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Population dynamics of the invasive lithodid crab, *Paralithodes camtschaticus*, in a typical bay of the Barents Sea

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We investigated population dynamics of the introduced red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), in Dalnezelenetskaya Bay, a typical coastal site of the Eastern Murman (Barents Sea) in summer over an 8-year period. In this bay, as in other coastal sites, juvenile crabs were most abundant. Among large crabs, the sex ratio was highly biased to females suggesting the important role of shallow water areas in reproduction of the red king crab. In 2002 – 2004, the carapace length (CL) frequency distribution of small crabs tended to be bimodal (30 and 60 mm). In 2005 – 2007 and 2009, crabs with a modal CL of 20 and 40 mm dominated. For small crabs, weight – length relationships were similar in males and females, while for large crabs the relationships differed significantly between sexes. Large males had a greater carapace width (CW) and merus length (ML), and higher CW/CL and ML/CL ratios, than large females due to sexual dimorphism. In 2002 – 2007, the total number of red king crabs was estimated to be 4100 – 7400 individuals; in 2008, we observed a marked decline to 350 individuals; in 2009, the total stock increased again to 3760 individuals. The observed patterns are in accordance with the stock dynamics reported for other coastal areas and could be associated with high levels of illegal fishing including recreational diving.

Keywords: Barents Sea, morphometric parameters, *Paralithodes camtschaticus*, population dynamics, stock decline.

Introduction

Members of the Lithodidae are popularly referred to as "king crabs" because of their high commercial value (Donaldson and Byersdorfer, 2005). King crabs belong to the infraorder Anomura, which includes both deep- and shallow-water species. The red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), is considered to be a shallow-water species and occurs in the North Pacific, spanning the Sea of Japan, the Sea of Okhotsk, the western and eastern Bering Sea as far north as Norton Sound, the Aleutian Islands and the Gulf of Alaska as far south as British Columbia, Canada (Donaldson and Byersdorfer, 2005).

There has been an increasing awareness of the potential effects of both intended and non-intended introductions of alien species around the world (Carlton, 1985; Carlton and Geller, 1993). During the 1960s and 1970s *P. camtschaticus* was intentionally introduced into the Barents Sea by Russian scientists (Orlov and Ivanov, 1978) to increase the economic potential of the local fishery. A Russian-Norwegian joint trial and research fishery for red king crab occurred from 1994–2001, during which this species was exempt from fishery regulations. In its new habitat the crab has formed a self-sustaining population (Kuzmin *et al.*, 1996; Kuzmin and Gudimova, 2002). In Russian waters of the Barents Sea, the number of legal-sized males (commercial stock) was estimated to be 4.3 million individuals in 2008 (Pinchukov, 2009). During the establishment of the population, red king crabs spread both to the west and east of the release sites in 1960–1970. Recently, the first findings of *P. camtschaticus* have been reported in the White Sea (Zolotarev, 2009), confirming continued range expansion. At present, the crab is common in Norwegian waters where its current commercial stock is estimated at 374 thousand individuals (Sundet and Berenboim, 2008).

The red king crab is among the world's largest arthropod, attaining weights > 10 kg and sizes of 220 mm in carapace length (CL) in the North Pacific (Powell and Nickerson, 1965) and up to 12 kg and 270 mm, in the Barents Sea (Kuzmin and Gudimova, 2002; Stiansen *et al.*, 2009). Red king crabs are high-level predators feeding on the most abundant benthic organisms, i.e. mollusks (bivalvia and gastropods), polychaetes and

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echinoderms (Kuzmin and Gudimova, 2002; Pavlova, 2008; Falk-Petersen *et al.*, 2011). In areas with intensive multispecies fishing, they predominantly feed on fish offal (Anisimova and Manushin, 2003). The main predators of red king crab in the Barents Sea are cod, wolffish and skates (Kuzmin and Gudimova, 2002). In Russian waters of the Barents Sea, red king crabs occur from shallow waters to > 335 m deep, at temperatures ranging from −0.8 to +8.5°C. In spring (April–May) they form mating aggregations at temperatures of 0–2°C. In autumn, August–September, red king crabs segregate by sex with males and females forming aggregations at temperatures of 4–6°C and 5–7°C, respectively (Stiansen *et al.*, 2009).

