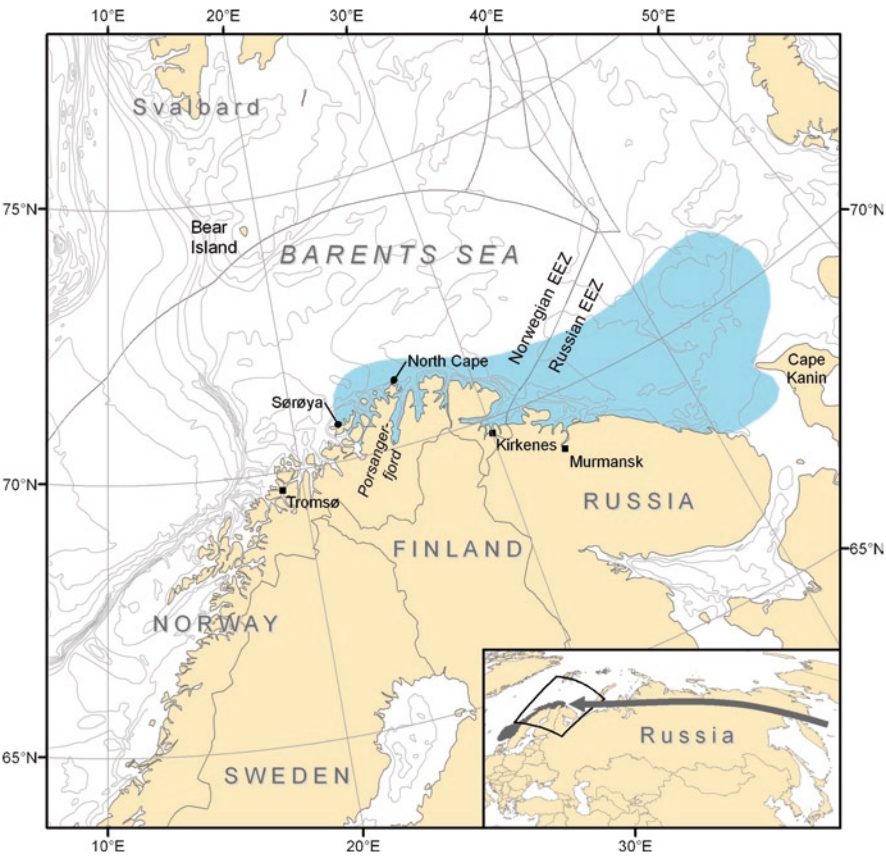

Fig. 3 Red king crab dispersal in the Barents Sea. Embedded map showing the translocation of crabs from West Kamchatka, North Pacific Ocean westwards into Kolafjord (see fig. 4), east Barents Sea

