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Marine Biology Research

ISSN: 1745-1000 (Print) 1745-1019 (Online) Journal homepage: http://www.tandfonline.com/loi/smar20

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To cite this article: Óskar Sindri Gíslason, Jónas P. Jónasson, Snæbjörn Pálsson, Jörundur Svavarsson & Halldór P. Halldórsson (2017) Population density and growth of the newly introduced Atlantic rock crab Cancer irroratus Say, 1817 (Decapoda, Brachyura) in Iceland: a four-year mark-recapture study, Marine Biology Research, 13:2, 198-209, DOI: 10.1080/17451000.2016.1240875

To link to this article: http://dx.doi.org/10.1080/17451000.2016.1240875

Published online: 09 Jan 2017.

MARINE BIOLOGY RESEARCH, 2017
VOL. 13, NO. 2, 198–209
http://dx.doi.org/10.1080/17451000.2016.1240875

ORIGINAL ARTICLE

Population density and growth of the newly introduced Atlantic rock crab *Cancer irroratus* Say, 1817 (Decapoda, Brachyura) in Iceland: a four-year mark-recapture study

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ABSTRACT

The Atlantic rock crab *Cancer irroratus* was discovered in Icelandic waters in August 2006 and spread rapidly along the coastline. The species has reproduced successfully in Iceland, and there have been strong indications that *C. irroratus* has become common on soft-bottom coastal habitats in south-western Iceland. To be able to evaluate the effect of such non-indigenous species on the ecosystem, population density estimates are required. In the years 2011 to 2014, a mark-recapture study was carried out on *C. irroratus* in a small inlet in the Kollafjörður fjord, south-western Iceland. In total, 6475 *C. irroratus* were captured and of them 4670 were tagged with sequentially numbered T-bar anchor tags. Of the crabs tagged, 155 were recaptured over the four years (3.3%), 34 had moulted and one of them presumably twice over the four-year period. The size range of recaptured crabs was 7.3–12.8 cm carapace width and the growth increment per moult ranged from 1.2 to 2.6 cm, with an average of 2 cm. Based on the mark-recapture analysis, the population at the study area in Kollafjörður was estimated to be about 107,000 individuals.

ARTICLE HISTORY
Received 22 January 2016
Accepted 20 September 2016
Published online 9 January 2017

RESPONSIBLE EDITOR
Roy Kropp

KEYWORDS
Growth; Iceland; mark-recapture; moulting; non-indigenous species

Introduction

Marine invasive species have been described as important drivers of ecological change, as their effects can lead to habitat changes, displacement of native species through predation or competition, spread of diseases and reduction of biodiversity (Bax et al. 2003). Once a marine non-indigenous species has become established, the chances that it can be eradicated are small (Thresher & Kuris 2004). A successful invasion depends on several steps. In addition to finding a route of dispersal to a new area, the colonizers may need to overcome numerous obstacles to establish in the new environment. Environmental conditions, such as temperature and salinity, have to be within the species' tolerance range for all life stages, so the species can grow, reproduce and spread successfully (Blackburn et al. 2011). Global warming, for instance, has led to opportunities for many species to expand their ranges to higher latitudes (Stachowicz et al. 2002), where the invader may outcompete native species, as the many examples of the invasive European green crab *Carcinus maenas* (Linnaeus, 1758) demonstrate (McDonald et al. 2001; Jensen et al. 2002; Rossong et al. 2006; MacDonald et al. 2007). However, most species fail to colonize new environments even though conditions seem favourable, possibly because of the negative effects of the transportation, unfavourable environmental conditions, competition or predation by native species, or a lack of genetic variation (Lockwood et al. 2005; Salmenkova 2008; Blackburn et al. 2011; Zenni & Nuñez 2013). For species that succeed, it can take a long time to establish in a new area, even decades or centuries (Crooks & Soulé 1999). Although some species that have established a colony may have no or little harmful effect on their new ecosystem (Bugnot et al. 2014), there are many cases of drastic ecological and/or economic effects, as has been seen for *C. maenas* (Klassen & Locke 2007), the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) (Roche & Torchin 2007), the Chinese mitten crab *Eriocheir sinensis* H. Milne Edwards, 1853 (Dittel & Epifanio 2009; Schrimpf et al. 2014) and the red king crab *Paralithodes camtschaticus* (Tilesius, 1815) that was intentionally introduced into the Barents Sea (Falk-Petersen et al. 2011; Dvoretsky & Dvoretsky 2013).

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Cancer irroratus Say, 1817, which is distributed along the eastern coast of North America, was discovered in Icelandic waters in 2006 but is thought to have been introduced as larvae via ballast water no later than 1999 (Gíslason et al. 2014). Relatively few large decapod crab species live in the coastal waters of Iceland, where the great spider crab *Hyas araneus* (Linnaeus, 1758) and *C. maenas* are the most abundant. Since *C. irroratus* was first discovered in Iceland, its population has been growing extensively. The crab has spread rapidly clockwise from south-western to northern Iceland and had colonized about 50% of the coastline in 2014. Studies on larval abundances (Gíslason et al. 2014) indicated that the crab has reproduced successfully and has maintained high genetic diversity (Gíslason et al. 2013b).