The population dynamics of *P. camtschaticus* in the Barents Sea has been extensively studied due to the species' high commercial value and non-indigenous status (Kuzmin and Gudimova, 2002; Sokolov and Milyutin, 2006). Other biological aspects are also well studied, such as distribution patterns (Sokolov and Milyutin, 2006), reproduction (Matyushkin, 2005), feeding (Anisimova and Manushin, 2003; Pavlova, 2008), molting (Kuzmin and Gudimova, 2002), limb injury patterns (Pinchukov, 2007; Sokolov and Milyutin, 2008; Dvoretsky and Dvoretsky, 2009b), migrations (Talberg, 2003; Jørgensen, *et al.*, 2007), behavior (Pereladov, 2003), and associated organisms (Bakay *et al.*, 1998; Dvoretsky and Dvoretsky, 2009a, 2010) in the Barents Sea. The main targets of these investigations, with some exceptions, were large crabs (legal-sized males with a carapace width (CW) >150 mm and egg-bearing females) because of traditionally used gears—trawls and bottom traps. In the Barents Sea, trawling is usually undertaken at depths >70 m and traps also may have depth limitations and are selective on the basis of crab size and sex (Zhou and Shirley, 1997; Zhou and Kruse, 2000; Stiansen *et al.*, 2008). Thus, at coastal sites, the most complete information on the population structure of red king crabs may perhaps be obtained by SCUBA diving. There are only a few studies of *P. camtschaticus* population biology in shallow (<60 m) coastal waters of the Barents Sea (Pereladov, 2003; Sokolov and Milyutin, 2006).

Dalnezelenetskaya Bay, a typical small bay of the Eastern Murman, is the area situated eastward from Kola Bay, in the southern Barents Sea. Dalnezelenetskaya Bay is known to be a site where *P. camtschaticus* larvae and juveniles were released as part of their introduction in the 1960s (Kuzmin and Gudimova, 2002). This shallow-water area is located near the margin of red king crab distribution in coastal waters of the Barents Sea. There are no previous complete records on population dynamics of the red king crab in Dalnezelenetskaya Bay (for some preliminary results see Britayev *et al.*, 2007, 2010). Therefore, the aim of this study was to investigate population dynamics and some biological aspects of the introduced crab in Dalnezelenetskaya Bay based on king crab sampled by divers from shallow water and supplemented by some large crabs for morphological studies. For this reason we studied (i) size–frequency distributions, (ii) morphological parameters, and (iii) population dynamics.

Material and Methods

Study area

Dalnezelenetskaya Bay is a semi-closed small bay with five islands delimiting the area of the bay from the open sea (Figure 1). Dalnezelenetskaya Bay is almost square with a length of 2 km. Two bights are situated in the southern part of the bay. The southeastern bight has a large sandy beach. High tidal levels (3–4 m) ensure intensive water exchange between the inner part of Dalnezelenetskaya Bay and the open sea. In winter, water temperature in the surface layer varies from −0.5 to +4.0°C, averaging +2°C. Mean salinity is typically 34.2 psu. In summer, water temperature ranges from 6.5–8.5°C and salinity from 32 to 34 psu (Matishov *et al.*, 2004).

Sampling and stock estimates

Red king crabs were collected in Dalnezelenetskaya Bay from late July to August, 2002–2009 by divers at shallow waters (from 5–40 m). In order to estimate stock of the crabs we used a transect method (Sokolov and Milyutin, 2006). The area of the bay was divided into several parts with the same types of biological community (benthic organisms living on hard and soft grounds, kelps and sand). A standard transect grid, which consisted of 12–25 transect lines covering a wide range of depths and different types of bottom communities, was established. Information about transect statistics is presented in Table 1. In 2004–2007, the area covered with transects was higher than in other years due to duplicate transects. Data on the depth, type of community and near-bottom water temperature were obtained from divers' reports.