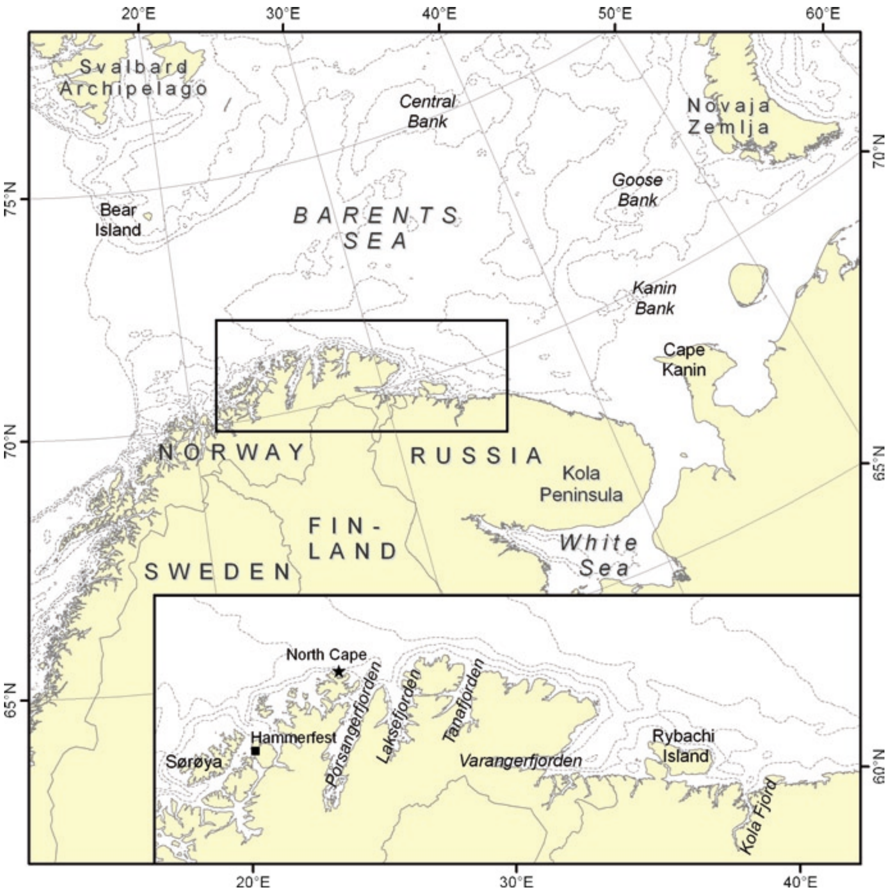

Fig. 4 The spreading of the red king crab along the northern coast of Norway

In 1992 the red king crab became abundant in Norwegian waters, initially reported from southern Varangerfjord (Fig. 4). By 1994 *P. camtschaticus* spread to the northern side of the fjord. The crab has increased fourfold in Varangerfjorden within 12 years (Table 1). In 1995 it was recorded in Tanafjord and the population has been relatively stable in the period 1999–2007 (Table 1). Further range extensions were noted in Laksefjord and Porsangerfjord during 2000, and by 2001 several adult crabs were caught west of Sørøya and west of the North Cape. In 2002 the crab were captured close to Hammerfest and three specimens were recorded about 120 nautical miles west off the North Cape (Hjelset et al. 2003; Sundet 2008).

The crab population along the northern coast of Norway was estimated to number 2.9 million individuals in 2001 and 3.5 million in 2003 (Hjelset et al. 2003). In 2007 the population in Norwegian waters was estimated at 4–5 million individuals (Sundet 2008). That number is an underestimate as only individuals with a carapace longer than 70 mm and at water deeper than 100 m are included.

Table 1 Average catch per unit of effort (CPUE) (number of crabs per trawl hour) with 95% CI (confidence interval) of the red king crab from the scientific cruises in the period 1995–2007 (From Hjelset et al. 2009)

Year	Varangerfjorden CPUE ± CI	Tanafjorden CPUE ± CI	Laksefjorden CPUE ± CI
1994	[a]		
1995	10.5 ± 3.6		
1996	19.1 ± 7.0		
1997	21.0 ± 7.7		
1998	13.7 ± 2.9		
1999	17.4 ± 4.5	18.3 ± 9.7	
2000	25.0 ± 13.3	5.2 ± 2.7	
2001	20.5 ± 10.0	6.0 ± 2.8	
2002	15.6 ± 5.8	18.9 ± 9.7	2.5 ± 4.9
2003	19.7 ± 7.5	38.8 ± 18.9	37.9 ± 71.7
2004	30.4 ± 17.2	25.8 ± 8.2	25.4 ± 39.1
2005	33.3 ± 21.9	23.5 ± 9.6	13.0 ± 16.0
2006	41.5 ± 25.4	31.0 ± 14.2	25.0 ± 31.0
2007	45.8 ± 25.7	24.8 ± 9.2	25.9 ± 19.1

[a] Not available

2 Spreading, Settling, Podding and Migration

The larvae of the red king crab develop in the coastal zone. In the 2 months after hatching, the pelagic larval stages can be transported by currents considerable distances (Pedersen et al. 2006). This period must be synchronised with the spring phyto- and zooplankton peaks in the upper 15 m of the water column (Shirley and Shirley 1989). The larvae settle in shallow waters (<20 m) on sponges, bryozoans and macroalgae (Marukawa 1933). Successful recruitment depends on a well-developed sessile community with extensive areas of dense concentrations of hydroids, bryozoans, and sponges needed to support a massive settlement of larvae.