The method of marking and recapturing has been used in biological studies since 1896 (Petersen 1896) to estimate population sizes and to gather information about migration, growth and mortality rates. This method is especially useful in the marine environment, where direct measurements and observations can be difficult to obtain. It has previously been used to estimate stock sizes of decapod crabs (Carroll 1982; Drummond-Davis et al. 1982; Munch-Petersen et al. 1982; McPherson 2002; Aedo & Arancibia 2003; Bell et al. 2003). The method is often applied by combining marking with commercial fisheries that are well designed to capture the target species and is used to improve stock estimates. For stock or population assessments, the effective fishing area of traps is an important consideration because it is known to vary greatly depending on the habitat quality and the crustacean species being trapped (Miller 1975, 1989; Melville-Smith 1986; Evans & Evans 1996; Aedo & Arancibia 2003).

Our aims were to obtain a better understanding of the colonization of Icelandic waters by *C. irroratus* and to evaluate whether the species may play a significant role in the coastal ecosystem. We assessed this at a selected site in the *C. irroratus* distributional range in south-western Iceland by estimating the population size, density and growth (moulting frequency and growth increment) of individual crabs. This study also aimed to determine whether T-bar anchor tags, which are cheap and easy to use, were useful for long-term monitoring, that is, whether *C. irroratus* could successfully moult with the tag retained, and, if so, estimate the moulting frequency and size increment per moult.

Materials and methods

Trapping and tagging

The study was carried out in a small inlet in the Kollafjörður fjord, south-western Iceland, in the latter part of September each year of 2011–2014 (Figure 1), a period of highest catches previously recorded in trap fisheries in Iceland (autumn/early winter) (Gíslason et al. 2014). Commercial crab fisheries in Iceland, though, are still small (<9 tonnes/year), and no commercial fisheries have been allowed in the study area. The selection of the sampling site, which is dominated by a fine substrate bottom, typical for other known *Cancer irroratus* sites in Iceland, was based on our previous studies and trap fisheries in that area. The depth at the study site was 4–12 m. Four trap strings were laid out, each string containing five box traps with 22 m between traps. The box traps were made by Carapax AB®, Sweden and are commercially used for brown crab, *Cancer pagurus* Linnaeus, 1758, fisheries. The traps (height 30 cm, length 80 cm, width 40 cm, volume 0.096 m^3, mesh size 4.8 cm) have entries at each end, but escape openings for juveniles were closed. The four strings were laid out in four lines, two on each transect (T1 and T2, Figure 1) with 50 m between the string ends and 200 m between transects. The four lines formed a square in the small inlet that is limited by land on two sides to the south-west and north-east, shallow waters to the south-east and east that are largely affected by tidal changes/movements, and a deeper and harder substrate to the north-west (Figure 1). Previous trap surveys in the shallower and deeper waters around the selected square indicated much lower *C. irroratus* abundance compared with the study site (Óskar Sindri Gíslason 2015, personal observation). The effective fishing area of the traps was estimated to extend to 150 m towards open sea and 100 m to land based on Miller (1989), suitable habitat and experimental trap fisheries in and around the area giving a total estimated sampling area of 0.22 km^2 (Figure 1). The traps were laid out five times each year in 2011–2013 and three times in 2014. On each occasion, the traps were retrieved after 48 h soak time, processed immediately and set out again. Each trap was baited with a mixture of about 250 g of cod *Gadus morhua* Linnaeus, 1758, saithe *Pollachius virens* (Linnaeus, 1758), haddock *Melanogrammus aeglefinus* (Linnaeus, 1758) and common dab *Limanda limanda* (Linnaeus, 1758).

All crabs were weighed using an electronic scale, with an accuracy of ± 1 g and measured across the two most distant points of the carapace (carapace width, CW) to the nearest 0.1 cm with a Vernier caliper. In the first four trips of each year 2011–2013, 4670 *C. irroratus* were captured and marked with sequentially numbered *T*-bar anchor tags. Crabs were not tagged in 2014. The recapture rate was documented for all four years (2011–2014). The highly visible,

