Research Article

Range extension of invasive *Cancer irroratus* and native *Carcinus maenas* polewards in the *Ascophyllum*-dominated intertidal zone in north-west Iceland

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Abstract

The rocky intertidal zone of sheltered shores in Breiðafjörður, north-west Iceland is dominated by monospecific stands of canopy-forming brown algae *Ascophyllum nodosum*, which provide habitat for mobile organisms and has been subjected to long-standing rotational harvesting. We investigated the assemblage composition of little-studied mobile brachyuran crabs in this area, to track distributional shifts in a native species responding to climate change and extent of occupancy of the intertidal by a primarily subtidal invasive non-native species. Potential interactive effects of seaweed harvesting were explored. Breiðafjörður was compared with two reference sites in Faxaflói, south-west Iceland. The study revealed clear poleward expansion of the native European green crab *Carcinus maenas* in the region, displacing the native spider crab *Hyas araneus* particularly at mid-shore levels. The invasive non-native Atlantic rock crab *Cancer irroratus* had negligible occupancy in the intertidal zone, indicating limited effects on the intertidal crab assemblage, composition, and abundance. The current harvesting regime of *A. nodosum* in Breiðafjörður did not affect the composition and abundance of the brachyuran crab assemblage in the rocky intertidal zone. *H. araneus* is likely being squeezed by displacement subtidally by *C. irroratus*, and intertidally by *C. maenas*. Overall, we provide insights into the potential interactions between climate change, invasive species, and human activities in the rocky intertidal zone.

Introduction

Species distributions are changing in response to global warming (Parmesan and Yohe, 2003; Chen *et al.*, 2011; Bellard *et al.*, 2012) and the introduction of non-native species (Parker *et al.*, 1999; Ricciardi *et al.*, 2013; Guo *et al.*, 2021), often acting in combination (Bellard *et al.*, 2013). Ranges are expected to move polewards as temperatures rise, with effects likely to be greater in low diversity systems in higher latitude areas (Bellard *et al.*, 2013). Such spread can potentially have consequences for resident species (Bellard *et al.*, 2012), especially in disturbed systems (Hobbs and Huenneke, 1992).

One recent case of invasion by a non-native species in Iceland is that of the Atlantic rock crab *Cancer irroratus* Say, 1817 from the east coast of North America (Galan and Eiríksson, 2009; Gíslason *et al.*, 2014; Gunnarsson *et al.*, 2015). First sightings date back to 2006 in Hvalfjörður, south-west Iceland (Gíslason *et al.*, 2014); since then *C. irroratus* has spread to north and east Iceland (Gíslason *et al.*, 2021), primarily in the subtidal zone but also occurring intertidally. Until at least 1973, the only brachyuran crabs inhabiting the rocky seashores of northwestern Iceland were the spider crabs *Hyas araneus* (Linnaeus, 1758) and *Hyas coarctatus* Leach, 1815 (Sæmundsson, 1936; Hauksson, 1977). The European green crab *Carcinus maenas* (Linnaeus, 1758), native to south-west Iceland, was later also found further north, in the Breiðafjörður area as its range extended polewards (Ingólfsson, 1996, 2004, 2006), probably in response to warming waters as a result of climate change (Kelley *et al.*, 2013; Goldsmit *et al.*, 2020). The spread of the invasive *C. irroratus* into Breiðafjörður after 2006 further increased the number of brachyurans in the area to four species (Gíslason *et al.*, 2017, 2021).

Invasive marine species can lead to negative ecological impacts (Hänfling *et al.*, 2011) such as displacement of native species by competition (MacDonald *et al.*, 2007; Byers, 2009) or predation (Rilov, 2009), leading to changes in community structure (Molnar *et al.*, 2008). Despite numerous studies on *C. irroratus* in the subtidal zone in Iceland, where it has been shown to outcompete its native counterparts (Gíslason *et al.*, 2021), the prevalence of this invasive species in the intertidal zone is yet unknown. Furthermore, in the context of marine ecosystem dynamics, there is a significant knowledge gap concerning the effects of *Ascophyllum nodosum* (L.) Le Jolis harvesting on associated mobile predators, and specifically crabs (Seeley and