Red king crabs smaller than 20 mm carapax length (CL) lives a cryptic and solitary life, sheltering beneath rocks and stones and in crevices. In the second year podding behaviour (Fig. 5) appears (Dew 1990). Podding is when the crabs congregate in large, tightly packed groups (Powell 1974). The smallest and largest crabs found in any pod are 24 and 69 mm CL, respectively. Pods therefore form during the latter part of the second year, exist throughout the third year, and continue a short time into the fourth (Powell and Nickerson 1965a, Powell and Nickerson 1965b). When the density of the crab approaches 6,000 individuals, pod structures transforms into elongate piles and dome shaped piles do not commonly occur until the fourth year when crabs are 60–97 mm CL (Powel and Nickerson 1965a). The pods are held during the daytime, but disperse into a nightly foraging aggregation. This was explained by changes in water temperature, crab weight, and time of

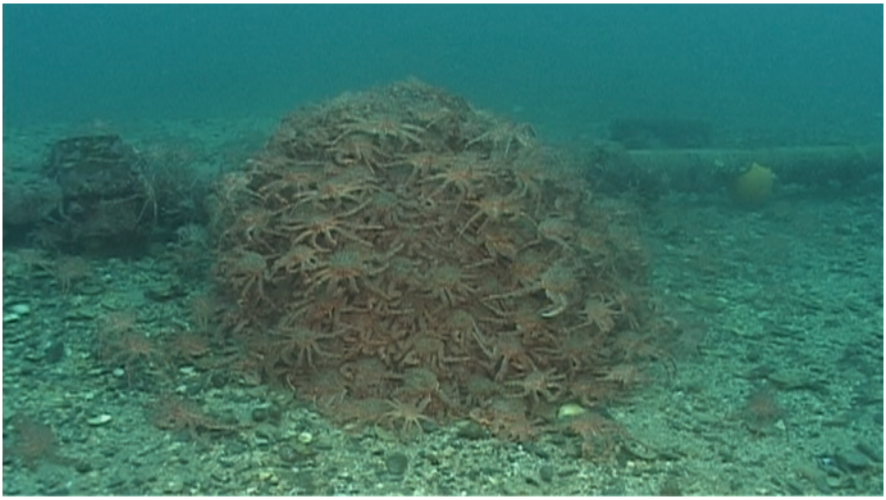

Fig. 5 Podding of juvenile red king crab (*Paralithodes camtschaticus*) in Norwegian fjord (Photographer: Geir Randby, Lillehammer Film)

sunset by Dew (1990). A trend of increased foraging time and movement to deeper, cooler water was apparent after mid-April, as water temperatures reached 4°C and began a sustained summer increase (Dew 1990).

Immature crabs (CL<120 mm), generally remain along the coast at 20–50 m depth (Wallace et al. 1949), and are seldom associated with adults in deep water.

Adults occur on sand and mud bottoms (Vinogradov 1969; Fukuhara 1985) and aggregate according to size, life history group or sex. The adult crab undergoes two migrations, a mating-moulting migration and a feeding migration (Fig. 6). The patterns of behaviour are similar off the coasts of Japan, Russia, and Alaska (Marukawa 1933; Powell and Reynolds 1965; Vinogradov 1969). The shoreward migration to shallow waters (10–30 m) takes place in late winter and early spring when the crabs mate, breed (Marukawa 1933; Wallace et al. 1949; Powell and Nickerson 1965a, b) and hatch their eggs (Stone et al. 1992). Extensive aggregations of both sexes occur during the spring spawning season. These spawning aggregations may also be found also in shallow water where kelp occurs (Powell and Nickerson 1965a, b). The kelp may provide shelter for the females following moulting ecdysis, and during mating (Jewett and Onuf 1988). Spawning is followed by migratory feeding movements, of both sexes, towards progressively deeper water (300 m). After this period, the sexes form separate aggregations for the remainder of the year (Fukuhara 1985), and are not found together until the following mating season (Cunningham 1969).

