

Invasion of the Atlantic rock crab (*Cancer irroratus*) at high latitudes

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Abstract With the increase in global oceanic trade the establishment of non-indigenous marine organisms has become a major environmental and economic problem worldwide. Recently, the Atlantic rock crab (*Cancer irroratus*) was reported in Icelandic waters, Eastern North Atlantic. This is the first record of this relatively large crab species outside its natural range, i.e. the east coast of North America. The crab was most likely transferred to Iceland as larvae in ballast water and has successfully established a reproducing population in Icelandic waters. The species is distributed

along the southwestern- and western-coast of Iceland. Adult specimens are now common in Faxaflói Bay, Southwest Iceland, but with sporadic occurrences in western and northwestern Icelandic waters. The green crab (*Carcinus maenas*) and the spider crab (*Hyas araneus*) are the only native brachyuran decapod species commonly found in its new habitat, but despite its recent colonization the rock crab was the most abundant brachyuran in the areas studied in southwest Iceland. Egg bearing rock crab and green crab females were found from June to October, while egg bearing spider crab females were seen from July to December. In Southwest Iceland both rock crab and green crab larvae were abundant in mid-summer but rare in both spring and autumn, which is opposite of what was observed for the spider crab. The size and abundance of adult crabs, their reproductive conditions, and occurrence of all larval stages, indicate that the Atlantic rock crab has successfully colonized Iceland.

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Introduction

Establishment of non-indigenous species has become a major environmental and economic problem worldwide with increasing global oceanic trade during the twentieth century (Brickman 2006; Cohen and Carlton

1998). Most marine invasions have resulted from commercial shipping, via the extensive unintentional transport of marine organisms in hull fouling and in ballast water (Ahyong and Wilkens 2011; Carlton 1996; Carlton and Geller 1993; DiBacco et al. 2012; Gollasch 2002; Ruiz et al. 1997; Ruiz et al. 2000). Despite extensive shipping in Nordic waters, relatively few anthropogenic oceanic introductions have been reported at high northern latitudes in the Atlantic Ocean. The most notable is the intentional introduction of the red king crab (*Paralithodes camtschatica*), a Pacific species successfully introduced for economic purpose in the Barents Sea in the 1960s and 1970s (Jørgensen 2006; Orlov and Ivanov 1978). Fewer introductions at high latitudes may reflect rapid dispersal following the retreat of glaciers about 10,000 years ago; the faunas of the northernmost Atlantic regions (Canadian Maritimes, Iceland, Norway) are closely related despite the long distances between these regions (see Ingólfsson 1992). The current maritime traffic, most often between low and high latitudes, might also contribute to the observed patterns as species from lower latitudes may have had difficulties establishing in the colder regions (Seebens et al. 2013). Alternatively, many historical introductions over the past 1,000 and more years may have been overlooked (Carlton 2003, 2009). In addition, future trans-Arctic maritime traffic may also increase introductions of non-indigenous organisms being transported between the high north of the Pacific and the Atlantic.

The oceanic island of Iceland has apparently not received many non-indigenous marine invertebrate species during the last decades. The only reported invertebrate introductions include the bivalves *Cerastoderma edule* and *Mya arenaria* (Óskarsson 1953, 1961), the decapod shrimp *Crangon crangon* (Gunnarsson et al. 2007), the algae *Codium fragile*, *Bonnemaisonia hamifera* and *Fucus serratus* (Ingólfsson 2008; Jónsson and Gunnarsson 1976; Munda 1979), and the planktonic diatoms *Stephanopyxis turris* and *Mediopyxis helysia* (Gunnarsson et al. 2010). These species have in common that man induced introduction, with ballast water or via ship hulls, is the most likely propagule pressure. Warming of Atlantic waters during the last 10–15 years (Astthorsson et al. 2012), may have aided in colonization of species occurring in Northeast Atlantic coastal waters (Cognie et al. 2006; Simon-Bouhet et al. 2006).

In this paper we present the first report of the occurrence of the Atlantic rock crab (*Cancer irroratus* Say, 1817) outside its natural range (Fig. 1). The species was first observed in the fjord Hvalfjörður in Southwest Iceland in 2006. Before that the species was only known to occur on the east coast of North America, from Florida to Labrador (Williams 1984). The distance from Iceland to the nearest land mass in North America where the crab can be found is over 2,200 km and includes long stretches of oceans with depths exceeding 1,000 m. The newly colonized population in Iceland is likely to be originated from the northern range of its native distribution (Gíslason et al. 2013a, b). The marine climate of Iceland is similar to that of the Atlantic Canada, although the sea surface temperatures in winter are generally higher and summer temperatures do not get as high as in Canadian waters, as reported by the Department of Fisheries and Ocean, Canada (DFO 2012) and Ingólfsson (1992).

In order to study the colonization of the rock crab in Icelandic waters, we sampled adults and larvae and studied the size structure and distribution of the species in the area where it was first found. Two native crab species, the European green crab (*Carcinus maenas*) and the spider crab (*Hyas araneus*), which inhabit the same areas, were studied in parallel for comparison. The former species is currently influencing the Atlantic rock crab in its natural habitat (see e.g. Matheson and Gagnon 2012). In addition we searched for rock crab larvae at selected sites in western and northern Iceland.

Materials and methods

The first reported specimen of the Atlantic rock crab was found 6 August 2006 in the fjord Hvalfjörður, Southwest Iceland at SCUBA depths (near 64°21.51'N, 21°29.45'W). In a preliminary survey using baited traps in late October 2006, Atlantic rock crabs (n = 12; males: 7.9–12.4 cm carapace width; females: 9.1 and 9.9 cm carapace width) were found to occur at several localities in Hvalfjörður at depths between 14 and 30 m.