Schlesinger, 2012; Borges *et al.*, 2020). This is particularly note-worthy when we take into account that *Ascophyllum* beds are nurseries for the vulnerable early life stages of many invertebrates (Schmidt *et al.*, 2011). Having a holistic understanding of the ecological consequences of seaweed harvesting, such as influences on the survival and distribution of associated fauna, can contribute to sustainable resource use and management. Global change often interacts with local or regional scale impacts (Firth and Hawkins, 2011; Hawkins *et al.*, 2017; Johnston *et al.*, 2017). *A. nodosum* has been harvested in Breiðafjörður for half a century, which may have had impacts on mobile predator populations. Here, we describe distribution, relative abundance, and population structure of crab species occupying the intertidal zone at eight sites within *Ascophyllum*-dominated sheltered shores of Breiðafjörður, where industrial-scale harvesting (∼15,000 tonnes of algae year^{-1}) occurs. We compare them to two sites further south in Faxaflói, south-west Iceland, with long-established populations of *C. maenas* and large adjacent subtidal populations of *C. irroratus*. Based on previous observations of population changes in the subtidal zone, we tested the hypothesis that *H. araneus* would diminish in abundance and show changed population structure in the face of spread by the other two species. We also examined the relationship between *Ascophyllum* harvesting, intertidal crab abundance, and assemblage composition in Breiðafjörður as a preliminary test of whether such disturbance affected the spread of *C. maenas* and *C. irroratus*.

Materials and methods

Surveys were made during the summer of 2020 at eight sites in Breiðafjörður, a large semi-enclosed bay (Figure 1A), north-west Iceland and at two reference sites in Faxaflói (Figure 1B), south-west Iceland in July 2022. The mean tidal amplitude at spring tide in Breiðafjörður is 4.3 and in Faxaflói 4.0 m. Both bays are characterized by extensive sheltered rocky shores (Ingólfsson, 2006; Georgsdóttir *et al.*, 2016), mostly dominated by the fucoid *A. nodosum* (Gunnarsson *et al.*, 2019). Eight sampling sites were chosen in Breiðafjörður based on ease of access and known history of harvesting, including some unharvested sites (see Supplementary Table S1). Sites dominated by *A. nodosum* (>95% cover; visually estimated) were targeted, with some having *Fucus vesiculosus* Linnaeus, 1753 in small amounts (<5%; visually estimated). The reference sites in Faxaflói additionally had *Fucus serratus* Linnaeus, 1753 present on the lower-most part of the shore, which is absent in Breiðafjörður. The survey sites had different histories of commercial harvesting of *A. nodosum*, with one site in Breiðafjörður (site 3, Maðkavík) and the two reference sites in Faxaflói (site 1, Sæbraut and site 2, Bolaklettar) never having been mechanically harvested. At the two reference sites in Faxaflói, the crabs *H. araneus*, *C. maenas*, and *C. irroratus* have coexisted since at least 2006 (Ingólfsson, 2006; Gíslason *et al.*, 2021).

Sites were surveyed during low water at spring tides either in the beginning of the afternoon or just after midnight, taking advantage of high latitude continuous daylight during summer. Site 10 (Fjörður) was the only site visited both at noon and midnight tides. At each of the ten sites, 6–15 replicated 5 min timed searches were made along a transect parallel to the shore (1–5 m wide depending on slope and 5–20 m long depending on abundance) to estimate relative abundance as catch per unit effort (CPUE) (except at site 2, Hnúksnes, when time was limited and reduced to 3 min). The searches were equally split between mid-shore and low-shore. During these 5 min searches, stones were lifted, the algal canopy and holdfast complexes were thoroughly searched to find as many crabs as possible. After each search, all crabs found were measured (maximum carapace length of

H. araneus and maximum carapace width of *C. irroratus* and *C. maenas*) to the nearest millimetre with a caliper, sex was determined, and the condition of the carapace and presence of eggs were noted. Crabs were released to from where they had been sampled. To maintain statistical independence, searches were always made at least one sampling unit away from each other (the shore length covered during the previous search).

Differences in abundance (CPUE as mean individuals found per min) with survey timing (noon *vs* non-dark midnight) were tested with a Wilcoxon rank sum test. Differences in CPUE among sites and shore levels were tested using a two-way non-parametric Kruskal–Wallis test, with subsequent pairwise comparisons using Wilcoxon rank sum test whenever significant differences were found. To overcome the considerable among-site variation a paired sample Wilcoxon test for mean CPUE between mid- and low-shore level was also performed.

To assess effects of *Ascophyllum* harvesting in Breiðafjörður, the total crab population was correlated with time since last harvest using Spearman's rank test. Planned comparisons using a Kruskal–Wallis were also made. This was done across the whole fjord between sites having 10+ years since last harvest (sites 3, 5, and 9) and those with less than 2 years since last harvest (sites 7 and 10). On the south side of the fjord, interspersed sites that had not been harvested for 15 years or more (sites 3 and 5) were compared with sites 4 and 6, that had had 4 years to recover from harvesting. On the north side of the fjord, it was possible to compare a site not harvested for 12 years (site 9) situated between two adjacent sites (7 and 10) that were last harvested respectively 1 and 2 years previously. When comparing years since last harvest and crab abundances in Breiðafjörður, Maðkavík [3] which has never been mechanically harvested was analysed as not having been harvested for 50 years. Certain limitations to the analysis in this study must be acknowledged. Firstly, statistical power of the analyses has been constrained by relatively small sample sizes due to a limited number of shores with accurate harvesting records. Secondly, the spread of *C. maenas* from the south-west has been into an area where shores that have not been harvested, confounding the two factors.