In Russian waters the crab occurs both along the coast and offshore, while in Norwegian waters, the crab is distributed solely along the coastline (Fig. 3). Since along the Russian coast the bottom slopes gradually, whereas in the Norwegian

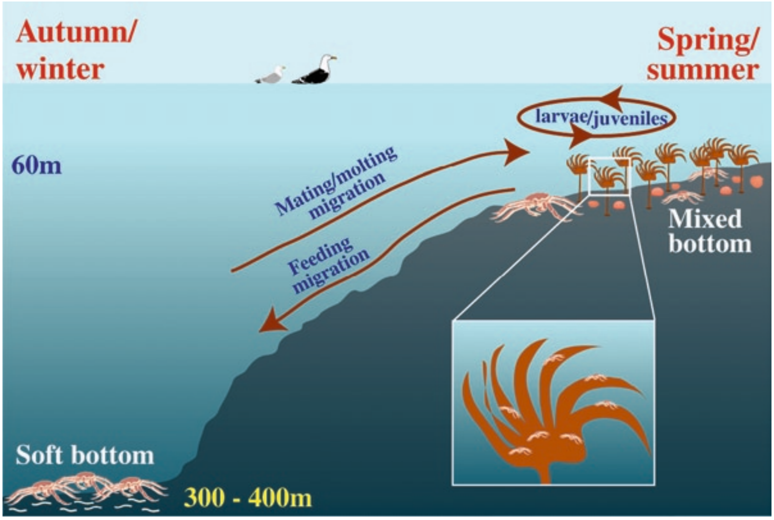

Fig. 6 Seasonal migration of *Paralithodes camtschaticus*: the mating-moulting migration in the spring/summer period to various substrates with benthic communities principally composed of calcified prey organisms, and a subsequent feeding migration in winter/autumn to soft substrate where annelids occur (*inset*: juvenile red king crabs associated with kelp)

fjords the bottom descends abruptly to deep water (300 m), it is proposed that the pattern of distribution is dependent on the coastal topography. This gently sloping coastal topography is also found in the north Pacific habitats, where the crab migrates far from the coast to reach deep water. The steeper topography may keep the Norwegian population close to the coast or inside the fjords year round.

3 Temperature Tolerance

The red king crab tolerates temperatures from −1.7 to at least +15°C (Rodin 1990), these tolerance limits vary at different stages of its life history. Temperature preferences of immature crabs (50–100 mm CL) are at <3°C as determined in laboratory studies (Hansen 2002). In the Barents Sea and the northern Norwegian Sea the temperature at 100 m depth in winter varies from 0°C to ~+6°C. Recently, it has been experimentally demonstrated that larval survival is affected by the water temperature in which the egg carrying females had been kept (Sparboe pers. comm.). Females acclimated to 14°C produced larvae with higher survival rates at high temperature compared with larvae from females acclimated to 4°C and 8°C. Survival was high (almost no mortality) for all crabs exposed to challenge temperatures from −1.7°C to 15°C independent of acclimation temperatures (4°C , 8°C and 14°C)

(Sparboe pers. comm.). This result may indicate that the red king crab may successfully invade also more southern habitats along the Norwegian coast (Larsen 1996; Sparboe pers. comm.).

The population of West Kamchatka overwinters on the continental slope where the warmer Pacific Ocean water mixes with the colder waters of the shallow shelf. The migration from the over wintering area to shallow water depends on bottom water temperatures, as well as the physiological conditioning prior to spawning and moulting (Rodin 1990). Large numbers of adult crabs assemble in shallow waters (10–15 m) in May–June when temperatures are approximately 2°C. Following reproduction in June and July, adults forage at around 50 m depth where the water is 2°C. Once temperatures decrease, the crabs disperse to deeper water for overwintering (Rodin 1990).

Amazingly, a single red king crab male was recorded in the comparatively "warm" Mediterranean Sea, though no explanation is given of its mode of introduction and survival so far south (Faccia et al. 2009).