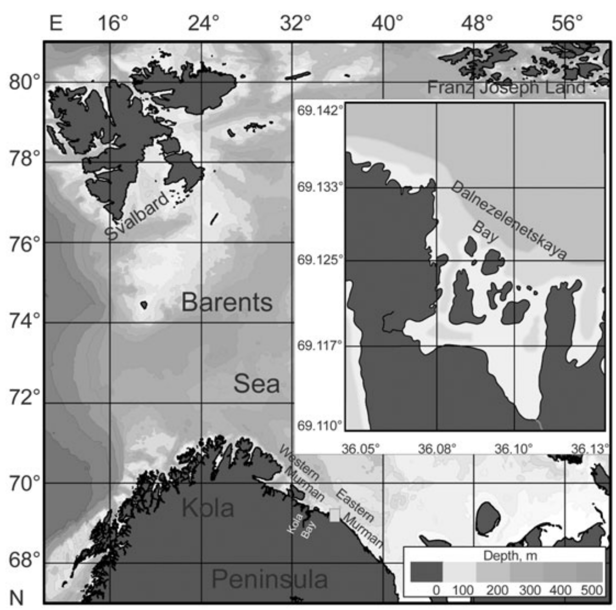

Figure 1. Study area, Dalnezelenetskaya Bay (Barents Sea).

Table 1. Transect data for red king crabs collected by SCUBA divers in in Dalnezelenetskaya Bay in summer 2002–2009.

Year	Transect number	Mean diving time per transect, min	Area examined, m^2
2002	13	28.7	23 030.3
2003	18	26.6	29 513.3
2004	21	31.1	40 318.4
2005	25	36.0	51 123.5
2006	22	31.2	42 417.7
2007	18	36.8	40 874.1
2008	14	33.6	24 873.7
2009	12	30.5	26 364.4

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The number of crabs on each transect line was then multiplied by the area of the bay sampled (1.7 km^2). For sites where transects were re-sampled, we used the mean density of crabs collected. For morphometric investigation we used additional measurements of 115 large male red king crabs (CL: range, 146.0–194.5 mm; mean ± SD, 166.9 ± 11.2) trapped in the open-sea area adjacent to Dalnezelenetskaya Bay.

Biological analyses

After being collected, the crabs were transported to the laboratory of the seasonal biological station of Murmansk Marine Biological Institute (MMBI) in Dalnezelenetskaya Bay. For each crab, the sex and shell condition (determined visually) were recorded following criteria in Kuzmin and Gudimova (2002) and Donaldson and Byersdorfer (2005). We also used standard crab measurements: (i) CW = the greatest straight-line distance across the carapace excluding spines, (ii) CL = the distance from the posterior margin of the right eye orbit to the medial-posterior margin of the carapace, (iii) merus length (ML) = distance from middle proximal notch to middle distal notch of the third right pereiopod, and (iv) chela height (CH) = greatest height measured on right chela excluding spines (Kuzmin and Gudimova, 2002; Donaldson and Byersdorfer, 2005). Additionally, we calculated the following ratios: CW/CL for all crabs and ML/CL for crabs with an intact merus only. Crabs were divided into two size classes: "small" crabs (CL < 90 mm) and "large" crabs (CL ≥ 90 mm). These size groups roughly correspond to immature and mature crabs, respectively (Sokolov and Milyutin, 2006). Though functional maturity of male red king crabs comes later than in females (Kuzmin and Gudimova, 2002), these size groups rather adequately reflect morphometric differences between sexes (Sokolov and Milyutin, 2006).

Statistics

Statistical significance of the deviations from a 1:1 sex-ratio was analysed using the Chi-square test. Weight–length and CH–CL relationships for small and large crabs were compared between males and females using an analysis of covariance (ANCOVA). The data were log-transformed for the allometric analyses. Differences in CW/CL and ML/CL ratios were compared between males and females using a one-way analysis of variance (ANOVA) for normally distributed data, or a Kruskall-Wallis test for data that did not meet this criterion. All statistical analyses were performed using STATISTICA (data analysis software system; http://www.statsoft.com/) v. 6 with a significance level of 0.05.