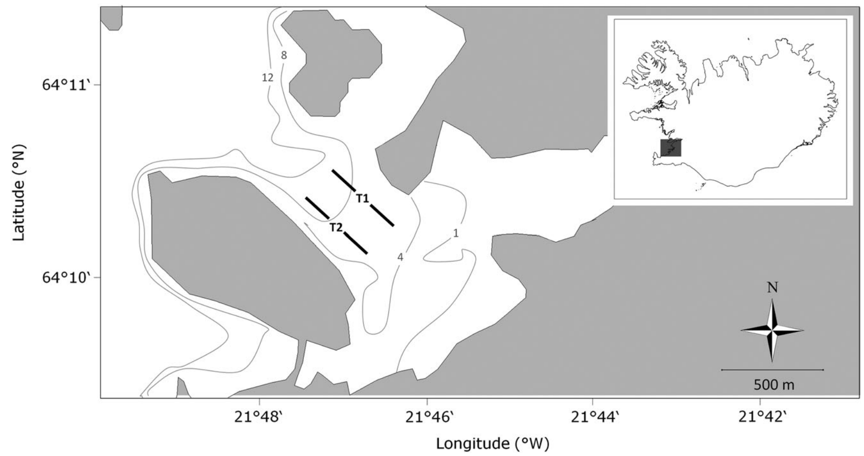

Figure 1. The Atlantic rock crab (*Cancer irroratus*) population study site in Kollafjörður, south-western Iceland. Strings were laid out in four lines, two on each transect (T1 and T2) with 50 m between the string ends and 200 m between transects. Depth contours are expressed in metres.

orange TBA-1 tags (Hallprint Fish Tags) used were 4.5 cm in total length with a 2.5 cm long marker. Moult of recaptured crabs was determined by changes in measured CW between captures.

The tags were always placed in the lateral ecdysial suture line at the same spot on the left side of the animal. The procedure was standardized to ease spotting the tags on recaptured individuals and for spotting lost tags (evident as clear pinhole) on individuals who had lost their tags. Crabs without tags but with worn pinholes were assumed to have been marked in the previous year based on moulting probability over time. All crabs were released about 50 m from the transect on which they were captured. A preliminary study carried out on 10 crabs for three weeks in laboratory tanks indicated that the tags had little or no effect on the crabs' behaviour, i.e. they all ate within one hour after being tagged and no mortality was observed.

Abundance estimates

Abundance estimates were calculated using two approaches based on mark-recapture methods. Firstly, crab counts were analysed over two consecutive years by using a maximum likelihood estimate of the population size N based on the binomial probability of sampling marked and unmarked individuals (G&S) as in Gazey & Staley (1986). Secondly, estimates for each year were obtained by fitting generalized linear models using the function *closedp*, implemented in the Rcapture package (Baillargeon & Rivest 2007), where the sampling was conducted over nine days, assuming a closed population with insignificant mortality and immigration/emigration during that short period. Sources of variation from temporal effects (t), heterogeneity between sampling units (h) (modelled three ways: Chao, giving a lower bound for the abundance, Darroch and Poisson; see further description in Baillargeon & Rivest 2007) and behavioural effects (b) were evaluated by different models denoted as M_0 (no source of variation) and: M_t, M_h, M_{th}, M_b, M_{tb}, M_{bh} and M_{tbh}. Thirdly, the population size of each year and over the whole period was estimated by considering the whole data set by applying the functions *robustd.0* and *robustd.t* and for the associated M models as listed above (Baillargeon & Rivest 2007). The robust functions are mixed, assuming closed systems within the study period within years but with possible arrivals and departures occurring between years; *robustd.0* uses the pooled frequencies of the observable capture histories in terms of number of captures within years, whereas the function *robustd.t* takes into account the capture success or failure of each capture occasion within each year. Lastly, the population size over the whole period was estimated using the *closedp* and the *openp* functions in Rcapture, where the latter allows arrivals and departures to occur between years. The best model was selected based on the Akaike information criterion (AIC). The population density of crabs in the study area was calculated by dividing the estimated abundance by the size of the assumed trapping area (0.22 km^2).

Statistical analysis

The deviations in size distributions of *Cancer irroratus* from normality were analysed for each year and both genders with the Shapiro–Wilk test (Shapiro & Wilk 1965), skewness (g1) (Sokal & Rohlf 2008) and Hartigans' dip test for multimodality (Hartigan & Hartigan

Table I. Total catch of Atlantic rock crab (*Cancer irroratus*) males (M) and females (F) in the mark-recapture study in Kollafjörður, south-western Iceland, during the years 2011–2014; *n* is the total number of crabs and n_{Traps} is the total number of traps.

		Gender		
Year	*n*	M	F (with eggs)	n_{Traps}
2011	1570	1229	341 (1)	100
2012	2331	2004	327 (1)	100
2013	1728	1530	198	100
2014	846	758	88	60
Total	6475	5521	954	360

1985), implemented in the R package *diptest* (Maechler 2015). Difference in size frequency distributions between genders was tested with the non-parametric Wilcoxon test (Wilcoxon 1945). Individual growth was studied by comparing the carapace width of individuals that had been marked and recaptured after one to three years with the size when marked. The probability of moulting was estimated by the relative frequencies of moulted individuals among recaptured individuals at a given size, and analysed by a logistic regression (Sokal & Rohlf 2008).

