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Population dynamics of three brachyuran crab species (Decapoda) in Icelandic waters: impact of recent colonization of the Atlantic rock crab (*Cancer irroratus*)

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The Atlantic rock crab (*Cancer irroratus*) was first found in Icelandic waters in 2006. Since then, the species has dispersed rapidly and is currently found clockwise from the southwest coast of Iceland to the east, corresponding to >70% of the coastline. Here, we present a monitoring study on this non-indigenous crab species in Iceland from 2007 to 2019. The study shows that the rock crab is now the most abundant brachyuran crab species on soft substrate bottoms in Southwest Iceland, both as adults and planktonic larvae, indicating that it is outcompeting its rival native species, the European green crab (*Carcinus maenas*) and the spider crab (*Hyas araneus*). The average size of the rock crab was similar over time (2007–2019), although it fluctuated between years in a pattern similar to that for the green crab, while significant reduction in size was observed for male spider crabs. The rock crab population is still in a growth phase in Icelandic waters, as seen in increasing distributional range, and can be found in densities comparable to the highest reported for the species in its native range in North America.

Keywords: *Cancer irroratus*, *Carcinus maenas*, competition, *Hyas araneus*, Iceland, invasive species

Introduction

Marine non-indigenous species are a worldwide problem, which has increased enormously in recent decades due to increasing world oceanic trade and travel by humans (Cohen and Carlton, 1998; Brickman, 2006). They are considered important drivers of ecological changes, as their impact can lead to habitat changes, displacement of native species through predation and/or competition, spread of diseases, and reduction in biodiversity (Bax *et al.*, 2003).

Crustaceans (Arthropoda) are among the most successful marine invaders, and one of their largest and most widespread groups is decapods (Hänfling *et al.*, 2011). Decapods play an important role in benthic communities, ranging from intertidal to deep waters. They are successful and versatile predators that prey on more than one trophic level and interact in various ways with their habitat and its inhabitants, as well as being prey for a large range of both vertebrates and invertebrates (Boudreau and Worm, 2012). Examples of the invasive decapod species include the European green crab (*Carcinus maenas*) (Klassen and Locke, 2007), the Harris mud crab (*Rhithropanopeus harrisii*) (Roche and Torchin, 2007), the Chinese mitten crab (*Eriochier sinensis*) (Schrimpf *et al.*, 2014), the red king crab (*Paralithodes camtschaticus*) (Dvoretsky and Dvoretsky, 2013), the Asian shore crab (*Hemigrapsus sanguineus*) (Jungblut *et al.*, 2017), and the Asian brush-clawed shore crab (*Hemigrapsus takanoi*) (Makino *et al.*, 2018).

Despite extensive shipping in Nordic waters, relatively few anthropogenic oceanic introductions have been reported at high northern latitudes in the Atlantic Ocean. That might be explained by a rapid dispersal following the retreat of glaciers about 10 000 years ago, as has been demonstrated by Ingólfsson (1992) that the faunas of the northernmost Atlantic regions (Canadian Maritimes, Iceland, Norway) are closely related despite long distances between them. As current maritime traffic is most often between low and high latitudes, the risk of invasion might be diminished as temperature may affect the establishment of species from lower latitudes to colder regions (Seebens *et al.*, 2013), although many historical introductions may have been overlooked (Carlton, 2003, 2009).

One of the most recent members of the invasive alien crustaceans in Icelandic coastal waters is the Atlantic rock crab (*Cancer irroratus*), which was first reported in Icelandic coastal waters in 2006 (Gíslason *et al.*, 2014) (Figure 1). Its occurrence in Iceland is the first discovery of the species outside its native range in North America. Its colonization may possibly be aided by the large-scale changes that started in the North Atlantic in 1996 that resulted in warmer waters around Iceland and led to noticeable changes in the Icelandic marine ecosystem (Anonymous, 2004; Astthorsson and Palsson, 2006; Astthorsson *et al.*, 2007, 2012; Stefansdottir *et al.*, 2010; Jochumsen *et al.*, 2016) and also to increased shipping in past decades. The apparent lack of founder effects, high genetic variation (Gíslason *et al.*, 2013), and apparently favourable environmental conditions may have led to the rapid spread of the rock crab since 2006 (Gíslason *et al.*, 2014). The success of the rock crab and its ability to thrive in Iceland is further demonstrated by the fact that it has been found in high abundance, comparable to the highest records in its native range (Gíslason *et al.*, 2017). In its new habitat in Icelandic coastal waters, the rock crab has few competitors for food and shelter, as there are only two native brachyuran decapod crab species commonly found in shallow coastal waters, i.e. the European green crab (*C. maenas*) and the great spider crab (*Hyas araneus*) (Gíslason *et al.*, 2014). All three species are known to display different life history traits (Supplementary Table S1), but very limited information is available for Iceland.

Our aims were to evaluate (i) population changes in the Atlantic rock crab in Southwest Icelandic waters during the latter stages of the colonization and (ii) the interaction of the rock crab and the two native brachyuran crab species, the European green crab and the spider crab. This was done by sampling larvae and adults of all species, comparing changes in abundance, and seeing if sampling areas differed in abundance, species composition, and size distributions of the three crab species.

Material and methods

Sampling

Trap fishing and plankton sampling were carried out in four areas in the inner parts of Faxaflói Bay, Southwest Iceland: Hvalfjörður, Kollafjörður, Skerjafjörður, and Borgarfjörður (Figure 2). Rock crabs and other decapod crabs were captured with commercial crab traps (depth range 7–80 m) at various times during 2007–2019 (Table 1). Twenty to 30 traps were used on each sampling trip (height 30 cm, length 80 cm, width 40 cm, mesh size 4.8 cm, escape opening for juveniles closed). Traps were baited with fish, always containing some gadoids (*Gadus morhua*, *Pollachius virens*, *Melanogrammus aeglefinus*, *Merlangius merlangus*). Mixed bait was placed in mesh bags hanging in the traps, ca. 250 g per trap. Baited traps remained in place for about 48 h before retrieval.