Results

Sex ratio

There was a difference in sex ratio between small and large crabs (Table 2). Juvenile sex ratio never differed statistically from 1:1, while adult sex ratio was female-dominated and varied from 4:1 in 2003 to 8:1 in 2004. We collected no adult male crabs in 2002, 2005, 2006 and 2008.

Size–frequency distributions and shell condition

Summer size–frequency distributions of red king crabs are presented in Figure 2. In 2002–2004, the majority of small crabs belonged to two modal classes—30 and 60 mm CL. In 2005–2007 and 2009, immature crabs were concentrated in modal classes of 20- and 40-mm CL. Mature females were mainly represented by individuals belonging to the 130- and 140-mm CL classes throughout the study period. In 2002, we observed the highest proportion of crabs of 70-mm CL and the lowest proportions of crabs <60-mm CL and of mature females compared to other years. This is connected with differences in study dates. In 2002, the majority of transects were done in late August when red king crabs migrate to the deep-water areas.

The majority of crabs collected had new shells representing molting <1 year prior to sampling: 94.1% among small crabs, 98.6% among large females, and 58.4% among large males. Premolt and soft-shell crabs were most frequent among small specimens (5.3%). Crabs with old shells represented 40.3% of large males compared to 0% of large females.

Morphometric parameters and relationships

The main size characteristics of the red king crabs captured in Dalnezelenetskaya Bay are presented in Table 3. Mean CL and CW were higher in females than in males. For our estimates we used simple linear relationships between CW and CL: CW = 1.21 CL − 6.297, $r^2 = 0.9975$, $n = 566$ (for males) and CW = 1.098 CL − 2.253, $r^2 = 0.9977$, $n = 736$ (for females). These relationships predict the CW of a specimen from its CL for comparison with other studies.

It is important to note that Russian scientists and fishermen use CW as the main size dimension in red king crabs, whereas foreign scientists use CL because it is measured more accurately than CW. Weight–length relationships found in small (CL < 90 mm) and large crabs (CL ≥ 90 mm) are presented in Table 4. In small crabs, these relationships were similar in males and females while in large crabs the parameters of the equations differed significantly between males and females

Table 2. Number of male and female red king crabs collected in Dalnezelenetskaya Bay in summer 2002–2009, and Chi-square tests for differences in observed sex ratios and the theoretical 1:1 ratio.

	Small crabs (CL < 90 mm)				Large crabs (CL ≥ 90 mm)			
Year	Male	Female	χ^2	p	Male	Female	χ^2	p
2002	74	54	3.125	0.077	0	1	N/A	N/A
2003	47	45	0. 043	0.835	21	81	35.294	<0.001
2004	42	28	2.800	0.094	10	77	51.598	<0.001
2005	92	93	0.005	0.941	0	151	151.000	<0.001
2006	86	73	1.063	0.303	0	19	19.000	<0.001
2007	60	50	0.909	0.340	4	22	12.462	<0.001
2008	2	3	0.200	0.655	0	0	N/A	N/A
2009	19	20	0.026	0.873	4	19	9.783	0.002

CL = carapace length, χ^2 = Chi-square value, p = significance level, N/A = not applicable.