Results

Mark-recapture

The total catch at the study site during the four years (2011–2014) was 6475 individuals in 18 fishing trips (Table I). In total, 4670 were tagged, 3992 males ranging with CW from 5.3 to 13.7 cm and 678 females ranging in CW from 5.8 to 11.0 cm (Table II). Males outnumbered females in all trap catches (Table I). The overall proportion of males was 85% during the four years, ranging from 78 to 90% per year. The average size of recaptured crabs was 10.5 cm CW, ranging in size from 7.3 to 12.8 cm. Only 10 individuals were smaller than 7 cm CW, the smallest one a male 5.3 cm CW. The proportion of egg-bearing females was very low (Table I).

The total number of individuals marked each year ranged from 1167 to 2041, and the recapture rate ranged from 0.5 to 3.1% within years and from 0.5 to 2.7% between years (Table III). Nine crabs were recaptured twice after being marked; three were recaptured two times in the same year, three with one year between and three with two years between recaptures. Seventeen recaptured crabs had lost their tags; two in 2011, one in 2012, nine in 2013 and five in 2014. In three cases, crabs had deformed carapaces where they had been tagged. All crabs captured with lost tags were marked with a new tag and released again.

Abundance

The estimated abundance of *Cancer irroratus* fluctuated over the years and was lowest in 2011 (*closedp*: 13,603 and *robustd.0*: 22,001) and largest in 2012 (*closedp*: 154,443 and robustd.0: 106,591), irrespective of the method applied (*closedp*, *robustd.0* and *G&S*) (Table IV, which shows only the results with the lowest AIC within each category of models). Although the average estimates varied somewhat among the models the confidence intervals overlapped. The same trend was observed with the G&S method as for the other methods, but as G&S includes the change over two years the numbers are not directly comparable with the within-year estimates. The estimated number of crabs over the study period ranged from 77,049 to 106,591 individuals and was largest for the *robustd.0* function, 106,591 (95% CI: 83,783–129,398), equal to the highest estimate obtained for 2012 (Table IV). The density of adult *C. irroratus* at the study site in

Table II. Carapace width characteristics (mean, range and standard error (SE)) for the Atlantic rock crab (*Cancer irroratus*) caught in traps in Kollafjörður, south-western Iceland in the years 2011–2014.

Sex/year	*n*	Mean	Range	SE	g1	dip test
$Male_{2011}$	1229	10.21	5.3–13.0	0.034	−0.670**	0.026**
$Male_{2012}$	2004	9.82	6.4–13.3	0.031	−0.018	0.026**
$Male_{2013}$	1530	10.55	5.9–13.7	0.030	−0.562**	0.021**
$Male_{2014}$	758	11.05	7.4–13.8	0.041	−0.812**	0.028**
$Male_{2011-14}$	5484	10.29	5.3–13.8	0.018	−0.448**	
$Female_{2011}$	341	8.15	6.8–9.7	0.032	0.172	0.042**
$Female_{2012}$	327	8.13	6.5–11.0	0.035	0.447**	0.033
$Female_{2013}$	198	8.30	5.8–10.0	0.049	−0.445**	0.038
$Female_{2014}$	88	8.80	7.2–10.4	0.070	0.166	0.058
$Female_{2011-14}$	954	8.23	5.8–11.0	0.021	0.171*	
All_{2011}	1570	9.76	5.3–13.0	0.035		
All_{2012}	2331	9.58	6.4–13.3	0.029		
All_{2013}	1728	10.31	5.8–13.7	0.032		
All_{2014}	846	10.81	7.2–13.8	0.044		
$All_{2011-2014}$	6475	9.98	5.3–13.8	0.018		

Significance: *0.05, **0.001.
Other parameters are: *g*1, size distribution skewness (departure from normality); *dip test*, results of Hartigan's dip test for multimodality.

Table III. The number of Atlantic rock crabs (*Cancer irroratus*) that were marked, recaptured and that had moulted by gender (M for male and F for female) during the study period of 2011–2014 in Kollafjörður, south-western Iceland.

					Recaptured crabs originally marked in		
Year	Captured	Marked	Recaptured M | F	Moulted M | F	2011	2012	2013
2011	1570	1167	35 | 1	0	36 (1)	–	–
2012	2331	2041	38 | 3	12 | 0	32	9	–
2013	1728	1462	57 | 2	14 | 1	21 (1)	31 (2)	7
2014	846	0	26 | 1	8 | 0	4	7	16

The number of recaptured crabs marked in certain years is also listed and individuals that were recaptured twice in the same year are shown in parentheses.

Kollafjörður ranged from 0.10 crabs m^{-2} (95% CI: 0.06–0.14) in 2011 to 0.48 crabs m^{-2} (95% CI: 0.38–0.59) in 2012 but declined in 2013 to 0.28 crabs m^{-2} (95% CI: 0.13–0.43).