All tests were performed by using R and RStudio 'Ghost Orchid' (version 2021.9.2.382) (R Core Team, 2022; RStudio Team, 2022).

Results

A total of 914 crabs were captured across all eight study sites in Breiðafjörður bay and the two reference sites further south in Faxaflói bay from nearly 900 min of searching (∼1 individual on average per minute of searching). Most of the crabs (67.2%) of all species were males, 21.3% were not sexually mature, and only 11.5% were females, none of which bore eggs. The commonest species across all sites was *H. araneus* (total 552; ♂: 392 [71%]; ♀: 38 [7%]; immature 122 [22%]; found at all sites in Breiðafjörður but absent from Bolaklettar, Faxaflói). *C. maenas* was dominant at the southern sites Sæbraut [1], Bolaklettar [2] in Faxaflói, and at Maðkavík [3], which was the southernmost site in Breiðafjörður (total 339; ♂: 201 [59%], ♀: 65 [19%]; immature: 73 [22%]; found at six sites). Very few *C. irroratus* were found intertidally (total 23; ♂: 21 [91%], ♀: 2 [9%]; immature: 0; found at six sites) (Figure 1; Supplementary Table S1).

Only two sites in the south-east of Breiðafjörður (Hnúksnes [4] and Skarðstöð [5]) had all three species present. Proportionally, *H. araneus* was numerically dominant at all sites except in the southernmost part of Breiðafjörður at Maðkavík [3], where *C. maenas* was advancing and becoming dominant, especially on the mid-shore (Figure 2). This site resembled the two reference stations in Faxaflói where *C. maenas* dominated both at low- and mid-intertidal
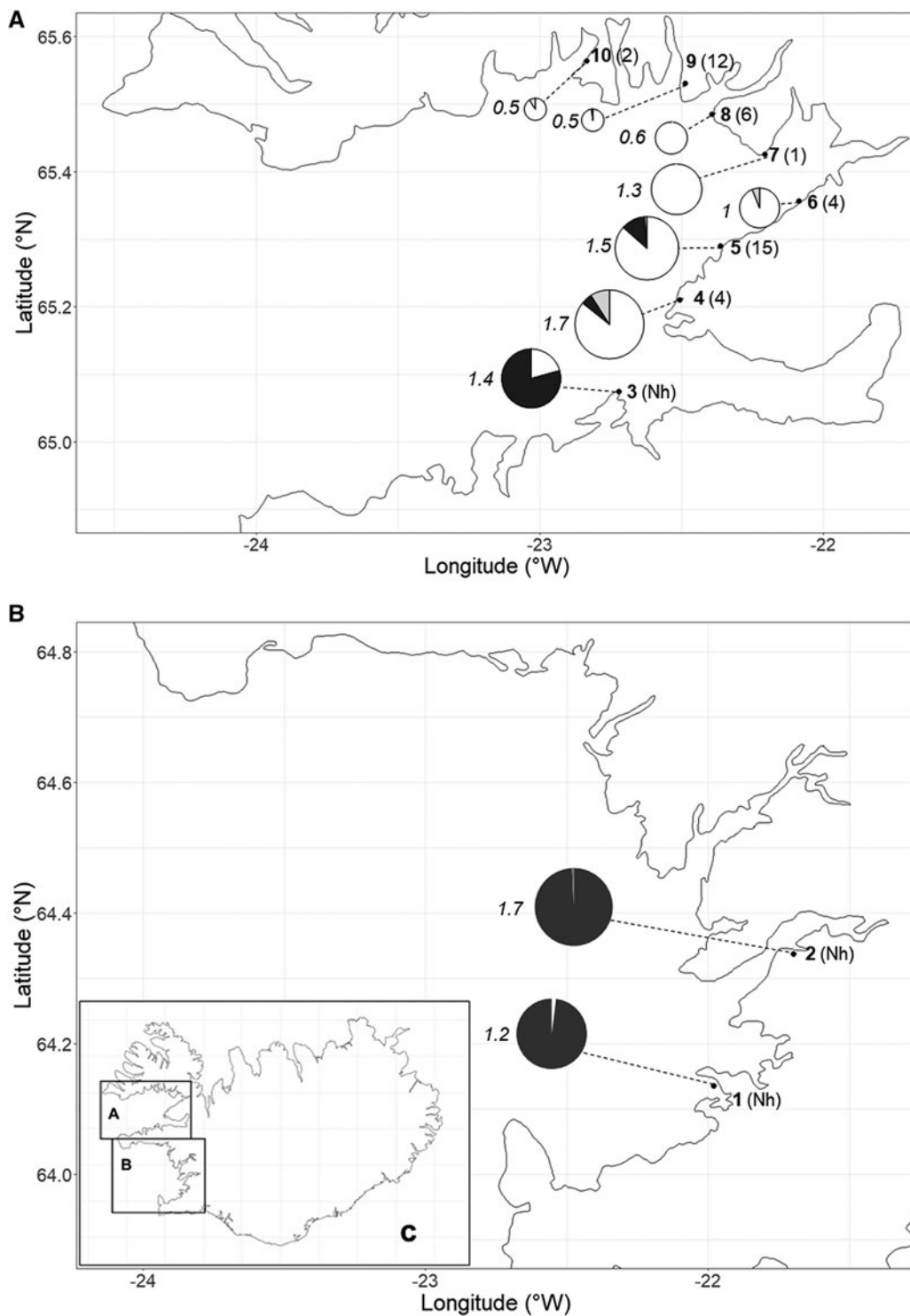
Figure 1. Breiðafjörður bay (A) and Faxaflói bay (B) in western Iceland with inserted map of Iceland (C) with sampling areas marked. Sampling sites marked with pie charts showing proportion of species found per minute. White: *H. araneus*, grey: *C. irroratus*, black: *C. maenas*. Size of the pie chart is scaled to abundance (mean number of crabs found per min. Exact mean values in italics to the left of pie chart). Numbers in brackets indicate years since last harvest (Nh = never mechanically harvested). (1) Sæbraut, (2) Bolaklettar, (3) Maðkavík, (4) Hnúksnes, (5) Skarðstöð, (6) Fagridalur, (7) Karlsey, (8) Klauf, (9). Kleifastaðir, and (10) Fjörður.