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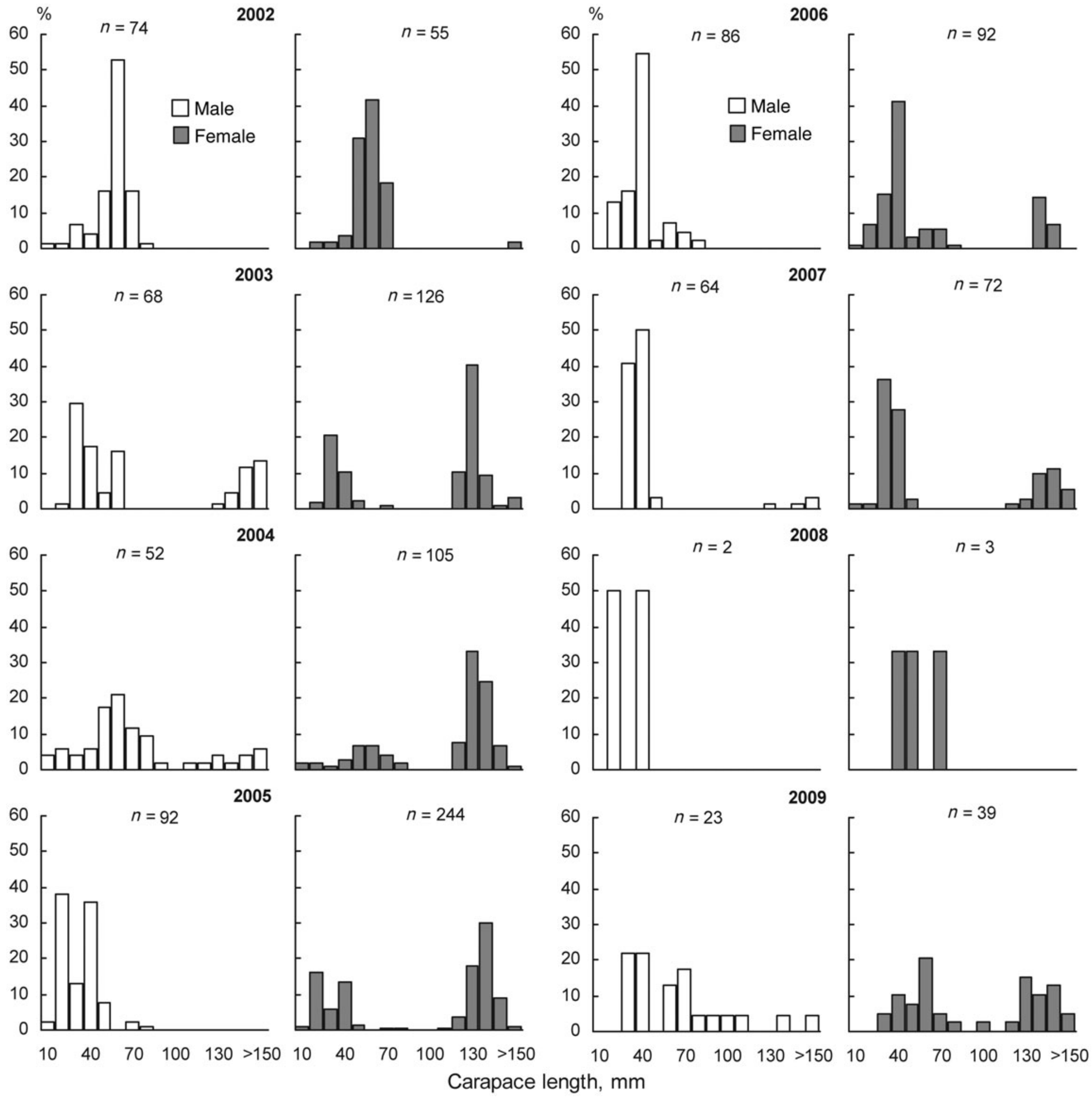

Figure 2. Size frequency distributions of *Paralithodes camtschaticus* collected in Dalnezelenetskaya Bay in summer 2002–2009. n = total sample size.

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Table 3. Morphometric characteristics of red king crabs collected in Dalnezelenetskaya Bay in summer 2002–2009.