Hvalfjörður was sampled during 42 trips during 2007–2019; 2016 is the only year with no data from that area (Supplementary Table S2). Each year and on each occasion, ten traps were placed out on a transect at a depth gradient (10, 20, 30, 40, and 60 m) for comparison with the former study by Gíslason *et al.* (2014), except in 2012, when traps were only laid out at 10-m depth. Kollafjörður was sampled during 27 trips in 2011–2019 (Table 1) in August and September. Borgarfjörður was sampled during two trips in 2013 and 2017 (Table 1) in September and October, respectively. Skerjafjörður was sampled during five trips in 2013, 2016, and 2017 (Table 1) in June, July, December, and March, respectively.

Most of the crabs were identified to species and gender. Presence or absence of egg remnants on females was determined, and the developmental stages of eggs in berried females were determined by their colour (bright orange = undeveloped; brown = developed). All three species are sexually dimorphic in size, with females considerably smaller than males.

Size and weight of Atlantic rock crabs, green crabs, and spider crabs were measured. Total body weight was measured using an electronic scale, with an accuracy of ± 1 g. The sizes of the rock crab and green crab, measured between the two most distant points on the carapace [maximum carapace width (CW)], and the lengths of the spider crab (maximum carapace length) were measured to the nearest 0.1 cm using a vernier calliper.

Plankton samples were taken in Faxaflói Bay (Figure 2) in 2012–2014 at the same stations as in our previous study (Gíslason *et al.*, 2014), when the peak in larval abundance was expected (July–August), with standard Bongo nets, 60-cm ring diameter, 250-cm net length, and 500-µm mesh size (Hydro-bios Apparatebau GmbH®, Germany). The nets were towed at 10-m depth at 1.3 m s^{-1} for 10 min at each sampling station. Filtered volume was estimated with a flow meter (Hydro-Bios Kiel, Model 438 110) fitted on one of the net's opening. Samples were immediately preserved in 10% formalin in seawater and later washed and preserved in 96% ethanol.

Statistical analysis

Variation in proportions of Atlantic rock crabs in Hvalfjörður and Kollafjörður was analysed with a linear regression of the relative frequencies against time and transformed with the arcsin of their square root (Sokal and Rohlf, 2008). Heterogeneity of the counts of different species within and among the sites were tested with a chi-square test.

Size distributions of the rock crabs were analysed in each sampling area with the Shapiro–Wilk test (Shapiro and Wilk, 1965) to estimate deviation from normality, i.e. skewness (g1) and kurtosis (g2) (Sokal and Rohlf, 2008). One-way analysis of variance was used to test variability in size between years. All calculations and graphical analyses were conducted in R (version 3.6.2; R Development Core Team, 2020).

Results

Distribution

The spread of the Atlantic rock crab in Iceland has been monitored through various indirect and direct sampling methods. After its first discovery in Hvalfjörður in 2006 (Southwest Iceland), it was reported in Breiðafjörður in 2008 (West Iceland), in Eyjafjörður in 2013 (North Iceland) and in Borgarfjörður Eystri in 2017 (East Iceland) (Figure 1), corresponding to >70% of the coastline.

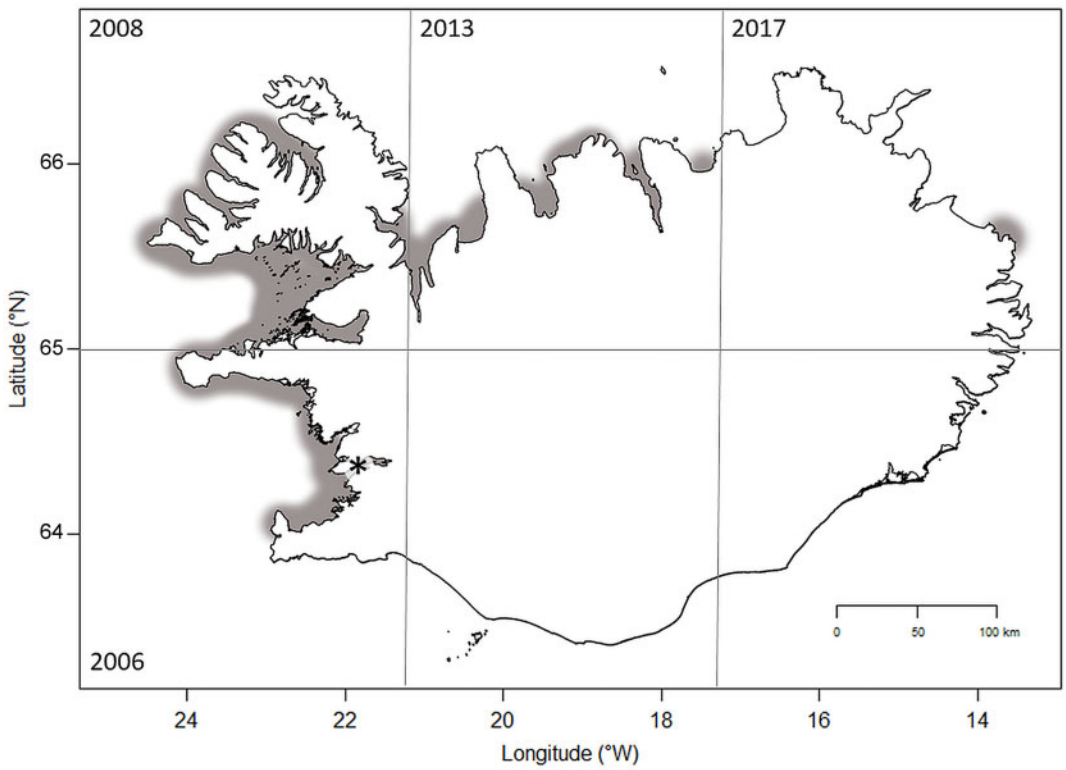

Figure 1. Known distribution of the Atlantic rock crab (*Cancer irroratus*) around Iceland in 2019 (grey shaded area). The map divides Iceland into six areas showing the year when specimens where first found. Asterisk shows the location where rock crab was first found in Hvalfjörður Southwest Iceland.