Quantitative samples were taken in four areas in Iceland, i.e. in Hvalfjörður and Faxaflói Bay (Southwest Iceland), Patreksfjörður and Tálknafjörður (Northwest Iceland), Álftafjörður (Northwest Iceland) and Eyjafjörður (North Iceland) (Fig. 2). Both trap

Fig. 1 World distribution of the Atlantic rock crab (*C. irroratus*) in dark grey shading

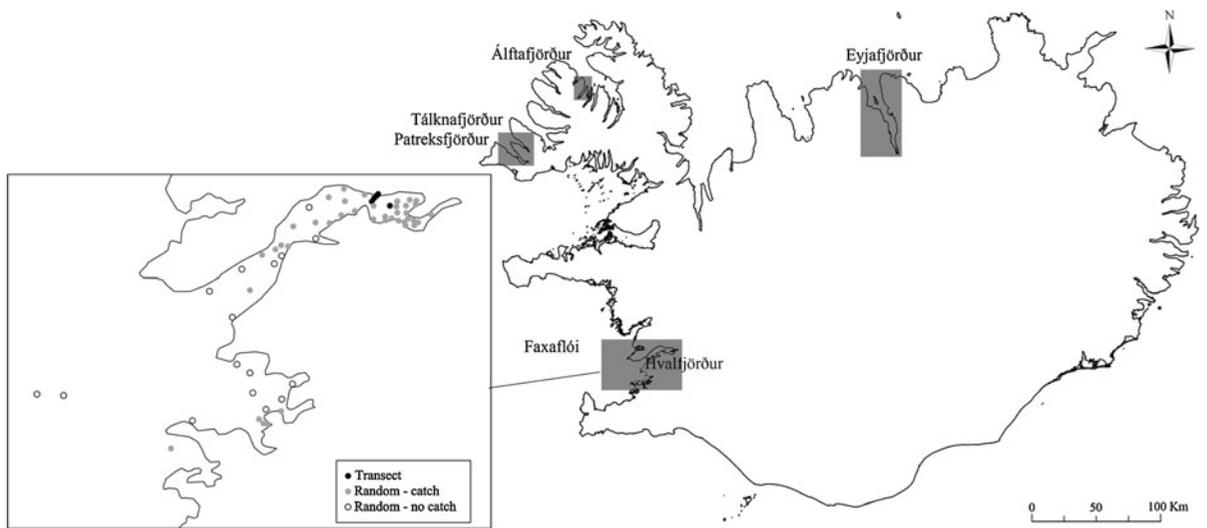
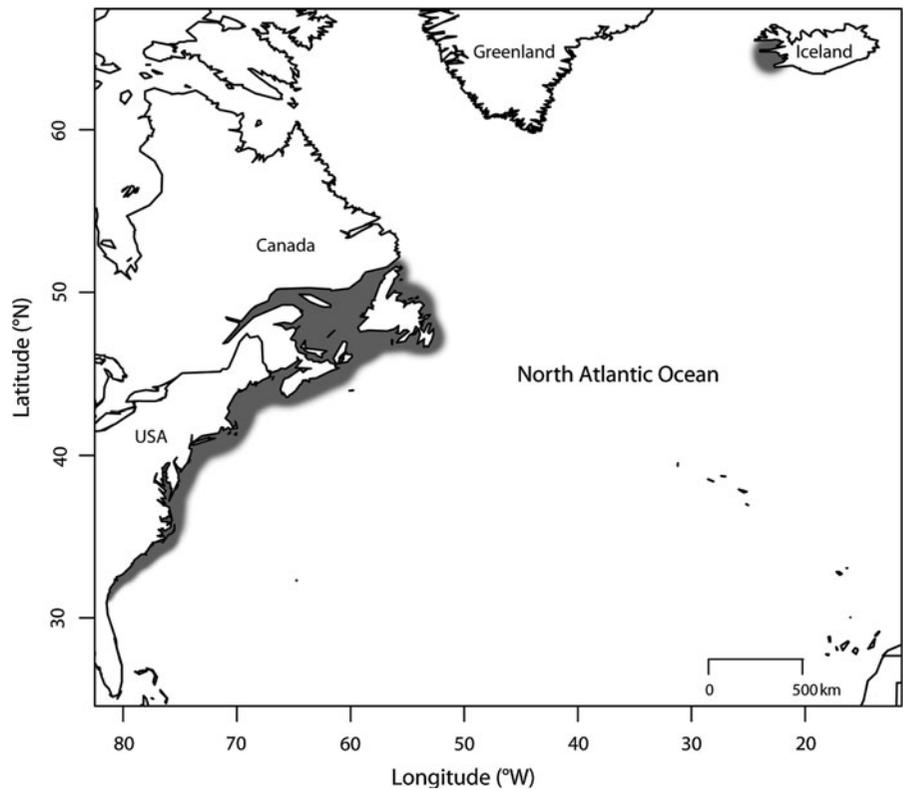


Fig. 2 The search for rock crab larvae in Iceland was carried out off the SW-coast (Hvalfjörður and inner Faxaflói Bay), Westfjords (Patreksfjörður, Tálknafjörður and Álftafjörður) and

in the North (Eyjafjörður). Baited traps were only laid out in Hvalfjörður and inner Faxaflói Bay in search for adult individuals (inserted figure)

fishing and plankton sampling were carried out in Hvalfjörður and the inner parts of Faxaflói Bay, but only plankton was sampled in the other areas.