levels. At the reference sites, *H. araneus* was present in Sæbraut [1] in very low numbers, but was not found at all in Bolaklettar [2]. *C. irroratus* was present in low numbers at the reference site Bolaklettar [2], but was not found at Sæbraut [1].

At the northernmost sites, Fjörður [10] and Kleifastaðir [9], sampling was repeated twice (site 9 twice at noon, site 10 once at noon and once at midnight) to increase sample sizes of crabs collected at these low abundance sites. There was no difference in CPUE when comparing those sites sampled at different times (1 crab min^{-1}, SE = 0.1, $N = 521$ at noon and 1 crab min^{-1}, SE = 0.2, $N = 389$ at midnight) (see Supplementary Table S1). There was no significant difference at Fjörður [10], where searches had been made at both times (Wilcoxon rank sum test; $N = 16$, $W = 19.5$, $P = 0.2$). Searches at mid-summer midnight (but not in the dark) were still effective. Sites were therefore subsequently compared irrespective of time of search.
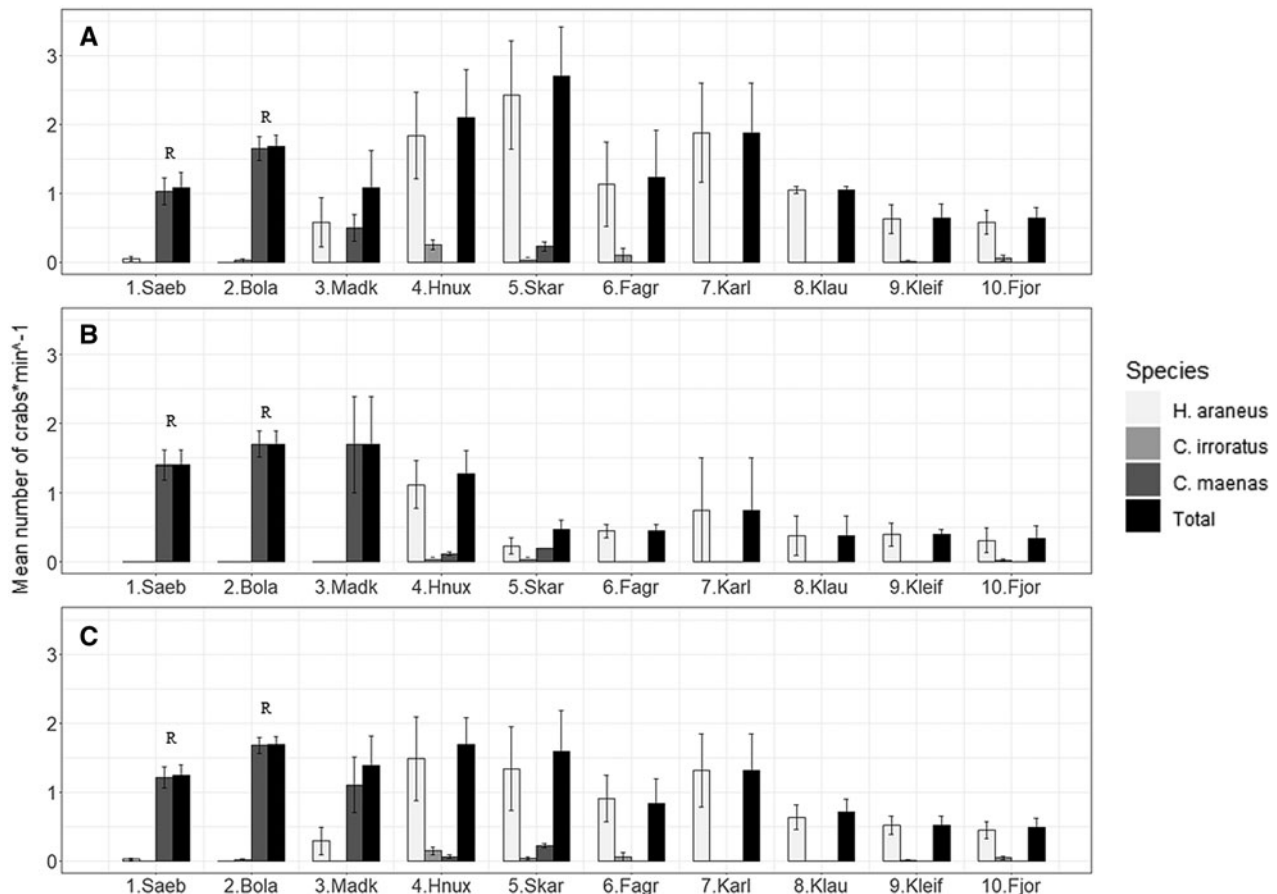
Figure 2. Mean number of crabs found per minute on each site (see Figure 1 for map) with SE: (A) low-shore level, (B) mid-shore level, and (C) both shore levels pooled together. R, reference sites located in Faxaflói bay.