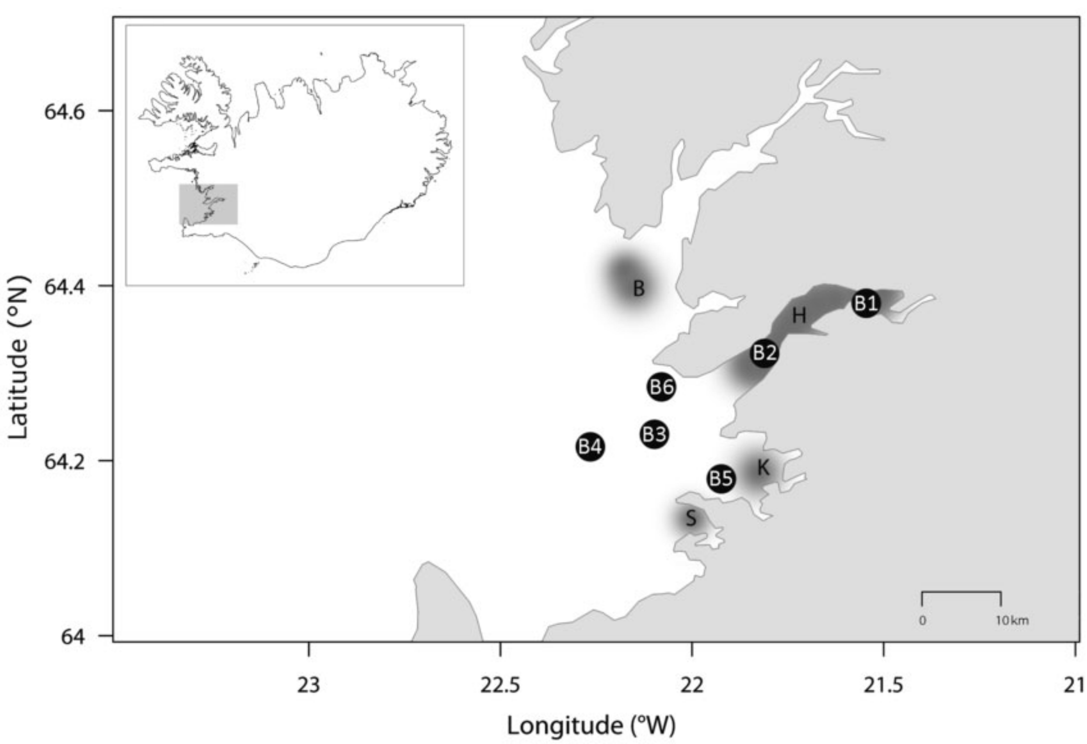

Figure 2. The sampling areas in Faxaflói Bay, Southwest Iceland: Skerjafjörður (S), Kollafjörður (K), Hvalfjörður (H), and Borgarfjörður (B). Trap fisheries were carried out in areas shaded with grey. Plankton sampling was carried out at six stations marked with black dots (B1–B6).

Table 1. Length and weight characteristics (mean, range, and standard error) for the Atlantic rock crab (*Cancer irroratus*), European green crab (*Carcinus maenas*), and spider crab (*Hyas araneus*) in four areas in Faxaflói Bay, Southwest Iceland.

					Carapace (cm)			Wet weight (g)		
Species	**Area**	**Sampling years**	**No. trips**	***N***	**Mean**	**Range**	**s.e.**	**Mean**	**Range**	**s.e.**
C. irroratus	Hvalfjörður									
	Males	2007–2019	42	9 361	11.7	6.5–15.1	0.012	256.2	60–487	1.235
	Females			1 347	8.8	5.8–11.7	0.020	116.2	59–254	1.574
	All			10 708	11.3	5.8–15.1	0.014	240.4	59–487	1.356
	Kollafjörður									
	Males	2011–2019	27	8 140	10.4	5.3–13.8	0.014	185.0	40–452	1.015
	Females			1 491	8.3	5.6–11.8	0.017	92.0	46–220	0.947
	All			9 631	10.1	5.3–13.8	0.015	174.1	40–452	0.997
	Skerjafjörður									
	Males	2013, 2016–2017	5	1 810	11.3	7.0–14.2	0.032	–	–	–
	Females			66	8.9	7.5-10.2	0.079	–	–	–
	All			1 876	11.2	7.0–14.2	0.031	–	–	–
	Borgarfjörður									
	Males	2013, 2017	2	994	12.8	8.2–15.3	0.033	–	–	–
	Females			968	8.9	7.0–11.1	0.019	–	–	–
	All			1 962	10,9	7.0–15.3	0.048	–	–	–
C. maenas	Hvalfjörður									
	Males	2007–2019	42	730	7.3	5.0–10.2	0.027	99.1	35–161	4.559
	Females			139	6.3	4.7–8.5	0.056	54.9	29–96	3.832
	All			869	7.1	4.7–10.2	0.027	86.4	29–161	4.221
	Kollafjörður									
	Males	2011–2019	27	4 741	7.1	5.1–9.9	0.008	100.1	40–196	1.055
	Females			306	6.5	4.5–7.9	0.030	63.5	20–120	1.331
	All			5 047	7.1	4.5–9.9	0.008	93.3	20–196	1.024
	Skerjafjörður									
	Males	2013, 2016–2017	5	467	7.9	6.2–9.6	0.030	–-	–	–
	Females			32	6.8	5.4–8.2	0.113	–	–	–
	All			499	7.8	5.4–9.6	0.033	–	–	–
	Borgarfjörður									
	Males	2013, 2017	2	4	6.8	5.8–7.5	0.382	–	–	–
	Females			5	6.3	5.9–7.2	0.231	–	–	–
	All			9	6.5	5.8–7.5	0.231	–	–	–
H. araneus	Hvalfjörður									
	Males	2007–2019	42	1 657	8.8	4.7–12.2	0.028	174.6	42–403	3.338
	Females			501	7.7	4.5–10.2	0.031	100.2	30–234	2.519
	All			2 158	8.6	4.5–12.2	0.025	156.6	30–403	2.917
	Kollafjörður									
	Males	2011–2019	27	597	8.8	4.5–11.5	0.050	177.3	36–310	5.389
	Females			78	6.8	5.4–9.9	0.094	61.0	30–136	3.446
	All			675	8.6	4.5–11.5	0.052	148.9	30–310	5.431
	Skerjafjörður									
	Males	2013, 2016–2017	5	189	8.1	5.5–10.9	0.082	–	–	–
	Females			29	7.2	5.7–8.3	0.134	–	–	–
	All			218	7.9	5.5–10.9	0.075	–	–	–
	Borgarfjörður									
	Males	2013, 2017	2	6	9.3	8.2–10.1	0.251	–	–	–
	Females			2	6.3	5.4–7.1	0.850	–	–	–
	All			8	8.5	5.4–10.1	0.548	–	–	–

Minimum catch size of crabs was 4.5 cm (carapace width/length). Trap catches were carried out in 2013 and 2017 in Borgarfjörður (September, October), in 2007–2019 in Hvalfjörður (April–December), in 2011–2019 in Kollafjörður (August and September), and in 2013, 2016, and 2017 in Skerjafjörður (March, June, July, December). Number of traps varied from 20 to 30 per sampling trip.