Rock crabs and other decapods were captured with commercial crab traps (height 30 cm; length 80 cm; width 40 cm; mesh size 4.8 cm; Carapax AB[®],

Sweden; traps commercially used for *Cancer pagurus*; escape opening for juveniles closed) in Faxaflói Bay at depths from 7 to 80 m, from April to December in the years 2007–2009. Twenty traps were used on each occasion where two traps were put out on each sampling station with 10 m distance between them. In each sampling trip ten traps were randomly deployed in the study area of Hvalfjörður and Faxaflói Bay and additional ten traps were placed out on a transect in Hvalfjörður, at a depth gradient (10, 20, 30, 40 and 60 m) (Fig. 2). About 250 g of bait was used in each trap, a mix of cod (*Gadus morhua*) and pollock (*Pollachius virens*). Baited traps were set on bottom for about 48 h before retrieval. All crabs were brought to land alive where their size was measured; their gender determined and examined if females carried eggs.

Total body weight was measured using an electronic scale, with an accuracy of ± 1 g. The size of crabs was always measured between the two most distant points on the carapace, therefore maximum carapace width (for the rock crab and the green crab) or length (for the spider crab) was measured to the nearest 0.1 cm using a vernier caliper. Size increment was estimated by calculating the change in the quantiles of the carapace width over the time period studied, from 2007 to 2008 and from 2007 to 2009.

Plankton samples were taken with standard Bongo nets (Hydro-bios Apparaturbau GmbH®, Germany). The Bongo nets have a 60 cm ring diameter, 250 cm net length and 500 μm mesh size. The nets were towed at 10 m depth at 1.3 m/s for 10 min at each sampling station. Filtered volume was estimated with a flow meter (Hydro-Bios Kiel, Model 438 110) that was fitted on one of the nets opening. Samples were immediately preserved in 10 % formalin in seawater and later washed and preserved in 96 % ethanol.

All larvae of the rock crab, the European green crab and the spider crab collected in Faxaflói and Patreksfjörður were determined to larval stages according to Sastry (1977), Ingle (1992) and Rice and Ingle (1975). In other areas (Tálknafjörður, Álftafjörður and Eyjafjörður) samples were only scanned for rock crab larvae.

Temperature data were acquired from auto logging temperature meters that the Marine Research Institute of Iceland has located in the fjords and nearby areas (MRI 2012).

Results

Trap fishing

In total 1,486 specimens of the Atlantic rock crab were caught in Hvalfjörður and in the inner parts of Faxaflói Bay in the years 2007–2009 (Table 1). Additionally, 550 specimens of the green crab and 643 specimens of the spider crab were caught.

The rock crabs were most abundant in the traps from the middle of July to October (Fig. 3). Of the 1,486 rock crabs, 1,117 were caught on the transect in Hvalfjörður and 369 on the random stations in Hvalfjörður and Faxaflói Bay. The average number of rock crabs on the transect was 9.6 crabs/trap (Fig. 3) and the average weight was 2.3 kg/trap (Appendix 1 in ESM). Seasonal changes and the overall catch remained relatively stable across the 3 years (Fig. 3 and Appendix 1 in ESM). The proportion of crab species changed, however, significantly on the transect with years ($p < 0.0001$) as the catch rate of rock crabs increased every year ($b = 0.237$).

The number of rock crabs decreased with greater distance from the transect ($b = 0.071$, $p < 0.05$), i.e. lower abundance of crabs was observed in the outer part of Hvalfjörður and in Faxaflói Bay, compared to the inner part of Hvalfjörður.

Significant difference in catch rate was observed with depth and years for the three species. Number of rock crabs decreased with depth in 2007 and 2009 ($b = -0.009$ to -0.03 , $p < 0.001$), but not in 2008 ($p > 0.05$). Number of green crabs increased with depth in 2008 ($b = 0.03$, $p < 0.0001$) but became less for the spider crab ($b = -0.139$, $p < 0.0001$). The rock crab was the most abundant ($p < 0.001$) of the three species at all depths on the transect in the two best fishing months, July and October, except at 10 m in October 2007 and at 60 m in October in all three sampling years (Fig. 4).

Size range

The average size of the adult Atlantic rock crab males was 11.4 cm in 2007, and the largest specimen was 14.2 cm (Fig. 5, Table 2). The average male crabs size was larger in 2008 (11.51 cm; largest crab = 13.5 cm) and still larger in 2009 (11.95 cm; largest crabs = 14.2 cm), with significant difference between 2007 and

Table 1 Annual catch of rock crab (*C. irroratus*), green crab (*C. maenas*) and spider crab (*H. araneus*) in 2007–2009 in Hvalfjörður and inner Faxaflói Bay, SW-Iceland. Number of

sampling trips, males, females and berried females (included in data for females) are shown

	Month	Trips	<i>Cancer irroratus</i>			<i>Carcinus maenas</i>			<i>Hyas araneus</i>		
			M	F	Egg bearing F	M	F	Egg bearing F	M	F	Egg bearing F
2007	April	1	1	0	0	0	0	0	0	0	0
	May	1	52	4	0	4	0	0	30	93	0
	June	1	17	1	0	1	0	0	0	0	0
	July	2	199	31	5	8	1	0	48	18	14
	August	1	85	14	1	9	1	1	21	18	15
	September	1	100	13	0	25	4	0	22	22	20
	October	1	121	5	0	125	10	1	25	53	42
2008	May	1	0	0		0	0		0	0	
	June	1	4	1	1	1	0	0	3	1	0
	July	2	139	16	0	12	7	1	33	13	9
	August	1	89	53	7	6	4	0	12	0	0
	October	1	105	9	0	105	55	0	56	15	12
	July	2	203	22	2	14	11	0	33	6	4
2009	October	1	127	4	1	134	1	0	54	5	4
	December	1	69	2	0	10	2	0	56	6	6
Total		18	1,311	175	17	454	96	3	393	250	126