Within Breiðafjörður, there were higher crab abundances as CPUE on the south side (Maðkavík [3], Hnúksnes [4], and Skarðstöð [5], maximum of 1.7 crabs min^{-1}) than at sites in the north side (Kleifastaðir [9] and Fjörður [10], both 0.5 crabs min^{-1}). The more abundant southern sites (Hnúksnes [4] and Skarðstöð [5]) had patchier distributions, reflected in larger SE. Abundances in the innermost part of Breiðafjörður (Karlsey [7] and Fagridalur [6]) were intermediate to those found to the south and north shores of Breiðafjörður. The reference sites in Faxaflói (Sæbraut [1] and Bolaklettar [2]) had higher abundances, being similar to Maðkavík [3]. *H. araneus* was dominant at the sites in Breiðafjörður except at Maðkavík [3]. CPUE of *H. araneus* was significantly lower at sites in Breiðafjörður with *C. maenas* present than those without it (Wilcoxon rank sum test; $W = 1173.5$, $P < 0.001$).

More crabs were found lower on the shore, except at the reference sites in Faxaflói (Sæbraut [1] and Bolaklettar [2]) and at Maðkavík [3] in Breiðafjörður where *C. maenas* dominated, being much more abundant on the mid-shore. Comparing abundance of all crab species across all sites in Breiðafjörður, except in Maðkavík [3], there were significantly more crabs at low-shore levels, being mostly *H. araneus* (one-tailed Wilcoxon matched pair test; $N = 7$, $T = 1$, $P < 0.025$), with on average 1.4 crabs min^{-1} on the low shore and 0.9 crabs min^{-1} on the mid-shore. CPUE of the most common species *H. araneus* was significantly higher on low-shore than on mid-shore levels (Kruskal–Wallis; $\chi^2 = 4.35$, df = 1, $P < 0.05$), but did not differ significantly among sites (Kruskal–Wallis; $\chi^2 = 12.57$, df = 9, $P = 0.2$).

The effect of harvesting was only assessed in Breiðafjörður to avoid geographically confounding factors. When abundances of total crabs on each shore were pooled across shore levels and compared with time since last harvest, there was also no significant relationship (Pearson's product–moment correlation; df = 72; $r = +0.2$; $P = 0.2$), but power is low with only eight locations. When testing the species separately, there was not a significant correlation of abundance of *H. araneus* with time since last harvest (Pearson's product–moment correlation; df = 72; $r = -0.2$; $P = 0.1$). A significant positive correlation with years since last harvest was found for *C. maenas* (Pearson's product–moment correlation; df = 72; $r = 0.7$; $P < 0.001$) (Supplementary Figure S1), but this is driven largely by high numbers at the unharvested site at the front edge of its poleward advance, combined with limited presence at other sites, leading to many zero scores. Correlation analysis for *C. irroratus* was not attempted because of their infrequent occurrences.