Trap fishing

In total, 24 245 specimens of the Atlantic rock crab were caught in the four areas (Hvalfjörður, Kollafjörður, Skerjafjörður, and Borgarfjörður) during 2007–2019. A total of 10 708 were size measured (Table 1) and 24 172 identified to gender (Supplementary Table S2). In addition, 6451 specimens of the European green crab (6424 measured and 6383 to gender) and 3797 specimens of the spider crab were collected (3059 measured and 3494 to gender).

Rock crab was the most abundant species in the trap catches in all four sampling areas (Figure 3a). The proportion of rock crabs was significantly different between sampling areas in 2013 ($p < 0.001$) and ranged from 64% in Kollafjörður to 99% in Borgarfjörður.

The average number of rock crabs per trap on the transect (10–60 m depth) in the inner part of Hvalfjörður in 2007–2015 (June–October) averaged 7.7 crabs/trap (±1.2 *SD*), showing no clear trend in the catch between years. The average catch has since increased significantly from an average catch of 13.8 crabs/trap in 2017 to 24 crabs/trap in 2019 ($p < 0.001$). However, the proportion of rock crabs in the total catch in Hvalfjörður increased significantly ($p < 0.001$) over the entire study period from 55% in 2007 to >95% in 2018 and 2019 (Figure 3b). In contrast, the proportional abundance of rock crab in Kollafjörður (sampling in 2011–2019) dropped significantly ($p < 0.01$) from 71% in 2011 to 52% in 2013 but increased steadily after that up to 87% in 2019 (Figure 3c).

Size frequency distribution and average sizes

The overall size frequency distribution and average size of the rock crab differed considerably among study areas (Table 1, Supplementary Figure S1). Significant size difference was observed among years for both males ($p < 0.001$) and females ($p < 0.05$), where the average CW fluctuated around the mean without clear trends over time (Figure 4). The variance in size was greatest in 2011 for both genders (males: 2.2 cm; females: 1 cm) but was ca. 1 and 0.5 cm for the males and females, respectively, in all other years (Figure 4). Significant size difference was observed for both males and females among sampling areas ($p < 0.001$, Figure 5). The average size of the males was lowest in Kollafjörður (10.4 cm CW), but highest in Borgarfjörður (12.8 cm CW). Exceptionally large rock crab males were caught in Borgarfjörður in 2013, the largest measuring 15.3 CW and 577 g in wet weight (Table 1). The male rock crab size frequency distribution in Skerjafjörður was similar to that in Hvalfjörður (Table 1).

The size frequency distribution of rock crabs in Hvalfjörður from 2007 to 2019 fluctuated over years ($p < 0.05$) with no temporal trend. It showed differences among years, with a slight increase in average size from 2007 to 2009, a decline until 2012, and an increase again in 2013 and since then has been relatively stable (Figure 4, Supplementary Figure S2). The multimodality indicates the occurrence of several cohorts of different ages among the adult crabs. The average male size may be influenced by an apparently strong cohort entering the fisheries in 2011 (Supplementary Figure S2).

The shape of the size frequency data of the rock crab also varied among regions. In all four sampling areas, samples deviated from a normal distribution for males ($p < 0.001$), being skewed to the left (Supplementary Table S3). When samples from each year were analysed separately, they were all skewed to the left for males, but differed from a normal distribution to skewness to either sides for females (Supplementary Table S3). Males in Hvalfjörður and Borgarfjörður also showed an overall significant leptokurtic distribution ($p < 0.001$), whereas males in Kollafjörður showed a platykurtic distribution ($p < 0.001$). Females in Hvalfjörður and Kollafjörður exhibited a significant leptokurtic distribution ($p < 0.001$) (Supplementary Table S3).

The average male and female CW of green crabs fluctuated over years ($p < 0.05$), with no temporal trend (Figure 4). A strong cohort of green crabs was observed entering the fishery in 2011 (Supplementary Figure S2). However, a significant reduction in size with time was observed for male spider crabs ($b = -0.03$, $p < 0.05$), female spider crabs ($b = -0.06$, $p < 0.05$), and female rock crabs ($b = -0.08$, $p < 0.001$).

Sex ratio

Overall, males outnumbered females in trap catches for all three species except for the spider crab in 2007 (Table 1; Supplementary Table S2). The proportion of males per year