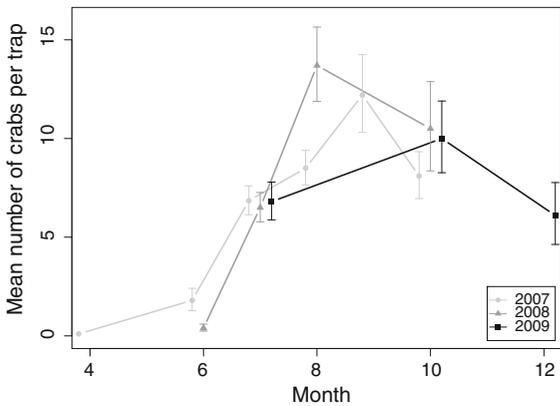


Fig. 3 Average number of rock crabs (\pm standard error) per trap on the transect in Hvalfjörður in the sampling years 2007–2009

2009 ($p < 0.001$), and showing consistent shift in size for all quantiles of the distribution (Fig. 6). The average size of females was significantly less in 2008 in comparison to 2007 ($p < 0.001$), but significantly larger in 2009 (Fig. 6, $p < 0.001$).

Sex ratio

Overall, males outnumbered females in trap catches for all three species, with the exception of May and

October in 2007 for the spider crab (Table 1). Interaction between depth and gender over the year was only observed for the spider crab ($p < 0.0001$) where the proportion of females increased with depth.

Berried females

Berried rock crab females were observed in 2007. Of the 175 female rock crabs caught in 2007–2009, only 17 (9.7 %) carried eggs. Berried females were caught from June to October (Table 1). All of them had well developed eggs, brownish in color, except a single female caught in October 2009 which had undeveloped bright orange eggs.

Only three (3.1 %) berried green crabs were caught, all carrying undeveloped reddish eggs. The proportion of berried spider crabs was much higher (50.4 %) than for the other two species where the spider crabs carried both undeveloped (orange) and developed (brown) eggs, from July to December (Table 2).

Larval abundance

Rock crab larvae were found in two of the four sampling areas, Faxaflói Bay and in Patreksfjörður. In

Fig. 4 Proportion of the three species (*light grey: H. araneus*, *grey: C. irroratus* and *dark grey: C. maenas*) in July and October in relation to depth on the transect in the sampling years 2007–2009. The number of crabs at given depth is given over each bar

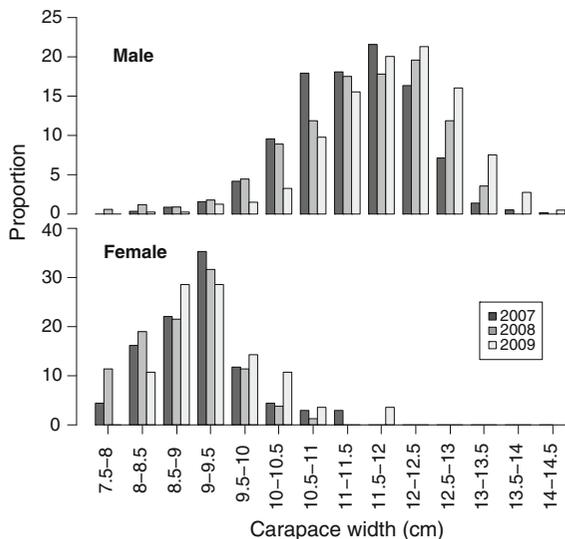
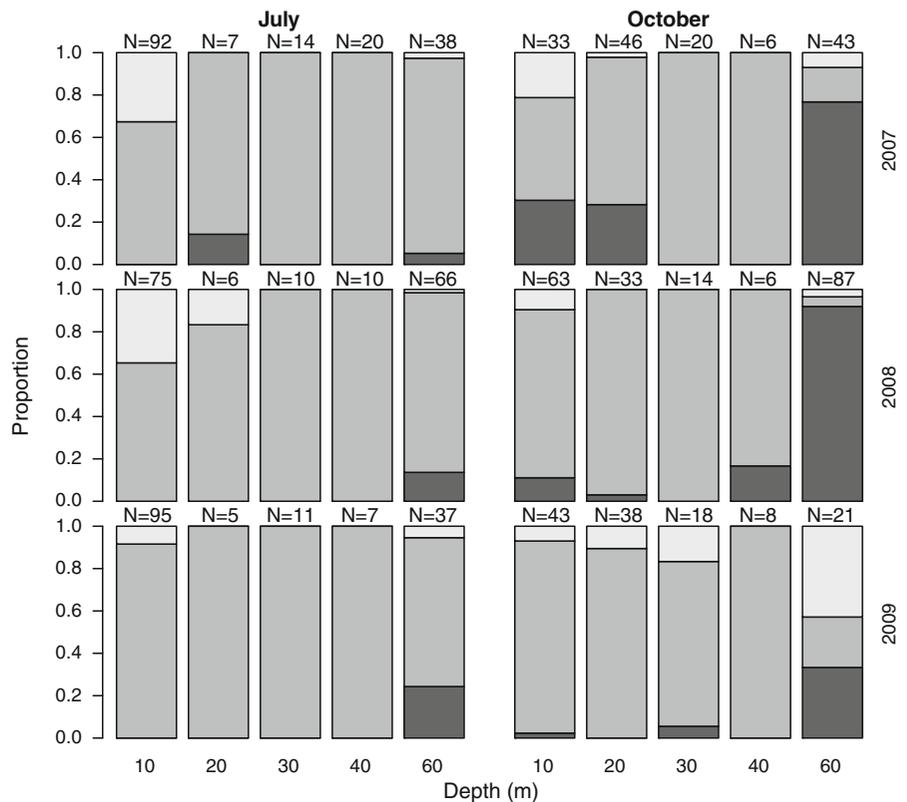