There were no significant differences when comparing crab abundances of each search of both shore levels at sites with different harvesting histories i.e. those with more than 10 years since last harvest (Maðkavík [3], Skarðstöð [5], and Kleifastaðir [9]) with sites with less than 2 years since last harvest (Karlsey [7] and Fjörður [10]) (Kruskal–Wallis; $\chi^2 = 6.2$, df = 4, $P = 0.2$). There were also no differences when comparing a control area with many years since last harvest such as Kleifastaðir [9] (12 years since last harvest) with two nearby sites more recently harvested like Karlsey [7] (1 year) and Fjörður [10] (2 years) (Kruskal–Wallis; $\chi^2 = 0.3$, df = 2, $P = 0.9$). On the south side of Breiðafjörður, we compared recently cut areas (Hnúksnes [4] and Fagridalur [6]; 4 years since last harvest) with those not harvested for over a decade or never mechanically harvested (Maðkavík [3] and Skarðstöð [5]). No significant differences in CPUE were found (Kruskal–Wallis; $\chi^2 = 0.2$, df = 2, $P = 0.9$).

At sites where *H. araneus* was the only species present in the intertidal zone (Figure 3) two different patterns in size structure were found. In Karlsey [7], there were large numbers of small individuals in the 10–12 mm size class, indicating a strong recruitment event. Klauf [8] had similar mean and medians to all other sites but differed from the rest in the size structure, as the dominating size class was larger (24–26 mm). The reference sites in Faxaflói (Sæbraut [1] and Bolaklettar [2]) and Maðkavík [3] in Breiðafjörður were dominated by *C. maenas*, showing large numbers of small crabs, indicating strong and recent recruitment, as well as some mature individuals. These sites had the lowest numbers of *H. araneus*.

The size frequency distributions of *H. araneus* were characterized by having two or three size classes and a majority of smaller individuals. There were very few, but larger *C. maenas* at Hnúksnes [4] and Skarðstöð [5], sites where all three species were found, indicating range edge populations with little recent recruitment. Similarly, few scattered individuals of *C. irroratus* were found at those sites, indicating very marginal intertidal populations of a predominantly subtidal species. Both Fagridalur [6] and Karlsey [7] are dominated by *H. araneus*, being the only species present at Karlsey and sharing part of the lower shore with low numbers of *C. irroratus* in Fagridalur. These sites also show the smallest mean carapace length for *H. araneus*, which could indicate that these sites have strong recruitment. Two-sample Kolmogorov–Smirnov tests showed significant differences in size frequency distributions of *H. araneus* in sites where it is the sole crab species (sites 7 and 8) *vs* sites where it is found with *C. maenas* (sites 1 and 3; $P < 0.001$, $D = 0.5$), with *C. irroratus* (sites 6, 9, and 10; $P < 0.001$, $D = 0.3$), or with both present (sites 4 and 5; $P < 0.001$, $D = 0.3$), indicating negative interactions with these newcomers (see Supplementary Figures S2–S6).

Discussion

Numerous studies have contributed to our understanding on the distribution of intertidal brachyuran crabs across various regions (e.g. Fukui and Wada, 1986; Flores and Paula, 2001; Silva *et al.*, 2009, 2014; Fatemi *et al.*, 2012; Ribero *et al.*, 2020). However, none have yet focused on *Ascophyllum*-dominated shores in Europe or Iceland. Our study was the first to successfully show considerable tide-out occupancy in the *Ascophyllum*-dominated intertidal zone by three brachyuran crabs (namely *H. araneus*, *C. maenas*, and *C. irroratus*). Populations of the most common crab *H. araneus* were composed of new recruits, immature individuals, and juvenile males with fewer females, suggesting a nursery function for a species that is found subtidally.

Prior to our research, there were no records of *C. irroratus* or *C. maenas* being present at these sites in Breiðafjörður. Historical records of the Icelandic intertidal zone showed that only *H. araneus* was found in Breiðafjörður prior to 1973 (Sæmundsson, 1936; Hauksson, 1977). The first occurrences of *C. maenas* in the area were in 1996 in the southernmost part of Breiðafjörður (i.e. at outer Snæfellsnes Peninsula as well as at the island of Flatey, Ingólfsson, 1996). Introduction of new brachyuran species into an ecosystem can have a wide arrange of effects, such as alteration of population dynamics (Sigurdsson and Rochette, 2013; Matheson *et al.*, 2016), resource competition (Epifanio, 2013), biodiversity loss (Falk-Petersen *et al.*, 2011; Clavero *et al.*, 2022), or impact on prey populations and predator–prey relationships (Lohrer and Whitlatch, 2002). Documenting the abundance and population structure of these crabs expands our understanding of global change in high latitude intertidal ecosystems by providing valuable insights into the changing distribution patterns.