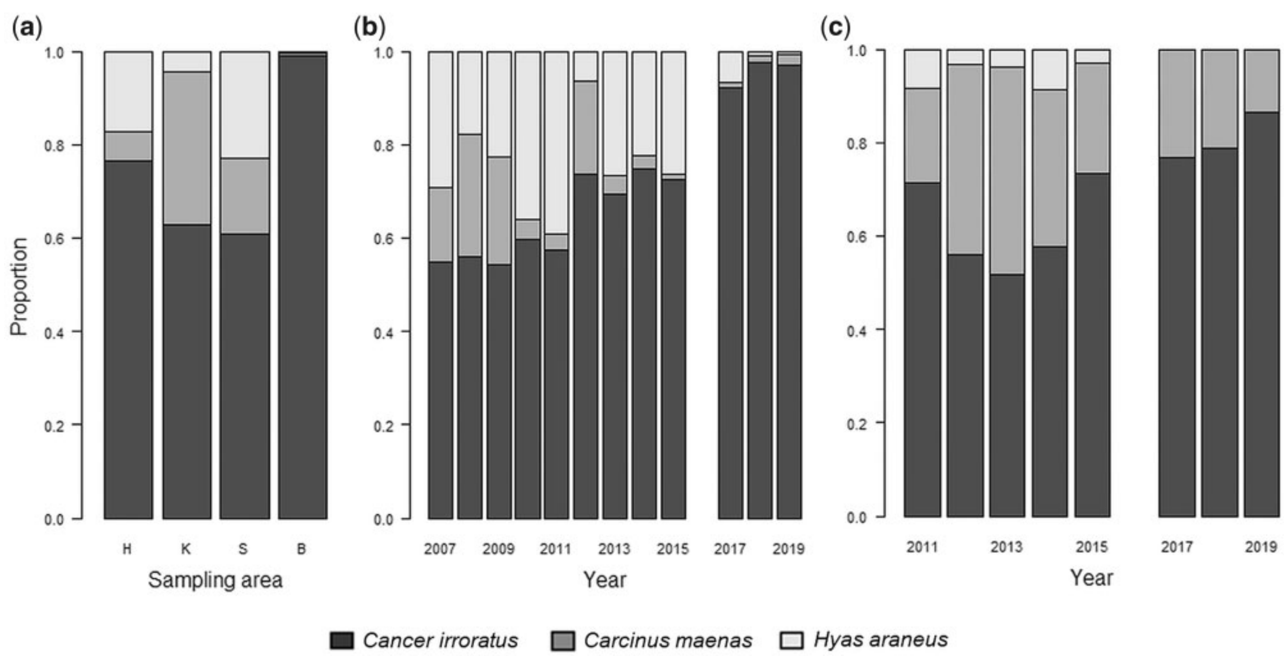

Figure 3. Proportion of the Atlantic rock crab (*Cancer irroratus*), European green crab (*Carcinus maenas*), and spider crab (*Hyas araneus*) in trap catches in (a) the four sampling areas: Hvalfjörður (H), Kollafjörður (K), Skerjafjörður (S), and Borgarfjörður (B), with total catch in each area; (b) Hvalfjörður in 2007–2019; and (c) Kollafjörður in 2011–2019. No sampling was carried out in Hvalfjörður and Kollafjörður in 2016.

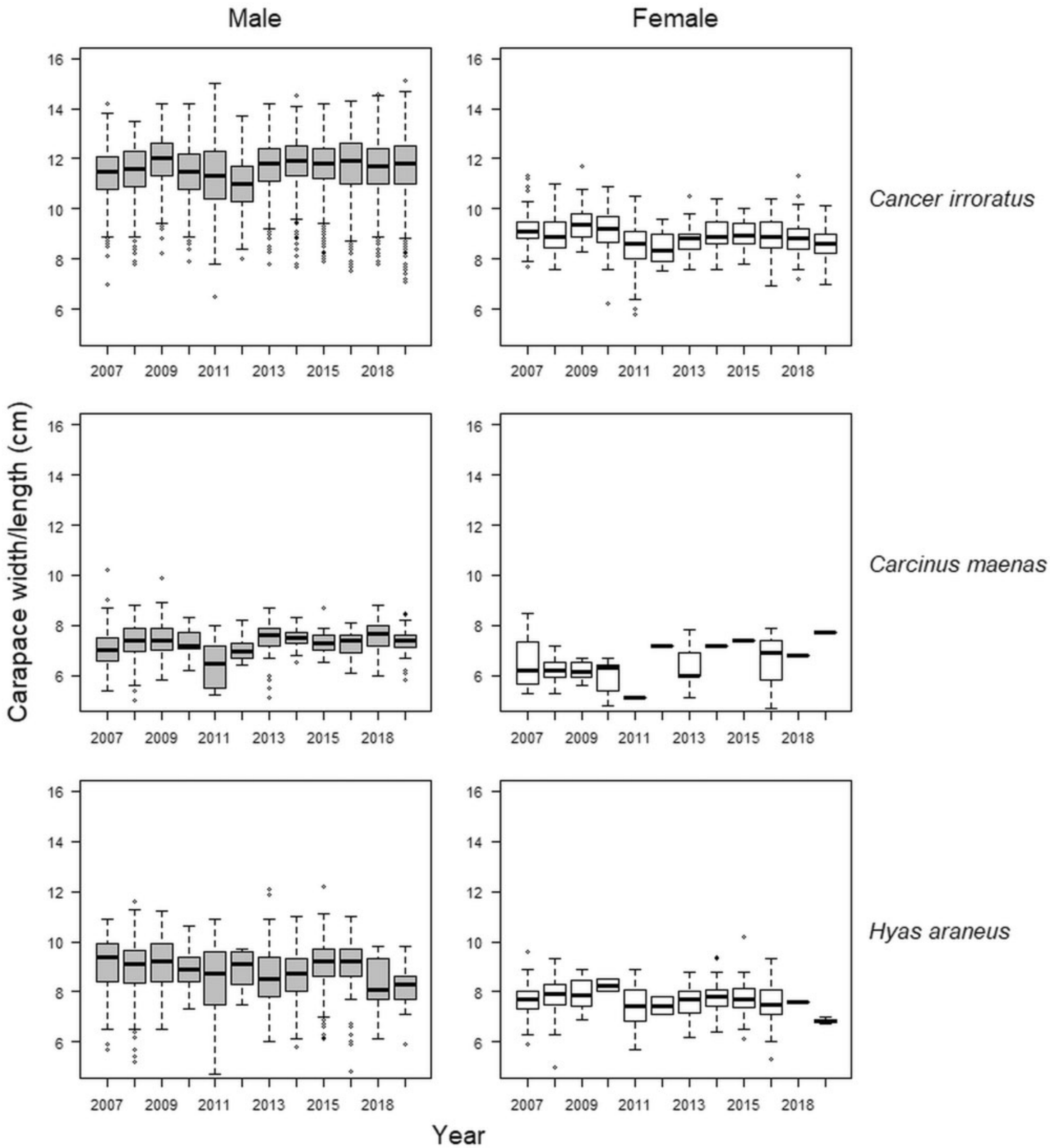

Figure 4. Difference in CW (with the median size ± standard deviation) with years in Hvalfjörður, Southwest Iceland, for both genders of the Atlantic rock crab (*Cancer irroratus*), European green crab (*Carcinus maenas*), and CL of the spider crab (*Hyas araneus*). No sampling was carried out in 2016. CL, carapace length.

ranged from 71 to 95% for the rock crab, 63–97% for the green crab, and 44–91% for the spider crab. Significant difference was observed in sex ratio of rock crab between both years and months ($p < 0.001$) (Figure 6). No significant difference in sex ratio was observed over months for the green crab, but they varied for the spider crab ($p < 0.001$), where females were most common in May (Supplementary Table S2).