	Males				Females			
Parameter	**Mean**	**SD**	**Min**	**Max**	**Mean**	**SD**	**Min**	**Max**
Carapace length, mm	46.1	33.7	9.2	191.0	83.8	50.0	8.5	172.6
Carapace width, mm	49.0	39.4	9.1	227.0	89.9	55.0	7.9	187.1
Merus length, mm	36.0	32.2	4.0	178.5	60.8	37.5	2.3	197.0
Weight, g	257.9	725.0	0.4	4972.0	856.2	871.7	0.2	6182.0

(Table 4). We did not find any differences between small males and small females in CW/CL ratio (Kruskall-Wallis test, df = 1, H = 2.770, $p = 0.096$) and ML/CL ratio (ANOVA, df = 1, F = 3.110, $p = 0.079$) (Figure 3). In contrast, these ratios were significantly higher in large males compared to large females (CW/CL, Kruskall-Wallis test, df = 1, H = 289.905, $p < 0.001$;

Table 4. Weight–length relationships in red king crabs collected in Dalnezelenetskaya Bay and adjacent open-sea waters, and results of analysis of covariance (ANCOVA) comparisons of the statistical significance of these relationships between males and females.

	Males			Females			ANCOVA statistics		
Category	**Equation**	r^2	*n*	**Equation**	r^2	*n*	**df**	*F*	*p*
Small (CL < 90 mm)	$W = 0.0005\ CL^{3.0759}$	0.9907	249	$W = 0.0005\ CL^{3.0884}$	0.9943	234	1	0.172	0.678
Large (CL ≥ 90 mm)	$W = 0.0005\ CL^{3.1027}$	0.9176	100	$W = 0.0049\ CL^{2.6225}$	0.7994	133	1	22.79	<0.001
Combined data	$W = 0.0004\ CL^{3.1317}$	0.9974	349	$W = 0.0005\ CL^{3.0787}$	0.998	367	1	128.39	<0.001

CL = carapace length, mm; W = weight, g

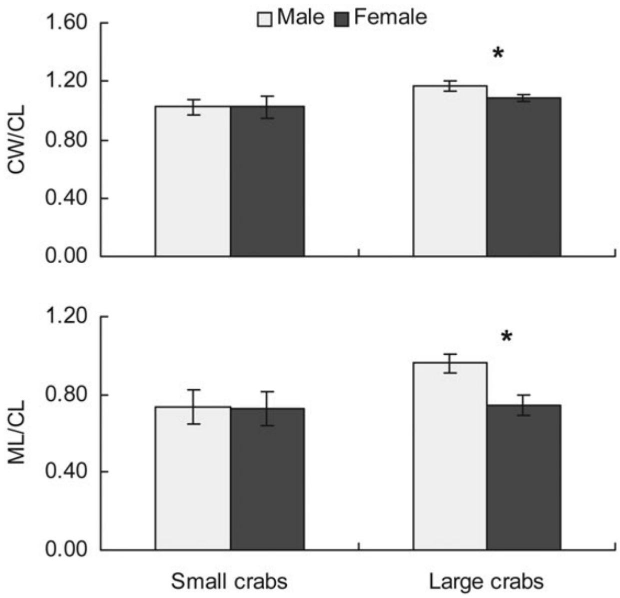

Figure 3. Estimated carapace width/carapace length (CW/CL) and merus length/carapace length (ML/CL) ratios in small (CL < 90 mm) and large (CL ≥ 90 mm) red king crabs collected in Dalnezelenetskaya Bay in summer 2002–2009. Vertical bars show standard deviations. Asterisks show significant differences ($p < 0.05$).

ML/CL, Kruskall-Wallis test, df = 1, H = 290.831, $p < 0.001$) (Figure 3).

Stock estimates

The estimated abundance of stock components varied interannually in Dalnezelenetskaya Bay (Figure 4). Based on diving results the number of individuals in the red king crab stock was estimated to range among 4100–7400 individuals over 2002–2009, except for 2008; in 2008, we observed a clear decline to about 350 individuals; in 2009, the estimated total stock increased again to 3760 individuals.