Within Breiðafjörður, *H. araneus* dominated all sites visited except in Maðkavík [3] where *C. maenas* was the most abundant, especially in the mid-shore level, where it has completely replaced *H. araneus*. We have confirmed that *C. maenas* is advancing polewards at the northern edge of its natural range in Europe and western Iceland. Increasing temperatures are driving changes in relative abundances (Harley *et al.*, 2006; Helmuth *et al.*, 2006; Van der Putten *et al.*, 2010; Poloczanska *et al.*, 2016) and enabling temperate and boreal intertidal species to shift polewards (Hawkins *et al.*, 2008, 2019; Cheung *et al.*, 2009). While *C. maenas* is considered native to Icelandic waters, its current expansion due to increasing temperatures raises the question about its ecological role in these receiving ecosystems, turning it into a potential 'climate migrant', with implications reminiscent of an invasive species. *C. maenas* advancing into new areas may lead to increased competition for food and/or refuges (Jensen *et al.*, 2002; Epifanio, 2013), or exclusion of prey species through predation (McDonald *et al.*, 2001; Brazão *et al.*, 2009). Studies conducted in areas where *C. maenas* has invaded outside its native range have demonstrated the competitive potential of the species, with documented cases of displacing and negatively affecting indigenous decapod populations
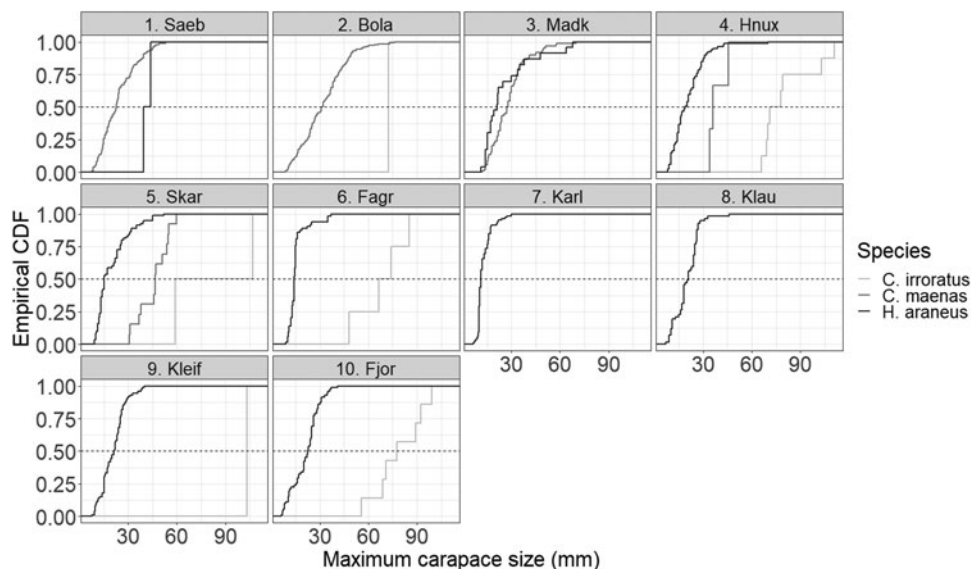

Figure 3. Cumulative frequency of maximum carapace size for *H. araneus* (length), *C. maenas* (width), and *C. irroratus* (width) per site.

(Grosholz et al., 2000; Williams et al., 2009; Gehrels et al., 2016; Ens et al., 2022), ultimately influencing species composition and relative abundance. As a predator with a diverse diet, C. maenas could affect lower trophic levels and disrupt populations of both higher and lower trophic levels (Grosholz and Ruiz, 1996). These findings suggest that the establishment of large C. maenas populations could have similar consequences for the intertidal community structure of the Icelandic Westfjords and the rest of Iceland. The extent of the impact the species will have on the area will depend on many factors, such as interspecific interactions, rate of expansion, community adaptability, and resilience or other changing ecological conditions. As C. maenas expansion continues, it is crucial that these changes are monitored to better understand further ecological consequences.

The occupancy of C. irroratus in the intertidal zone was limited. Despite being present in six out of ten sites in Breiðafjörður and at one of the reference sites, abundances were always low. Even with these low densities, our study found some changes in the size structure of H. araneus when comparing sites with the presence of C. irroratus to those where it was absent. These findings suggest that interspecific interactions between both species exist, underscoring the importance of considering such ecological interaction when examining community dynamics and population structure in the future. Previous studies in our reference area in the south-west of Iceland show abundances of C. irroratus being greater than C. maenas and H. araneus in the subtidal zone (Gíslason et al., 2021), where it has become the dominant species. Relative proportions of brachyuran crab species in the intertidal zone of Breiðafjörður differ from those reported in the subtidal habitat (Gíslason et al., 2014, 2021). This could be due to differences in life history and niche partitioning. All three species have different life-history traits (Gíslason et al., 2021) and therefore might use the intertidal and subtidal zones differently. But how these brachyuran species use this zone is still relatively unknown. Our study also showed that the shore was predominantly used by new recruits, immature and male juveniles, with no egg-bearing females being found. In many crab species, females stop eating, foraging, and move to deeper areas when ovigerous (Howard, 1982; Shields, 1991), which could explain the lack of females and berried females in our study.