Berried females

Of the 3870 rock crab females caught in 2007–2019, only 86 (2.2%) carried eggs. Berried females were caught from May to October (Supplementary Table S2). Fourteen of the berried females (16%) had undeveloped eggs, 26 had well-developed eggs (30%), but about half (41 individuals, 47%) had recently lost/hatched their eggs, only carrying egg remnants. Only 14 (3%)

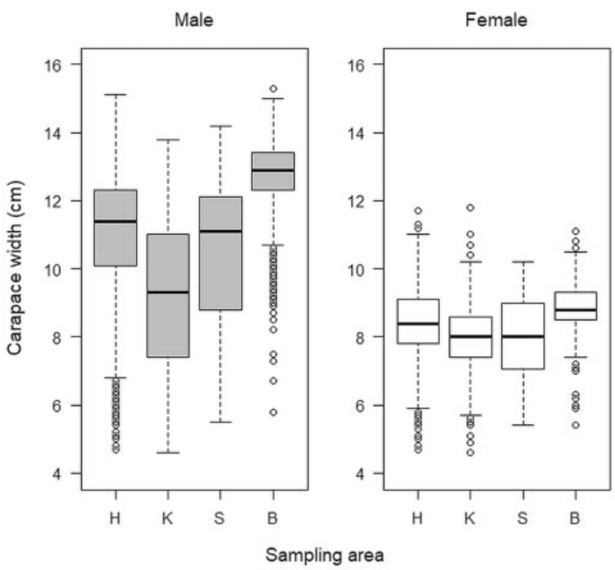

Figure 5. Difference in CW (with the median size ± standard deviation) for both genders of the Atlantic rock crab (*Cancer irroratus*) at the four sampling areas: Borgarfjörður (B), Kollafjörður (K), Hvalfjörður (H), and Skerjafjörður (S).

berried green crabs were caught, carrying either orange or brown eggs. More than half of all 641 captured female spider crabs caught from May to December were carrying eggs (71%) (Supplementary Table S2). Half of the berried spider crab females were carrying orange eggs (50%), 19% were carrying brown eggs, and 2% had egg remnants.

Larval abundance

Larvae of two of the three species, rock crab and green crab were present in plankton samples during the summer months (June–August). The mean abundance of rock crab larvae in July ranged from 0.5 to 2.3 larvae m^{-3} in 2007–2008 and from 7.6 to 10.7 larvae m^{-3} in 2012–2014, with the highest abundance in 2012 and 2014 (Figure 7). Proportion of Atlantic rock crab larvae was significantly higher ($p < 0.05$) at the sampling sites in Faxaflói Bay (B3–B6) than within Hvalfjörður (B1 and B2); however, abundance varied extensively (Table 2, Figure 8) and no significant differences in proportions of larval species were detected among years within sampling sites.

Discussion

The Atlantic rock crab is now well established in Icelandic waters. Since first recorded in 2006 (Gíslason *et al.*, 2014), the rock crab has spread rapidly and is now found along >70% of the coastline, i.e. clockwise from Faxaflói in Southwest Iceland to East Iceland. The population is still in a growth phase, as seen in a rapid increase in distributional range, and is now found in densities that are among the highest reported for the species in its native range (Gíslason *et al.*, 2017). According to the present study, the rock crab is the most abundant brachyuran crab species on soft-bottom habitats in Southwest Iceland. The proportion of rock crab in trap catches increased from 55% in Hvalfjörður in 2007 to >95% in 2018 and 2019, and the abundance of rock crab larvae in July, when the annual peak was seen in larval abundance (Gíslason *et al.* 2014), was sevenfold higher in 2014 than in 2007.

Size distribution

The mean size of rock crabs in Hvalfjörður fluctuated between years, with no clear trend over time, showing a pattern in fluctuations similar to that seen for green crab. This indicates that the same environmental factors are affecting both species. The size distribution of the rock crab was left-skewed and leptokurtic. Right skewness, however, applies in general for most species on a large geographical scale (Kozlowski and Gawelczyk, 2002). This might be due either to the crab still colonizing the local area or simply that the trap catches are not representing the smaller individuals in the population. It is known that crab traps are both size and sex selective (Workman *et al.*, 2002; Smith *et al.*, 2004; Hernaez *et al.*, 2012), and trap fishing may also be affected by moulting period, reproductive status (berried females), and health condition of the animals. The much higher catchability of male rock crabs compared to females in trap fishing in Iceland, as for many decapods elsewhere, is presumably because the commercial traps used are more efficient at retaining larger crabs, which are predominantly males (Smith and Jamieson, 1991; Workman *et al.*, 2002). Presence of large aggressive individuals in the traps has also been considered to affect the catchability of smaller animals such as juveniles and females by restricting their entrance into the traps (Fischer and Wolff, 2006).

The different size frequency distributions of the rock crab, seen here partly in very large crabs in Borgarfjörður, may indicate that favourable local conditions in the absence of other crabs may lead either to larger sizes or that an additional moult would occur. The former explanation is probably more likely, as a small increase in size increments between moults under favourable conditions could easily lead to the ca. 1 cm increase in the size of males in Borgarfjörður compared to other areas. Furthermore, to our best knowledge, the maximum size of rock crab males and females in Iceland is substantially larger than documented in its native range (Bigford, 1979; Robichaud *et al.*, 2000; Robichaud and Frail, 2006). Little information is available on the number of moults undertaken by the Atlantic rock crab, except for Reilly's (1975) estimator on age and number of moults of the rock crab. Gíslason *et al.* (2017) found size increments between moults of adult rock crabs in Kollafjörður to be ca. 2 cm.