4 Food and Feeding

The crab's food preference varies with age and stage. The pelagic larvae feed on both phytoplankton and zooplankton (Bright 1967). Once settled, the juveniles feed on hydroids, the dominant component of the epifauna on the Kamchatka shelf (Tsalkina 1969). Dew (1990) reported that young crabs (CL > 20 mm) feed on sea stars, kelp, *Ulva* spp., red king crab exuviate, bivalves of the genera *Protothaca* and *Mytilus*, nudibranch egg masses, and barnacles. Occasionally, crabs were observed dragging around large sea stars during the nocturnal foraging period. These stars were sometimes left near the base of the pod in the morning, and taken up again upon pod break-up. Adults are opportunistic, omnivorous feeders (Cunningham 1969). They feed on the most abundant benthic organisms, though usually one food group/species dominate their diet and this varies regionally (Kun and Mikulich 1954; Kulichkova 1955; Jewett et al. 1989). Most common food items are echinoderms (*Ophiura* spp., *Strongylocentrotus* spp.) and molluscs (*Nuculana* spp., *Clinocardium* spp., buccinid and trochid snails) (Cunningham 1969). Calcareous-shelled food items are more frequent in the diet of post-moult crabs (Herrick 1909; Fenyuk 1945; Logvinovich 1945). Kulichkova (1955) suggested that crabs need to replace calcium carbonate lost during moulting and that the young clams and barnacles in shallow waters fulfill this need. At times of moulting, growth and reproduction, the food intake declines but such pauses do not normally last more than 2–3 weeks (Kulichkova 1955) and thereafter the crabs feed avidly (Takeuchi 1967). The crabs feed on bivalves and echinoderms during spring and summer months when in shallow areas, and polychaetes in autumn and winter where they migrate to deeper water (Gerasimova 1997). Crabs contain significantly more food in their guts during spring-early summer (Takeuchi 1967; Jewett et al. 1989) when compared with the late summer-autumn-winter (Jewett and Feder 1982).

Adult crabs feed either by grasping and tearing apart larger invertebrates or by scooping sediment by the lesser chela and sieving it through the third maxillipeds. Scooping sand was often observed by Cunningham (1969) during periods when no larger food was immediately available. Logvinovich (1945) referred to the frequent presence of sediment in the stomachs and intestines of crabs. Foraminifera, minute molluscs and amphipods found in stomach contents probably result from feeding by sieving, as these either burrow in or occur on sediments. Logvinovich (1945) suggested this as an alternative method of feeding when larger prey is unavailable. Observations on the degree of gut fullness would indicate that crabs browse on food as it is encountered (Cunningham 1969). Calculations indicate that a young adult crab consumes 6 g, and juvenile crab 1.7 g within 25 h at 3°C, and 16 g and 3.5 g respectively at 6°C (Jørgensen et al. 2004). Laboratory studies indicate a daily ingestion rate of more than 70 g (squid) for young adult crabs at 5–9.4°C (Zhou et al. 1998). Pavlova et al. (2007) showed that juveniles consume a mixture of polychaetes, bivalves, ophiuroids, echinoids, asteroids weighing 0.7–26 g daily, based on soft tissues. However, identification of prey items and calculation of their weight from gut contents is inaccurate because decapods rarely swallow prey whole, rather they tear it apart. These fragments are shredded further in the gastric mill and are mostly unidentifiable. If to the weight of consumed soft tissue are added the undigested shells (*Chlamys islandica*, *Strongylocentrotus droebachiensis*, *Modiolus modiolus*, *Astarte* sp., *Buccinum undatum*, *Asterias* sp. or *Henricia* sp.) mature and immature crab show a daily foraging rate (killing or mortally damaging) between 150 and 300 g at 5–6°C (Jørgensen 2005; Jørgensen and Primicerio 2007), 17–408 g when feeding solely on scallops within 24 h (Anisimova et al. 2005; Jørgensen and Primicerio 2007), and 1–101 g per 24 h when feeding on sea urchins (Gudimov et al. 2003; Jørgensen and Primicerio 2007).

The above results might indicate a range from “low” (high abundance of prey, high species richness, prey of low foraging preferences, or not foraged benthic species) to a “strong” (low abundances of prey, species richness is low, highly preferred and flat-bodied prey species) impact on native local communities depending on the abundance of prey and the number of red king crabs. Because food appears to be the sole factor that could limit the increase in red king crabs numbers within the Southern Barents Sea (Gerasimova 1997), it is most likely that the invasive species, particularly in high abundances, will have a measurable effect on native prey populations.