Size range and size distribution

The mean CW of males over the years was 10.3 cm (range 5.3–13.8 cm) and 8.2 cm for the females (range 5.8–11.0 cm) (Table II). Males were significantly larger than females within years and overall ($P < 0.001$). The size distribution differed among the years (Figure 2). The distributions deviated from normality, showed signs of multimodality for males in all years and females in 2011 ($P < 0.001$, Table II) and were skewed to the left for males (negative $g1$ value, $P < 0.001$) but skewed to the right for females (positive $g1$ value, $P < 0.05$) (Table II).

Moulting and growth

In total, 155 male *Cancer irroratus* were recaptured, of which 34 had moulted (21%) (Table III). Nine females were recaptured, of which one had moulted. The proportion of moulted crabs, recaptured one year after being marked, ranged from 0 to 29% during the different sampling years. One crab was captured three times during the four-year study period and had, when considering the size increment in percentages, moulted at least twice (Table V). The probability for males to moult decreased with CW as shown by the logistic regression ($P < 0.001$, Figure 3). The mean inter-moult CW of crabs that had moulted was 8.9 cm and was 11.1 cm for those who did not moult. Among the recaptured male crabs, 27.5% had moulted after one year, 34.6% after two years, and the two recaptured after three years had both moulted (Table III).

The average moulting increment in CW of the marked and recaptured crabs was 2 cm (±0.33 SD), ranging from 1.2 to 2.6 cm (Table V), excluding a single individual who had grown by 3.4 cm over a two-year period. Assuming a normal distribution in growth rate the probability of observing such a large growth is about 1.1×10^{-5}. The size increment in percentage was independent of the body size (correlation test, $P > 0.05$) and varied from 5 to 26% after taking the intervals in years between moults into account (Figure 4a), based on Reilly's (1975) estimated annual

Table IV. Abundance estimates of the Atlantic rock crab (*Cancer irroratus*) in Kollafjörður, southwestern Iceland in 2011, 2012 and 2013.

Years (period)	Function	Model	Open/closed population	Abundance with CI	AIC
Within year					
2011	*closedp*	Mt	Closed	13,603 (10,213–18,726)	155.003
2012	*closedp*	Mt	Closed	154,443 (88,366–307,165)	85.518
2013	*closedp*	Mt	Closed	55,556 (35,039–95,992)	79.667
2011	*robustd.0*	M0	Mixed	22,001 (13,397–30,606)	92.402[a]
2012	*robustd.0*	M0	Mixed	106,591 (83,783–129,398)	92.402[a]
2013	*robustd.0*	M0	Mixed	61,919 (28,591–95,247)	92.402[a]
Over two years					
2011–2012	*G&S*	–	Closed	74,400 (53,800–107,200)	–
2012–2013	*G&S*	–	Closed	143,300 (103,000–208,000)	–
2013–2014	*G&S*	–	Closed	77,000 (49,000–131,000)	–
Overall years (whole dataset)					
2011–2013	*closedp*	Mth Chao	Closed	77,049 (63,660–94,590)	244.851
2011–2013	*openp*	–	Open	81,208 (41,723–120,686)	92.934
2011–2013	*robustd.0*	M0	Mixed	106,591 (83,783–129,398)	92.402[a]

[a]Based on a single model across years, including all the data.

The estimates were based on mark-recapture over a single period *G&S*: (Gazey & Staley 1986) and on logistic regression over the sampled periods based on (1) closed function (*closedp*) within years, (2) open function (*openp*) over years and (3) mixed open and closed function (*robustd*) within and over years. Best models for closed populations were M0 (no source of variation), Mt (temporal effect), and Mth (temporal effect and heterogeneity between units) (Baillargeon & Rivest 2007). Abundance is given with 95% confidence intervals (CI). The lowest Akaike information criterion (AIC) indicates the best estimate.