Fig. 5 Size frequency distribution of rock crab (*C. irroratus*) for the sampling years 2007–2009

Faxaflói Bay rock crab larvae were present in surface waters (~10 m depth) between May and November in 2007 and 2008 (no sampling in 2009). Peak period of

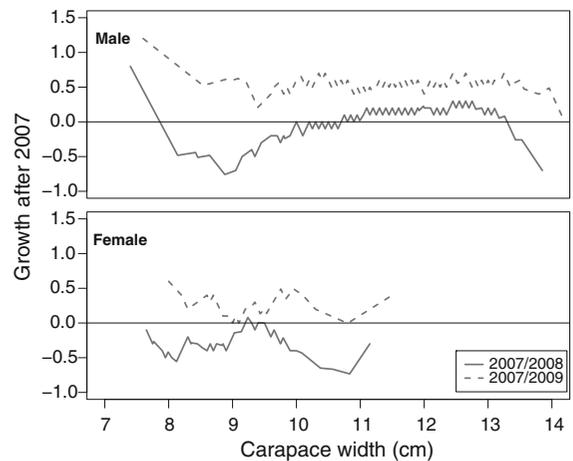


Fig. 6 Growth in carapace width (cm) of *C. irroratus* in Faxaflói, SW-Iceland in 2007 with respect to size classes. The growth is estimated by the difference in quantiles over one (*solid line*) and 2 years (*broken line*)

larval abundance was in July in both years, i.e. 1.5 larvae/m³ in 2007 and 2.1 larvae/m³ in 2008, when annual surface water temperature was highest,

i.e. 12.1–12.5 °C (Fig. 7). Only zoea I larvae were observed in May and June in both sampling years, but from July to November the later larval stages were found (Fig. 8). The first four larval stages, zoea I–IV, were observed in 2007 while in 2008 all the six stages were found in surface waters. In Patreksfjörður rock crab larvae were found in July 2008 at low density, 0.03 larvae/m³.

Green crab larvae were present in surface waters from June to October. Abundance of green crab larvae showed similar pattern to the abundance of rock crab larvae with a peak period in July (Fig. 7). In 2007 the abundance of green crab larvae was highest in early July (1.1 larvae/m³) and in late July in 2008 (2.2 larvae/m³). The spider crab showed much lower larval density than the other two species, with the highest

Table 2 Length and weight characteristics (mean, range and standard error) for rock crab (*C. irroratus*), green crab (*C. maenas*) and spider crab (*H. araneus*). Individuals with missing leg/claw were excluded from the data

	N	Carapace (cm)			Weight (g)		
		Mean	Range	SE	Mean	Range	SE
<i>Cancer irroratus</i>							
Males	1,137	11.6	7.8–14.2	0.029	247.3	72–443	1.860
Females	220	9.1	7.6–11.7	0.048	118.6	63–220	1.938
All	1,357	11.2	7.6–14.2	0.036	226.2	63–443	2.047
<i>Carcinus maenas</i>							
Males	126	7.1	5.2–9.9	0.058	96.1	35–198	2.460
Females	33	6.2	4.5–7.4	0.107	56.8	20–96	3.106
All	159	6.9	4.5–9.9	0.059	88	20–198	2.410
<i>Hyas araneus</i>							
Males	200	8.8	5.9–11.2	0.081	170.3	42–403	5.351
Females	45	7.6	5.7–8.9	0.132	96.3	30–169	4.964
All	245	8.6	5.7–11.2	0.076	156.7	30–403	4.821

Fig. 7 Mean density (larvae/m³) of three crab species; rock crab (*C. irroratus*), green crab (*C. maenas*) and spider crab (*H. araneus*), each sampling day in inner Faxaflói Bay in the years 2007 and 2008. Sea temperature is also shown. Line segment on x-axis mark the beginning and end of each month