Berried females

Proportion of berried females varied among the three species. Berried rock crabs were caught from May to October, which is similar to what is seen in the native habitat of the crab in North America. In Canada and Maine, females with well-developed eggs or egg remnants are mainly seen from June to August (Krouse, 1972; DFO, 2008), but from March to June for more southern rock crab populations (Reilly, 1975; Reilly and Saila, 1978). The proportion of berried green crabs was low compared to rock crabs and was caught from June to October. Proportion of berried green crabs varies greatly between regions, where berried green crabs have been caught from April to August in Maine, United States (Berrill, 1982), from February to June in Swansea, United Kingdom (Naylor, 1962), and year-round in Portugal (Baeta *et al.*, 2005). The proportion of berried spider crabs was much higher than for the other two species, or >60% in total, and they were captured from May to December, which is consistent with Einarsson (1988), where spider crab females were reported to carry undeveloped (orange) and developed (brown) eggs year-round in Iceland.

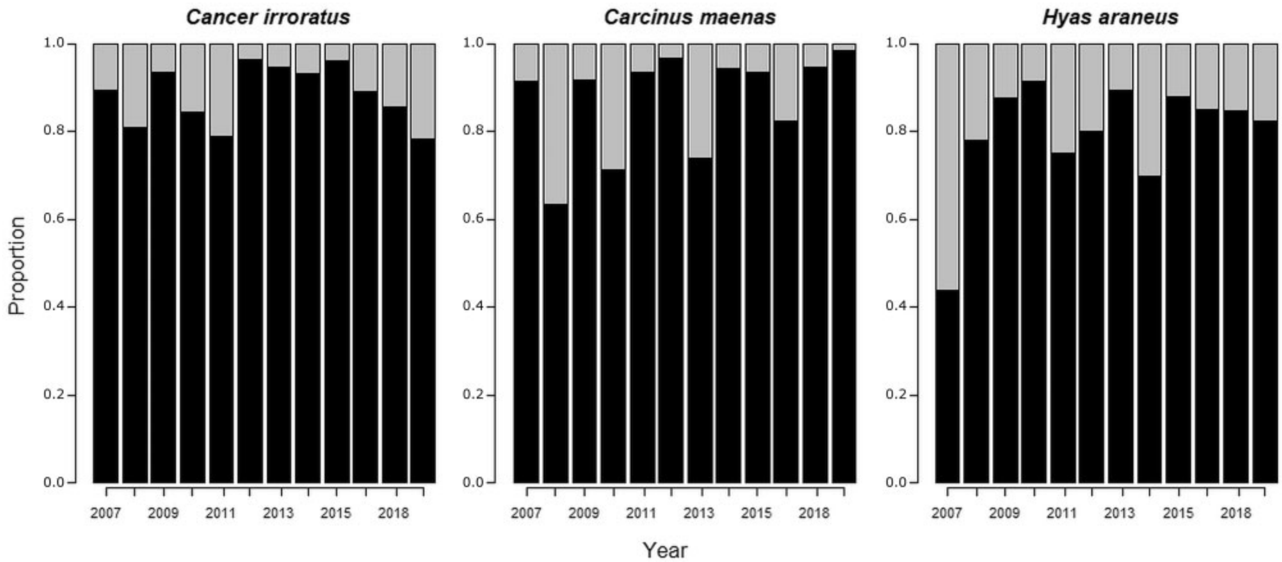

Figure 6. Proportion of male (black bars) and females (grey bars) for the Atlantic rock crab (*Cancer irroratus*), European green crab (*Carcinus maenas*), and spider crab (*Hyas araneus*) per year in Hvalfjörður during 2007–2019. No sampling was carried out in 2016.

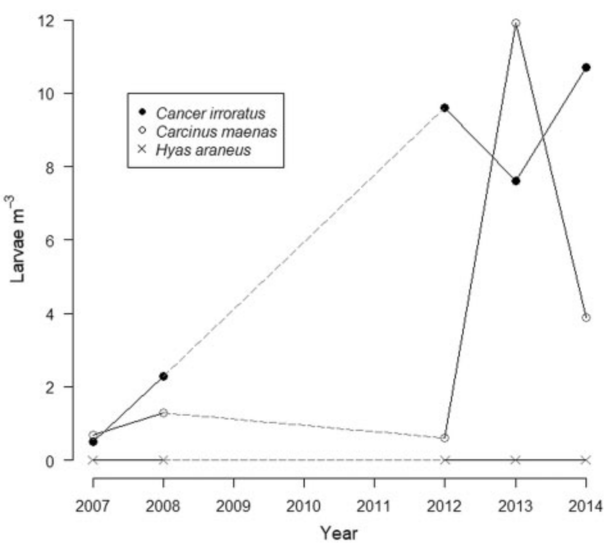

Figure 7. Mean density (larvae m − 3) of three brachyuran crab species: the Atlantic rock crab (*Cancer irroratus*), green crab (*Carcinus maenas*), and spider crab (*Hyas araneus*) in July in Faxaflói Bay, Southwest Iceland, in 2007–2008 and 2012–2014.

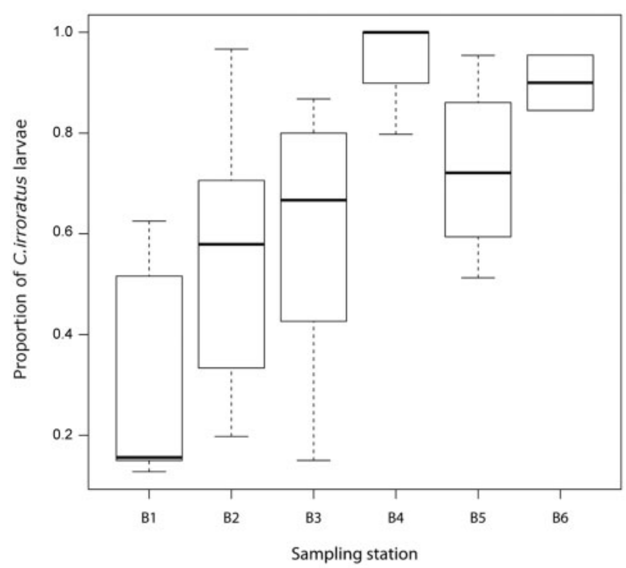

Figure 8. Proportion of Atlantic rock crab (*Cancer irroratus*) larvae in relation to other brachyuran decapod larvae per sampling station in July in 2007–2008 and 2012–2014 in Faxaflói Bay, Southwest Iceland.