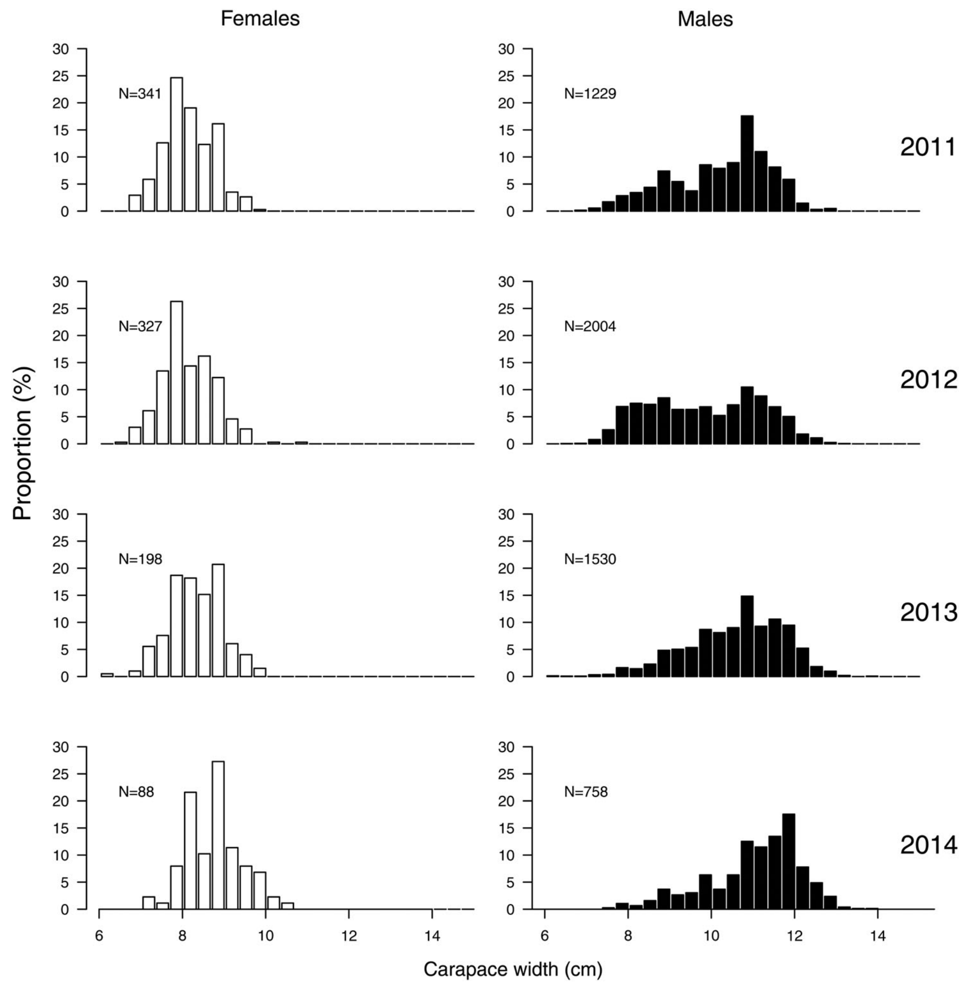

Figure 2. Size (CW) distribution of the Atlantic rock crab (*Cancer irroratus*) in Kollafjörður, south-western Iceland in the years 2011–2014. There were five sampling trips in 2011–2013 (100 traps per year) and three trips in 2014 (60 traps). The number of individuals of each gender caught each year is shown.

moult cycle for *C. irroratus*. Considering solely the individuals that were recaptured after one year, two groups are observed, one larger with increments from about 20 to 26% per moult and one with three individuals with lower increments of about 15% (Figure 4a). The observed increment of crabs recaptured after two and three years (Figure 4b) corresponds to the annual increment presented in former studies (Haefner & Van Engel 1975; Reilly 1975), indicating one moult during the period (except for a single individual, marked with [b] in Table V). Similar patterns are observed for the adjusted values as for the individuals recaptured after one year (see Figure 4a), where 12% in total showed the lower proportional increment in size (Figure 4b).

Discussion

The rock crab, *Cancer irroratus*, was most likely introduced into Icelandic waters no later than 1998 or 1999 via ballast water, and the species is now thriving well in its northernmost habitat in the Atlantic Ocean (Gíslason et al. 2014). Our study further supported the suggestions of Gíslason et al. (2014) and Jónasson & Gíslason (2014) that the rock crab is now established in the Icelandic coastal ecosystem.

Population density estimates for *C. irroratus* in its native range have been based on various methods, including transect counts with divers and trap catches (Scarratt & Lowe 1972; Miller 1989; Wells et al. 2010), marking and recapturing by engraving numbers on the carapace of *C. irroratus* from trap catches (Drummond-Davis et al. 1982) and trawl surveys (Hanson et al. 2014). T-bar tags have not been used previously in studies on *C. irroratus* but have been successfully used to tag other decapods such as the Dungeness crab *Metacarcinus magister* (Dana, 1852) (Diamond & Hankin 1985; Smith & Jamieson 1991; Taggart et al. 2004; Hildebrand et al. 2011) and *Paralithodes camtschaticus* (Windsland et al. 2013).

Table V. Size (CW) difference of marked and recaptured Atlantic rock crabs (*Cancer irroratus*) in Kollafjörður, southwestern Iceland after moulting.