Studies on H. araneus in the rocky intertidal zone are scarce (although see Hartnoll, 1963), and many of the life-history traits are unknown (Gíslason et al., 2021). A study by Einarsson (1988) indicates that H. araneus can be found everywhere from 2 m down to depths of 60 m all around Iceland, but it should be noted that any study before 2006 did not account for what effects C. irroratus might have on the native species. In other instances, co-existence of crab species in the same habitat and with similar niches have led to competitive exclusion or to changes in diet (Al-Wazzan et al., 2019). A possible explanation for the differences in distribution and abundances in the subtidal and the intertidal zones is that, intertidally, H. araneus has a different niche foraging under the Ascophyllum cover, making it easier for larger populations to be sustained – the exception being sites where C. maenas is found in large numbers, which may lead to a competitive displacement of H. araneus. In the subtidal, C. irroratus might have an advantage in niche utilization as their maximum size is bigger and may therefore displace both native species. This leads us to hypothesize that, in the near future, H. araneus may be excluded from the intertidal zone at progressively northern sites by advancing C. maenas, particularly at mid-shore levels. Such a pattern reflects what is found further south in Europe and around the British Isles, where H. araneus is primarily subtidally distributed (Hartnoll, 1963), only occasionally found intertidally usually in low-shore pools, and never under Ascophyllum canopies (Golletty et al., 2011, S. J. Hawkins,

unpublished observations over four decades of observations on Manx, Welsh, and south-west shores). Additionally, its subtidal niche could also be compromised as C. irroratus proliferates; essentially being squeezed from below by C. irroratus, a proliferating non-native in the subtidal zone and from above by C. maenas, an advancing native in the intertidal zone.

The ecological importance of seaweed canopies is widely recognized. Large changes in seaweed canopy or complete canopy removal can lead to major changes in community organization and habitat provision, particularly when considering understorey species and more complex epiphyte communities on intact fronds that contribute to overall productivity and heterogeneity (Ang et al., 1996; Jenkins et al., 2004; Ingólfsson and Hawkins, 2008; Stagnol et al., 2013; Lotze et al., 2019). The present study found no effect of harvesting on the mobile brachyuran crab community of Breiðafjörður. Correlations were found between abundance of crabs with time since last harvest for only C. maenas, but not for the brachyuran community. Sample sizes of sites were small, limiting the power of the analysis, and the spread of C. maenas from the south-west into unharvested sites is a confounding factor. The nearly significant ($P = 0.1$) negative correlation may indicate some benefit from harvesting for H. araneus among bushier plants but is likely to be driven by the large numbers of C. maenas at the unharvested site at its invasion front.

The overall impact of harvesting on the benthic community will highly depend on frequency, tools, seasonality, and magnitude of harvesting as well as the phenological attributes of the community (Vasquez, 1995). Moderate harvesting of A. nodosum canopy has little long-term effects on the algal and associated benthic faunal community (Kelly et al., 2001; Lauzon-Guay et al., 2021). However, more intense harvesting can have longer-lasting negative effects on the number of species, or animal and algal cover (Boaden and Dring, 1980; Fegley, 2001; Gendron et al., 2018). Nevertheless, our results showing undetectable effects – albeit with low power and some confounding factors – are consistent with studies and reports from Ireland (Kelly et al., 2001) which found very minor effects of Ascophyllum harvesting on megafauna. Bertness et al. (1999) found that the main positive effects of Ascophyllum cover were found to be higher on the shore, where algal canopy ameliorates the effects of the harsh physical conditions, while effects on the lower tidal heights were offset by increased consumer pressure. Therefore, harvesting strategies should be in line with the phenological characteristics of the canopy species as well as the ecological characteristics of the community to allow fast recovery, maintain a sustainable biomass, and avoid long-term degradation of the benthic community (Seeley and Schlesinger, 2012; Lotze et al., 2019).

Conclusion

Quantifying and mapping species distribution are essential for understanding the interplay of anthropogenic impacts such as climate change, introduction of non-native species, and harvesting of habitat-forming species. In our study we demonstrated that, currently, the presence of C. irroratus in the intertidal zone was negligible and that C. maenas is advancing northwards. Successful establishment of C. maenas populations in the intertidal zone in Breiðafjörður bay has led to a displacement and substantial reduction of H. araneus probably by competition for resources. Given its displacement in the subtidal by C. irroratus, current squeezing of H. araneus may accelerate with warming and further spread of C. maenas. This warrants further tracking. Ascophyllum harvesting was not linked to effects on crab species. Nevertheless, a precautionary approach should always be practiced, as juvenile individuals are susceptible to nursery habitat degradation should harvesting intensify.

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