Discussion

The balanced sex ratio of small *P. camtschaticus* in shallow waters of Dalnezelenetskaya Bay is an expected finding. Small crabs do not migrate far offshore and tend to aggregate in the coastal areas of the Barents Sea. A similar tendency was noted by Sokolov and Milyutin (2006) in the Eastern Murman coastal sites during 2003. However, in our study, females dominated crabs in the large size category. In spring, after mating, most of the large males migrate to deeper water, whereas the females tend to not move as far offshore, causing the sex ratio in shallow

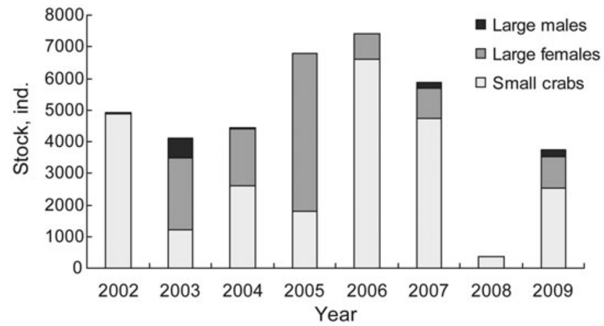

Figure 4. Stock dynamics of small (CL < 90 mm) and large (CL ≥ 90 mm) *Paralithodes camtschaticus* in Dalnezelenetskaya Bay in summer 2002–2009.

water to be highly biased towards females (Kuzmin and Gudimova, 2002). In this sector of the Barents Sea, an opposite pattern with large males predominating over large females was found in 2003 (Sokolov and Milyutin, 2006), but the period of those investigations was limited to 1–4 days, in comparison to our 15–25 days. This result may also be related to interannual fluctuations of the red king crab stock. For example, in 2003, large male crabs also predominated in trawls (70%, Pinchukov *et al.*, 2003) and it is in that year that we recorded the highest number of large males (21 individuals) in our own dive surveys (see Figure 2).

Two modes were observed in size frequency distributions for juvenile red king crabs. These modes changed between 2002–2004 and 2005–2009, being 30 and 60 mm CL, and 20 and 40 mm CL, respectively (Figure 2). These size classes may be attributed to the age classes 2+ and 3+ of red king crabs as suggested by Pereladov (2003). The downward shift observed in mode size classes may reflect differences in juvenile mortality rates between the years. As a rule, the mortality rate is higher in small than in large crabs due to their higher frequency of molting that makes them more vulnerable to predator attacks (including cannibalism). Increased mortality in 60-mm CL crabs may be connected with an increased anthropogenic impact, especially, recreational diving (Dvoretsky and Dvoretsky, 2009b). Previous studies have shown that recreational fishing can produce strong direct and indirect effects in aquatic ecosystems (Magnuson, 1991) and has led to severe declines in marine commercial crustaceans (Haaker *et al.*, 1996; Eggleston and Dahlgren, 2001). Our own observations have shown that in Dalnezelenetskaya Bay, the number of divers collecting both small crabs for souvenirs and large crabs for food significantly increased in the last years, coincident with increased levels of limb injury in large crabs and overall high autotomy levels for all red king crabs at the study site (Dvoretsky and Dvoretsky,

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2009b). This pattern is also in accordance with the stock dynamics observed in Dalnezelenetskaya Bay (see below). The increased number of divers is associated with the presence of a relatively good road for cars and a changed status of the area. Recently, special permissions required to visit Dalnezelenetskaya Bay were abolished, and citizens of the Russian Federation can now reach this area by car or ship. So, the number of tourists visiting the area has gradually increased. According to anecdotal information, a similar situation has been observed in other coastal sites of the Barents Sea.

The predominance of new-shell crabs is not surprising. Small crabs molt 2–4 times per year and they would not be expected to have old shells. Large male crabs molt typically once per year in spring after mating. The relatively high proportion of old-shell crabs among mature males is explained by their lower molting probability. In the Barents Sea, male red king crabs of > 110-mm CW can skip-molt, and some large males molt only once every 3–4 years (Kuzmin and Gudimova, 2002).