Gender	CW_{2011} (cm)	CW_{2012} (cm)	CW_{2013} (cm)	CW_{2014} (cm)	Increment	
					cm	%
F	7.3		8.5		1.2	16.4
M	7.5	9.2		11.8	1.7 | 2.6	22.7 | 28.3
M	8.3	10.4			2.1	25.3
M	8.3		10.3		2.0	24.1
M	8.4			10.2	1.8	21.4
M	8.6	10.7			2.1	24.4
M	8.7	9.9			1.2	13.8
M	8.7	10.9	10.9[a]		2.2	25.3
M	8.7	10.7			2	23
M	8.7	10.8			2.1	24.1
M	9	10.8		10.8[a]	1.8	20
M	9	11.2			2.2	24.4
M	9.1	11.1			2.1	22
M	9.1	11.2			2.1	23.1
M	9.3		11.6	11.6[a]	2.3	24.7
M	9.3	11.4			2.1	22.6
M	9.3		11.6		2.3	24.7
M	9.4		11.7		2.3	24.5
M	9.6	11.5			1.9	19.8
M	9.8		11.8		2.0	20.4
M	10.2			11.8	1.6	15.7
M		7.5		10.9	3.4[b]	45.3
M		8.3	10.3		2.0	24.1
M		8.5	9.8		1.3	15.3
M		8.6		10.5	1.9	22.1
M		8.7	11.0		2.3	26.4
M		8.8	10.1		1.3	14.8
M		8.8	10.7		1.9	21.6
M		8.8		10.9	2.1	23.9
M		8.8	10.9		2.1	23.9
M		9.1	11.1		2.0	22
M		9.3	11.3		2.0	21.5
M		9.5	11.7		2.2	23.2
M		9.5		11.7	2.2	23.2

[a]Same weight as in previous measurement.
[b]Likely moulted twice.
Crabs were tagged in 2011, 2012 and 2013 and recaptured in 2012, 2013 and 2014.

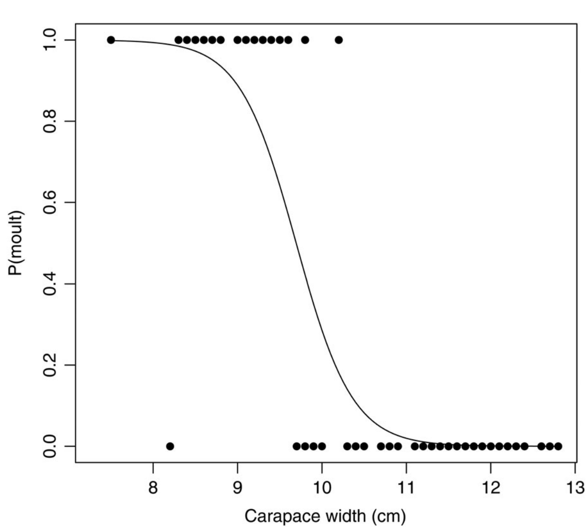

Figure 3. The probability of moulting for male Atlantic rock crabs (*Cancer irroratus*) with respect to size (CW) based on mark-recapture data from Kollafjörður, south-western Iceland during the years 2011–2014. The dots present observed values and the line indicates the prediction from a logistic regression.

Our study showed that *C. irroratus* is abundant in the study area in Kollafjörður, with the abundance of adult crabs around 107,000 individuals, giving an estimated density of around 0.5 crabs m^{-2}. This is high compared with the population densities reported for the crab in its native range. The highest densities reported by Scarratt & Lowe (1972) and Hanson et al. (2014) for *C. irroratus* on bedrock, gravel and sand bottom habitats in the Northumberland Strait were 0.04 and 0.03 crabs m^{-2}, estimated by observations of divers and catches in bottom trawls, respectively. In kelp and barren habitats in Nova Scotia, the highest densities were 0.09 and 0.095 crabs m^{-2}, obtained by divers and using traps, respectively (Miller 1989). The most similar densities to the present study were 0.5 crabs m^{-2} in a kelp forest in New England, estimated by divers (Wells et al. 2010). Fogarty (1976), however, reported a high density of 2.1 crabs m^{-2} on a sandy bottom substrate in Narragansett Bay, also obtained by divers. Previous studies in the sampling area and in the Hvalfjörður fjord, SW Iceland (Gíslason

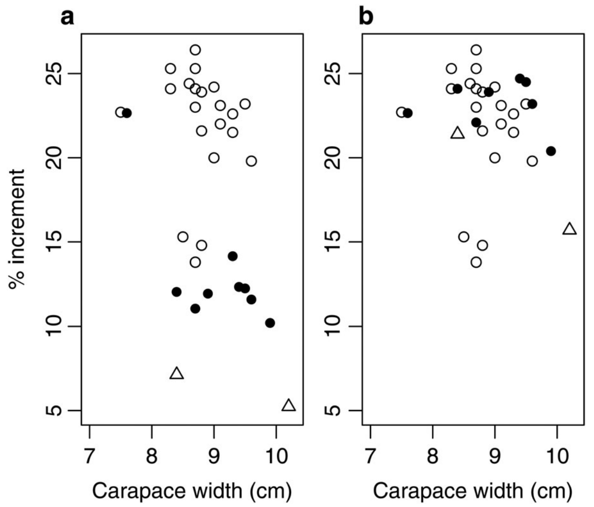

Figure 4. Per cent moulting increment for male Atlantic rock crabs (*Cancer irroratus*) in Kollafjörður, south-western Iceland. Different symbols refer to crabs marked and recaptured at intervals of one year (open circles), two years (filled circles) and three years (triangles). (a) Assumed annual moult increment (cm) (based on Reilly 1975). (b) Measured increment, assuming a single moult per time interval based on confirmed single moult increments in the present study and published moult increment data for *C. irroratus* (e.g. Haefner & Van Engel 1975; Reilly 1975).

et al. 2013a) based on observational counts by divers, were not successful since the number of crabs seen by the divers was less than 1% of the total crabs that were caught in traps. This could have been due to poor visibility, the habitat, patchy distribution and/or nocturnal activity of the crabs that may have been hiding in the soft bottom during daytime. Whether this can explain the large difference in the population density estimates between this study and studies from the native range is not known.