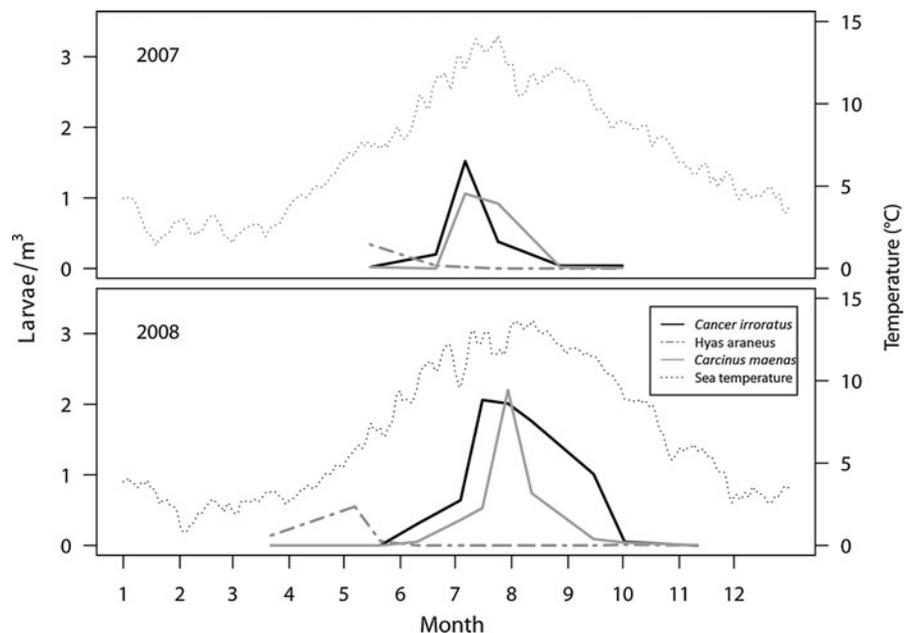
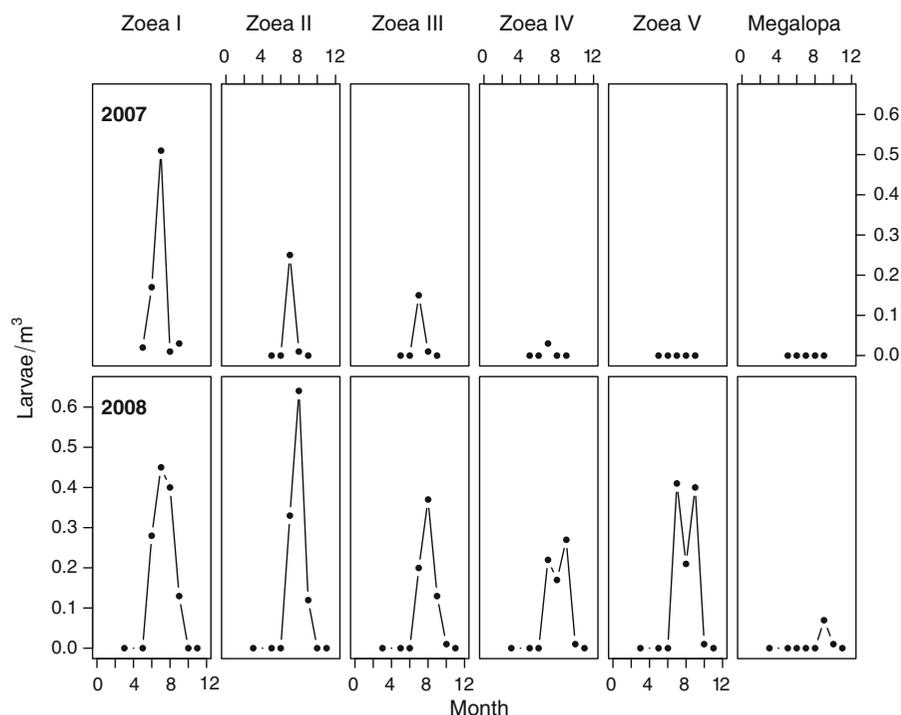


Fig. 8 The mean number of rock crab (*C. irroratus*) larvae at each larval stage per m³ in Hvalfjörður and inner Faxaflói Bay in the years 2007 and 2008



larval abundance in spring, from March to May (0.14–0.6 larvae/m³). In other sampling months spider crab larvae were either absent or only observed in very low density (<0.04 larvae/m³).

The proportion of larvae among the three crab species differed both within and between sampling stations in inner Faxaflói Bay (Fig. 9). In the year 2007 green crab larvae were most abundant (~70 %) in the inner part of Hvalfjörður. In the outer part of the fjord the proportion was more similar between green crab and rock crab but out in Faxaflói Bay the rock crab was predominant (98 %). In the year 2008 green crab larvae were still most abundant in the inner part of Hvalfjörður (~70 %) but numbers reduced greatly in the outer part of the fjord where rock crab was predominant (>67 %). The proportion of spider crab larvae was low in both sampling years showing more scattered distribution compared to the other species.