5 Ecological Impact

There is a growing recognition that aliens may interact negatively with the native species in the recipient communities (e.g., Elton 1958; Lodge 1993; Carlton 1996; Ruiz et al. 1997; Walton et al. 2002; Ross et al. 2003). Due to the body size, long life span, predaceous behaviour, large population size and rapid dispersal of the red king crab, questions have been raised as to its impact on the native benthic community.

Since the establishment of the crab in the Barents Sea, studies on its predatory effect have been undertaken (Sundet et al. 2000; Haugan 2004). The crab feeds on a range of molluscs, sea urchins (*Strongylocentrotus droebachiensis*) and other echinoderms, crabs, polychaetes, sipunculids and fish (Sundet et al. 2000). Indeed, it was shown that some benthic taxa decreased considerably in abundance since its introduction, and that changes have occurred in the benthic community structure in the investigated fjords (Anisimova et al. 2005). It was calculated that the crab preys upon 15% of the total coastal population of *Strongylocentrotus* urchins (Gudimov et al. 2003; Pavlova 2009). Experiments of the potential impact of the invading crab on the beds of the native scallop, *Chlamys islandica*, showed that the scallop had no size refuge. The scallop's flat shell is easily handled by both small and large crabs (Jørgensen 2005; Jørgensen and Primicerio 2007), though small crabs seem to prefer smaller scallops (Gudimov et al. 2003). Larger prey items with dome shaped bodies, sponges, sea cucumbers and sea anemones were not preyed upon (personal laboratory observations made by the author). Scallop beds with a rich associated fauna are less vulnerable to predation than beds with few associated species, had several possible prey items to forage in the rich species associated scallop bed compared to the scallop bed with few other species than the scallop (Anisimova et al. 2005; Jørgensen 2005; Jørgensen and Primicerio 2007).

Anisimova et al. (2005) calculated that the crab population consumes 37 tonnes of capelin (*Mallotus villosus* Cuvier, 1829) eggs in a Barents Sea fjord during 3 months, and extrapolated this value to the whole Barents Sea crab population. The study concluded that the crab may impact 0.03% of the egg mass laid by the capelin.

In order to forecast possible impact in new or in already invaded areas, a study of the quantitative values of the prey (killed or mortally damaged specimens) is needed, and possible recipient areas need to be surveyed ahead of the crabs' arrival. The baseline surveys should include epifauna and infauna as the crab preys on components of both.

6 Economic Impacts

The development of the crab fishery in Norway is illustrated in Table 2. The data indicate that from 1994 to 2007 the total allowable catch (TAC) and effort increased dramatically. The overall increase in number and size of fishing vessels indicate the development of the economic importance of the crab. After 2001 the overall harvest rate increased along with the growth of the stock.

The increase in crab stocks in recent years has resulted in severe by-catch issues, particularly in the cod gillnet fishery. However some available size distribution data for crabs caught by the gillnet fishery show that few juvenile specimens are caught. Most crabs seem to be larger than CL 120 mm. More than 60% of the crabs caught in the gillnet fishery in Varangerfjord were females, while large males dominate the by-catch in the lumpsucker gillnet fishery during early summer. The by-catch of crabs increased from 1997 to 1999, but declined in 2000–2002, and the estimated number

Table 2 The number of vessels, fishing effort in traps allowed per boat, TAC, and size of the vessels participating in the research- and commercial fishery of the red king crab in Norwegian waters from 1994 to 2007 (From Hjelset et al. 2009)

Year	Number of vessels	Fishing effort traps per boat	TAC (legal males)	Harvest rate (%)	Overall vessel length(m)
Research fishery					
1994	4	20	11,000	41	7–15
1995	4	20	11,000	11	7–15
1996	6	20	15,000	17	7–15
1997	6	20	15,000	14	7–15
1998	15	20	25,000	17	7–15
1999	24	20	38,000	[a]	7–15
2000	33	20	38,000	6	7–15
2001	116	20	100,000	22	7–15
Commercial fishery					
2002	127	30	100,000	13	7–15
2003	197	30	200,000	15	7–15
2004	260	30	280,000	21	6–21
2005	273	30	280,000	34	6–21
2006	264	30	300,000	29	6–21
2007	253	30	300,000	31	6–21

[a] Not available

in 2002 was a third as large as in 1999 (Sundet and Hjelset 2002; Hjelset et al. 2003). This is probably due to the decline in the cod gillnet fishery. Low abundance of cod has forced the fishermen to move further west along the coastline in search of fish, thereby reducing the by-catch of the crab. The crab impacts the longline fishery by removing the bait off the hooks, thereby reducing catches of target fish.