Our results showed that weight–length relationships were similar in small male and female crabs; this corresponds to the findings of other authors indicating that sex-specific growth rates are not apparent in red king crabs until maturity (Weber, 1967; Dew, 1990). This also explains the similarity in CW/CL ratio of immature males and females. Large male crabs collected in Dalnezelenetskaya Bay tended to be heavier than females of the same CL. Such a sexually dimorphic pattern may be associated with a higher energy investment in reproduction by females than by males, which can invest more energy in somatic growth. Moreover, this also explains why the ML/CL ratio was found to be higher in males than in females. Another possibility is connected with higher migration activity in male crabs which requires longer, more powerful legs, as has been suggested for *P. camtschaticus* both in the native and new places of its habitat (Kuzmin and Gudimova, 2002; Klitin, 2003). Immature crabs do not migrate over long distances and the MLs and the ML/CL ratios in small males and females are similar. The differences in weight–length relationships in large crabs may be also explained by differences in shell thickness (thicker in males due to the irregular molt), and differences in body proportions (males certainly have thicker and longer legs).

In the present study, the total number of red king crabs was relatively stable over the period 2002–2007 with some fluctuations caused by mass recruitment in 2006, which was preceded by the large proportion of females in 2005 (Figure 4). Recruitment was also high in 2002 and 2007. In 2008, we observed a decline of the total stock of *P. camtschaticus*. This decline corresponds to a decrease in the stock of red king crabs in coastal waters of the Barents Sea (Pinchukov *et al.*, 2011). Furthermore, in 2009 we observed a higher crab stock than in 2008; its value was lower than in the previous period 2002–2007. This rehabilitated level could be a result of a restriction of red king crab fishing that was forbidden from January–September 2009. Therefore, in general, the decline of the red king crab abundance could be associated with illegal fishing that led to a decrease of the total number of crabs in coastal waters of the Barents Sea in 2008 (Dvoretsky, 2011). A high level of illegal fishing is supported by the finding of red king crabs with fragments of forbidden gears. It should be noted that in the commercially fished areas the stock index of red king crab declined from 4.2 million individuals in 2008 to 1.5 million individuals in 2009, and the main reason for this event is considered to be illegal fishing (Pinchukov, pers. comm.). A second possibility is connected with the invasive status of *P. camtschaticus*. The red king crab, being an alien species, could have reduced their food resources especially in the areas of high abundance (Western Murman). However, recent studies have shown a negligible effect of this introduced species on local bottom communities (see review Britayev *et al.*, 2010), and this hypothesis should be rejected. A third consideration is survey measurement errors. Red king crabs from the study area are not truly a closed population. So, low estimated numbers of king crabs observed in 2008 could be due to changes in their distributions relative to the SCUBA depths of our transects (<40 m). For instance, movements of female king crabs have been reported in the North Pacific in association with life history events and in response to temporal and spatial variability in environmental conditions (Stone *et al.*, 1992, 1993). The increase in large females and large males observed in 2009 suggests that crab abundance was underestimated in 2008. Owing to the extremely small sample size, the size distribution and sex composition is poorly defined in 2008. However, a decline in total stock of both large males and females was also observed in adjacent deep-sea waters (Dvoretsky, 2011). Environmental conditions in the study area did not vary significantly in 2008 compared with 2007 and 2009 (Dvoretsky and Dvoretsky, 2013 and references therein). Moreover, the location of a transect grid in 2008 was similar to that of previous periods. Thus, we think that migrations of male and female crabs have lower significance than illegal fishing.

Our study has shown that the red king crab is well adapted to the environmental conditions of the Barents Sea. The population dynamics of the invader in a typical coastal site of Eastern Murman are in accordance with that observed for *P. camtschaticus* in other parts of the Barents Sea. Due to its relatively low stock size, the local sub-population is high sensitive to human impact, especially illegal fishing based on forbidden gears and traps as well as SCUBA diving. This increased level of human activity (mainly illegal fishing of crabs, including recreational diving) in coastal sites of the Barents Sea may be considered a consequence of red king crab introduction to the Barents Sea. This and other social aspects of the red king crab introduction should be considered in future studies. On the other hand, overfishing of *P. camtschaticus* could lead to a decrease in its abundance, as has recently been reported for native parts of its habitat (Orensanz *et al.*, 1998). Monitoring of red king crab sub-populations is required to save the commercial stock of *P. camtschaticus* in the Barents Sea for future exploitation.

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