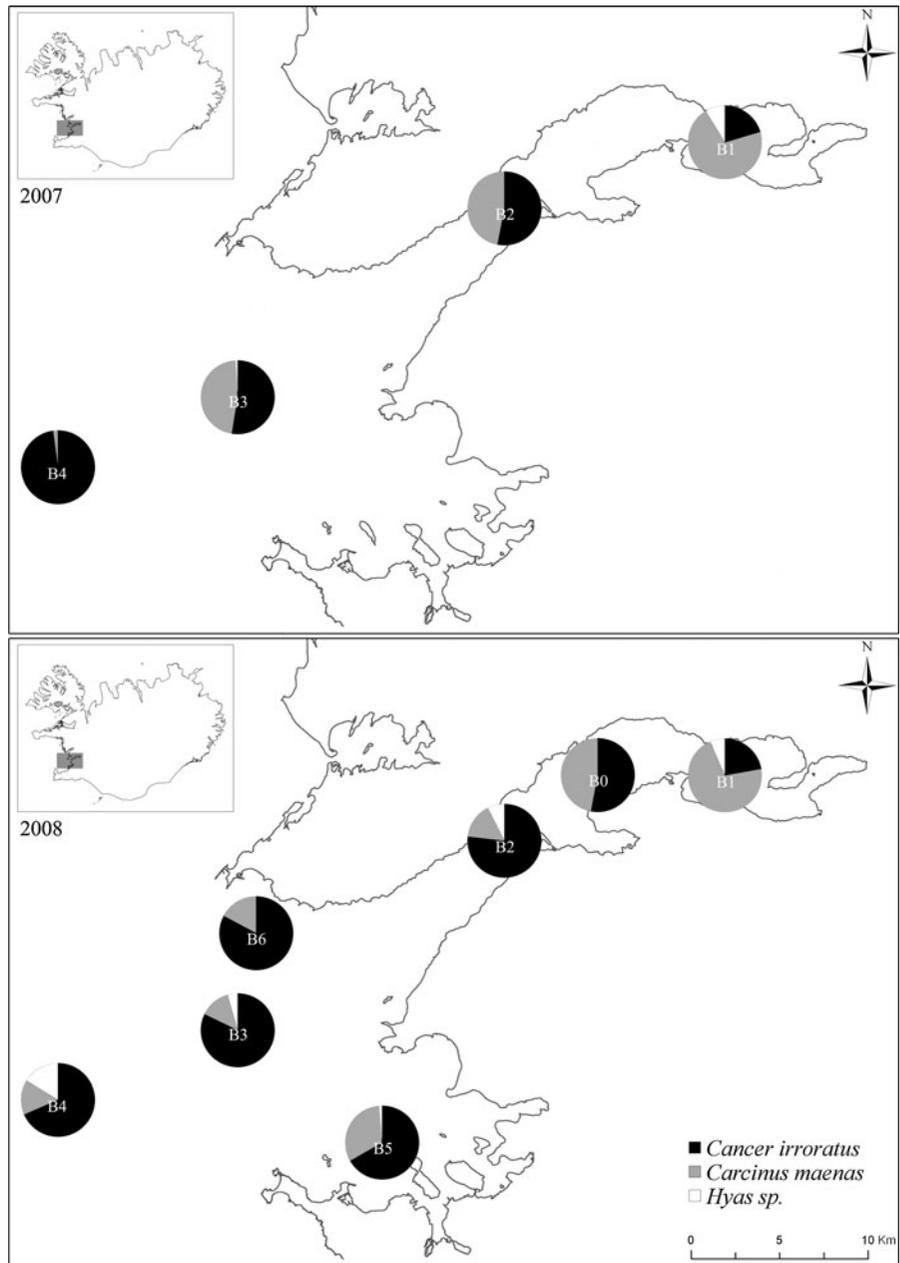
Discussion

The rock crab *C. irroratus* was most likely introduced as larvae to Iceland with ballast water. Natural dispersal by currents can be ruled out as south of Iceland there is a huge anti-clockwise sub-polar gyre,

which makes a fast drift from Canada to Iceland impossible (Jakobsen et al. 2003). The possibility for larvae to cross the Labrador Current along the Canadian coast, to enter the Atlantic Drift, hence into the eastern branch of the gyre, drift north-eastward, and finally northward to Iceland is very small. The length of this dispersal route would be around 5,000 km and with an average speed of around 10 cm/s, the transport would thus take around 600 days for the larvae. Considering that the pelagic phase of larval development for the rock crab varies from 17 to 50 days depending on temperature (Johns 1981) this possibility can be ruled out. In contrast, successful transport of larvae of *C. irroratus* in ballast water from North America to Europe has been shown (Hamer et al. 1998), although colonization in European waters has not been observed until now. Migration of adult rock crabs to Iceland is highly unlikely, first because of the great distances between the coasts of Iceland and North America, and second due to the depth of the Atlantic ocean, especially considering that the species has never been reported below 750 m depth (Haefner 1976).

A previous natural occurrence of the crab in Icelandic waters can be ruled out. Extensive studies of the marine biota have been conducted in Iceland in

Fig. 9 Proportion of the number of each crab larvae species with all larval stages included; rock crab (*C. irroratus*), green crab (*C. maenas*) and spider crab (*Hyas* spp.) on plankton stations in Hvalfjörður and inner Faxaflói Bay during the sampling years 2007 and 2008



the past (e.g. the Danish *Ingolf* Expedition 1895–1896) including analysis of museum material for the series Zoology of Iceland (Christiansen 1969; Stephensen 1939), in 1978–1979 a large survey was undertaken in Hvalfjörður, including sledge samples (Aðalsteinsdóttir and Garðarsson 1980) and the large BIOICE project mapping the benthic fauna around Iceland during 1992–2002 (e.g. Moreira and Parapar 2012). Studies were done on *H. araneus* in Iceland

using traps in the years 1983–1995 (Einarsson 1988; Sólmundur Tr. Einarsson, personal communication) and again in 2004 (Sólmundur Tr. Einarsson, personal communication). None of these studies found *C. irroratus* in the region.

The Atlantic rock crab seems to have colonized Icelandic waters in Hvalfjörður. This is a fairly long and narrow fjord, about 35 km long and 3.5 km wide, with maximum depth of 84 m. A harbor serving a few

large cargo vessels has been located at the northern side of Hvalfjörður (64°21.21'N, 21°46.40'W), 13 km from the mouth of the fjord, since 1978. The vessels serve to transport raw material and processed products from a Ferrosilicon (FeSi) plant (since 1979) and an aluminum factory (since 1998). Different vessels are used for raw materials and products and accordingly large vessels without cargo, but with extensive ballast water, enter the fjord to pick up factory products.

Despite its recent colonization the rock crab is currently the dominant brachyuran crab species in coastal waters of Faxaflói Bay. The maximum size of the rock crabs in Iceland is similar to what is found in its native habitat in North America, which is noteworthy considering the recent colonization in Iceland. However, in Icelandic waters the species is not influenced by one of the main competitor in its natural environment, the American lobster (*Homarus americanus*) (Hudon and Lamarche 1989; Sainte-Marie and Chabot 2002; Wells et al. 2010). Based on the size of individuals caught in 2006 the rock crab may have arrived in Iceland either in the year 1998 or 1999, considering Reilly's age estimator (1975). The narrow bell-shape of the male population (and lack of small males in 2007–2009; the traps did not have any escape openings) and clumping of the bulk of the population in a restricted area, indicates a single cohort, presumably flushed out in the ballast water of a large vessel or vessels. However, subsequent fisheries (unpublished data) and studies on the genetic variation of the Icelandic population sampled in 2007 point to recruitment in Icelandic waters and did not detect any clear evidence of genetic founder effects in the population (Gíslason et al. 2013a, b).