In order to compensate the fishermen for the loss of the traditional fishery and equipment (i.e., gillnets, long-lines) caused by the invasion of the crab, the criteria for participation in the annual fishery are set in favour of the local fishermen. This is generally acknowledged by fishermen from other parts of Norway, since the presence of the crab directly impacts the local fishermen (Jørgensen et al. 2004).

7 Management and Future Challenges

From 1994 to 2001, the newly introduced red king crab stock was exploited through a research fishery limited by TAC numbers (Table 2) in the territorial waters of Russia and Norway. The harvest rate of the crab was relatively low (Sundet and Hjelset 2002). Thereafter the management regime and the following harvest pattern ensured that the largest males were removed from the population (Nilssen and Sundet 2006).

In 2002, the fishery had become commercial, and the Norwegian quota was set at 100,000 crabs (Nilssen and Sundet 2006), and increased to 300,000 crabs in 2006 (Table 2). The management of the fishery was based on annual joint agreements between Russia and Norway through the Mixed Russian-Norwegian Fishery Commission. During 2004, Norway and Russia agreed to limit the spread of the crab westwards by establishing a border at 26°E in the Norwegian zone (Fig. 3 North Cape). West of this longitude Norway was given free rein to apply all necessary management methods with a view to limit the spread of the crab. The joint Norwegian and Russian management ended in 2007. Since then management has been continued by each country within their respective fishery zones in the Barents Sea.

At present two management regimes are implemented in Norwegian waters and located to two different geographical areas/regions. One commercial eastern area from the Russian border at 31°E to North Cape at 26°E which are controlled by the governmental management plan for a king crab fishery where the population of king crabs are managed in order to give the best possible biological and economical output. The second area is the western area, south and west of 26° E, with a free fishing of the red king crab in order to reduce the rate of spreading south along the Norwegian coastline (St. meld. 40 2006; Øseth 2008).

The commercial stock in the eastern area is managed according to the '3-S' regime (sex, size and season) and only males with a CL > 137 mm may be landed (Nilssen and Sundet 2006). This strategy is similar to the Alaskan management model (Otto 1986; Kruse 1993). In the western "free fishing area" all crabs are landed without regard to size and sex.

It was not legal to land females CL > 137 mm in the eastern commercial management area before 2008, but now allowed. This regime with an eastern commercial managed area and a western free fishing area is still under evaluation and king crab assessment and management in relation to harvest strategies, by-catch problems, changes in gear technology, targeting ground fish and reducing the spread of this invasive species is still under consideration (Jørgensen et al. 2007).

Both extended periods of heavy fishing pressure (Pollock 1995; Jørgensen et al. 2007) and lack of food can affect the life history traits of crustaceans. There will always be a trade off between food available and the investment in growth, size/age at maturation and reproductive output (Stearns 1992). Reduction in reproductive output could be effected by lack of food which will be a consequence of the increased biomass of crab. It is therefore necessary to investigate the variation in size at sexual maturity and reproductive output in the population along the Norwegian coast in order to establish a baseline for future management and monitoring (Hjelset et al. 2009). Therefore, registration of size at sexual maturity, fecundity and moulting frequencies of the crab has been collected since 1992 and will be published in nearest future.

Precise scientific predictions cannot be given concerning the future impacts of the red king crab in the Southern Barents Sea. All indications suggest that this invasive species will spread further north in the Barents Sea, as well as southwards along the coast of Norway. The possibility of transporting larvae in ballast water to other regions is an alarming reality, especially as the traffic of oil and gas vessels around the Barents Sea and northern Norway is likely to increase in the near future.

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