Environmental conditions and larval abundance

Environmental conditions in Southwest Iceland seem to be favourable for larval development of the rock crab. Gíslason *et al.* (2014) showed that rock crab larvae are present in surface waters from May to November, with a peak period in July when temperature is near maximum in Icelandic waters. Since 2007 and 2008, larval abundance has increased significantly up to sevenfold in 2014, as shown in the present study. Similar results were observed for larval density of the green crab, with significant increase in 2013 and 2014 from previous years (Gíslason *et al.*, 2014). This may reflect the expansion phase of the colonization process, but as for the green crab, environmental conditions have been improving, which are likely linked to the large-scale changes occurring in the North Atlantic in recent years (Anonymous, 2004), which has led to noticeable changes in Icelandic marine ecosystems (Astthorsson and Palsson, 2006; Astthorsson *et al.*, 2007, 2012; Jochumsen *et al.*, 2016). Spider crab larvae were absent in plankton samples in July. This is in good agreement with what is known about spider crabs in the North Sea where hatching occurs mainly in late winter to early spring (Anger, 1983a; Kunisch and Anger, 1984) and to results previously reported by Gíslason *et al.* (2014) in Iceland.

Table 2. Abundance of the Atlantic rock crab (*Cancer irroratus*) and the European green crab (*Carcinus maenas*) larvae in Faxaflói Bay, Southwest Iceland, in July 2007–2008 and 2012–2014.

Year	N	Station	Abundance (larvae m^{-3}) C. irroratus	C. maenas	Proportion of C. irroratus (%)
2007	2	B1	0.3	1.7	16
		B2	1.1	0.8	58
		B3	0.3	1.7	14
		B4	0.4	0.0	100
		B5	–	–	–
		B6	–	–	–
2008	3	B1	0.6	4.1	12
		B2	1.2	0.5	71
		B3	5.9	0.9	87
		B4	0.04	0.01	74
		B5	2.7	1.3	67
		B6	1.8	0.5	85
2012	1	B1	0.5	0.3	58
		B2	2.9	0.1	98
		B3	0.8	0.2	77
		B4	–	–	–
		B5	39.5	1.9	95
		B6	4.2	0.3	96
2013	1	B1	6.1	33.0	16
		B2	1.8	7.3	20
		B3	5.8	7.8	43
		B4	14.2	3.6	80
		B5	10.1	9.6	51
		B6	–	–	–
2014	1	B1	1.6	1.5	52
		B2	2.0	4.0	33
		B3	2.8	1.4	67
		B4	2.9	0.0	100
		B5	41.6	12.6	77
		B6	–	–	–

N is the number of samples taken yearly in July at each station (see Figure 1).

Impact and competition

The rock crab expansion phase, which is marked by an increasing spread rate, fits well with the second classification of the invasion process by Arim *et al.* (2006), indicating that the rock crab has enough resources in its new habitat in Iceland and that both competition and predation are weak or lacking. In its native range, the rock crab has been shown to be a major player in structuring benthic communities by influencing species composition and abundance. In an experiment where the crab was excluded from a region where it was the most abundant and frequently encountered predator, the polychaete *Pholoe tecta* and the clam *Macoma calcarea* became the dominant benthic infauna and the overall species richness increased (Quijon and Snelgrove, 2005a, b). The effects of the rock crab colonization in the Icelandic ecosystem are still unforeseen, though it is highly likely that a large species, like the rock crab, found in such high densities has a significant impact on coastal biota. By outnumbering its rival native species, the spider crab (*H. araneus*) and the European green crab (*C. maenas*), on soft-bottom substrates, the rock crab shows its fitness. Comparative density studies on the rock crab and green crab in North America on various substrates have shown that both species are found in highest densities on sandy bottom substrates (Fogarty, 1976). Belair and Miron (2009) showed that predation rates and stomach contents of the rock crab and the green crab remained unaffected by the presence of each other and that the two species avoided each other passively and actively, which could enable them to coexist and reduce competition. The rock crab is both bigger and bulkier than both the spider crab and the green crab, which makes it a harder competitor for food and shelter. The size advantage is also likely to make the rock crab less vulnerable to predation. However, despite the smaller size of the green crab and that it is not as well adapted to low water temperatures (<10°C) as the other two species (Anger, 1983b; Belair and Miron, 2009), which may inhibit feeding (Berrill, 1982) and moulting (Audet *et al.*, 2003), the green crab is considered to be the most aggressive and generally the fittest of the three species being listed among the most successful alien species in the world (Klassen and Locke, 2007). It has, for example, invaded North America (Cohen *et al.*, 1995; Audet *et al.*, 2003, 2008), where it is regarded as a potential threat to native species. Abiotic factors in Iceland, whether temperature or others, constrain the green crab distribution to the southwest and west coasts of Iceland (Ingólfsson, 1996). The rock crab, on the other hand, new in the ecosystem, has spread fast along the Icelandic coastline and has now established itself in the Westfjords and North Iceland, where the green crab is absent. Of the three species, coexistence has only been studied to some degree between the rock crab and the green crab. Matheson and Gagnon (2012) observed that medium-sized rock crabs (which were as big as large green crabs) won <20% of their contests with large green crabs, whereas large rock crabs won as many contests, demonstrating that large green crabs can outcompete rock crabs even if the latter is larger.

Conclusion

Whether it is fitness, size advantage over the native species, or preference for the soft-bottom substrates that make the rock crab more abundant in such habitats in Iceland, it is clear that the rock crab is thriving well. The successful establishment of the rock crab in Icelandic waters is of concern as the magnitude of environmental and ecological effects is not fully known at this stage. The recent record of a single specimen of rock crab in southern Kattegat, Sweden (Berggren, 2019), raises wariness of further spread and establishment of the species, and the possible role of Iceland as a stepping stone for the rock crab to mainland Europe.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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