Seasonal variation in catch rate illustrate that catch was lower in spring than in late summer and fall. Similar seasonal differences in trap catch have also been described for other decapods, such as the Dungeness crab (*Metacarcinus magister*) (Taggart et al. 2004), edible crab (*Cancer pagurus*) and the lobster (*Homarus gammarus*) (Bennett 1974). The catch rate of male rock crabs was preponderant and without substantial seasonal variation between years. The low catch rate of females could simply be explained by the fact that during the main fishing season (April–October) mature females are egg bearing or molting and therefore not very active (Haefner 1976; Krouse 1972; Tremblay and Smith 2001). This behaviour is well known for other species, e.g. the

edible crab (Howard 1982). Studies on the Dungeness crab have also shown that ovigerous females move less frequently, slower and have lower feeding rate than males or non-ovigerous females (O'Clari et al. 1990; Taggart et al. 2004), and might therefore be less attracted to bait. Furthermore, the catchability of decapods in traps has also been shown to be effected by both sex and size, whereas females and small individuals are less catchable (Miller 1989; Tremblay and Smith 2001). In North America the sex ratios of the rock crab appear to vary both with seasons and locations (Bigford 1979; DFO 2000; Krouse 1972; Robichaud and Frail 2006). These differences have been explained as possible population movements/migrations which are restricted to one sex (Bigford 1979). However, no conclusive explanations have been revealed for this different catch rate of the sexes in Icelandic waters.

Proportion of berried females was different between the three species. Berried rock crabs were caught from June to October and their proportion was similar between years. This is similar to what is seen in its distribution in North America. Females with well developed eggs or egg remains are mainly seen from June to August in Canada and Maine (DFO 2008; Krouse 1972) but from March to June for more southern populations (Reilly 1975; Reilly and Saila 1978). The proportion of berried green crabs was low although a number of small egg-bearing green crab females was observed in cod stomachs in July 2007 in Hvalfjörður (in cod that were caught for bait in crab traps, personal observation), while no females were caught in traps. This clearly indicates that trap fishing can be biased, thus only giving limited information about sex ratios. This seems to vary between distribution areas. For example, berried green crabs have been caught from April to August in Maine, USA (Berrill 1982), from February to June in Swansea, UK (Naylor 1962) and all year around in Portugal (Baeta et al. 2005). The proportion of berried spider crabs varied from 45 to 82 %, between years in this study. In accordance to Einarsson (1988), spider crab females have been found with both undeveloped (orange) and developed eggs (brown) all year around in Icelandic waters.

Environmental conditions in Southwest Iceland seem to be appropriate for larval development of the rock crab. Rock crab larvae were present in surface waters from May to November, with peak period in

July when the temperature is near maximum in Icelandic waters. This is in harmony with seasonal changes in both biomass and density of zooplankton (Bot et al. 1996; Gislason and Astthorsson 1995). Larval abundance seems therefore to be closely linked to surface temperature. This is similar to what is known in Canada where larval abundance is highest in August–September, when surface water temperatures are beginning to decline and bottom water temperatures are approaching their maximum (Petrie and Francis 1993; Scarratt and Lowe 1972). Interestingly rock crab larvae were found in Patreksfjörður in low numbers. It is however uncertain if the species is successfully reproducing in Patreksfjörður or if the occurrence of larvae was caused by larval drift from the south, with the coastal current that runs in a clockwise direction around Iceland (Valdimarsson and Malmberg 1999). Similar results were observed for larval density of the green crab in Icelandic waters, with a peak in July. The larval period of the green crab in Iceland is similar to what it is seen in Canada, from June to October (Cameron and Metaxas 2005). In Britain the larval period is earlier, i.e. from February to July (Naylor 1962). Larvae are, however, found all year around in Portugal (Baeta et al. 2005; Queiroga et al. 1994). This indicates a latitudinal pattern of the species, from north to south. In comparison with the rock crab and the green crab, the larval density of the spider crab was low. Unlike the other two species, the peak in larval abundance of the spider crab was in May. Only a few spider crab larvae were found in the summer and autumn samples. These results indicate that the spider crab larvae hatch earlier in the year and develop at lower temperatures. This is similar to what is known about the spider crab in the North Sea where hatching occurs mainly from February to April, when water temperature is 3–6 °C (Anger 1983; Kunisch and Anger 1984). In Newfoundland the spider crab larvae are present later in the year or from June to August (Squires et al. 1997), although water temperature is similar to what it is in Iceland over the summer months (Lawson and Rose 2000; Nakashima and Wheeler 2002).

This study shows that the rock crab has a well established stock in Icelandic waters. The successful colonization of the rock crab may be linked to the large scale changes that have been observed in the North Atlantic Ocean in recent years (Anonymous 2004). Since 1996, Icelandic waters have become warmer

which has led to noticeable changes in Icelandic marine ecosystems (Astthorsson et al. 2007, 2012; Astthorsson and Pálsson 2006). In comparison to its two main competitors, the rock crab seems to be becoming a dominant crab species off the southwest coast of Iceland. In light of its size and generalist diet (Drummond-Davis et al. 1982; Scarratt and Lowe 1972) the species may have significant effect on a variety of native benthic organisms, e.g. through direct predation, competition for habitat or indirect trophic cascades.

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