The mean carapace width (CW) in the present study was much larger than those measured in the studies mentioned above; 6.4 cm (Scarratt & Lowe 1972), 3.6 cm (Wells et al. 2010) and 6.2 cm (Fogarty 1976), with only 4.2% of the Icelandic individuals smaller than 8 cm. The females, which are in general smaller than the males, only counted for 14.9% of the total catch. The low proportion of small individuals and the skewed sex ratio toward males were consistent with previous studies in Iceland (Gíslason et al. 2014). Multimodality and skewness in size distributions varied over the years, which may indicate different cohorts or differences in intermoult time.

Crab traps can be size and sex-selective (Workman et al. 2002; Smith et al. 2004; Hernaez et al. 2012), and the trap fishing may also be affected by moulting, reproductive status, health condition of the animals and different habitat selection of juveniles and females compared with males. The much higher catch of male *C. irroratus* in the trap fishing in Iceland, as for some decapod species elsewhere, is presumably because the commercial traps used are more efficient at retaining larger crabs, which are predominantly males (Smith & Jamieson 1991; Workman et al. 2002). Trap selectivity is also thought to be affected by more aggression of larger individuals where smaller animals such as juveniles and females may have restricted entrance into the traps (Fischer & Wolff 2006). It is therefore likely that our population density estimate is cautious and presumably underestimated the population size in the study area because it mainly reflected mature individuals that were predominantly males. Furthermore, in comparison to other studies on decapods (Miller 1975, 1989; Melville-Smith 1986; Evans & Evans 1996; Aedo & Arancibia 2003), the estimated effective fishing area for *C. irroratus* in this study was substantially larger, which may indicate a conservative density estimate. It should be noted that compared with other *C. irroratus* studies in Iceland, the number of crabs per trap in this study was high, although a direct comparison can be difficult because of differences in the timing of the fisheries and the types of traps used. *Cancer irroratus* has become widespread in other areas in south-west and western Iceland (Gíslason et al. 2014; Jónasson & Gíslason 2014). In general, there are very limited studies on decapod crabs and on shallow water habitats in Iceland, making extrapolation of the current population density estimates difficult.

The effects of the occurrence of *C. irroratus* in the Icelandic marine ecosystem are still poorly known, although it is likely that a large species like *C. irroratus* occurring in such high densities can have significant effects on its ecosystem. A proportional increase of larvae and adult *C. irroratus* has been observed in recent years, compared with the other crab species, *Hyas araneus* and *Carcinus maenas*, living on shallow-water soft-bottom substrates in south-western Iceland (Gíslason et al. 2014). Comparative population density studies on *C. irroratus* and *C. maenas* in North America on various substrates have shown that these species overlap and are found in the highest densities on sandy bottom substrates (Fogarty 1976). A study by Bélair & Miron (2009) showed the potential coexistence between both species, although *C. maenas* is considered to be the most aggressive and generally the fittest compared with *C. irroratus* and *H. araneus*, and it is listed among the most successful alien species in the world (Klassen & Locke 2007). However, *C. maenas* is smaller and not considered as adapted to cold water as *C. irroratus* (Bélair & Miron 2009) and *H. araneus* (Anger 1983), which may inhibit *C. maenas* feeding (Berrill 1982) and moulting (Audet et al. 2003) in cold regions. Whether it is the reproductive success, high genetic variation, size advantage over the native species, use of an open niche and/or adaptation to the soft-bottom substrates that make *C. irroratus* more abundant in such habitats in Iceland (Gíslason et al. 2014), it is clear that *C. irroratus* has been successful in establishing a population in Iceland.

Crustaceans grow by moulting, but the moulting frequency varies considerably among species, sex and size classes (Vogt 2012). Adult *C. irroratus* females generally mate following moulting in the period between the summer and winter solstice when the photoperiod is decreasing (Krouse 1972; Scarratt & Lowe 1972). Moulting of adult males occurs from November to mid-March, when bottom-water temperatures are decreasing (Scarratt & Lowe 1972; Haefner & Van Engel 1975). Previous moulting information for *C. irroratus*, with size-increment data, have mainly been gathered in laboratory studies (Haefner & Van Engel 1975; Reilly 1975). The field studies have all been conducted by divers that either observed the moulting, or captured the crabs together with their recently cast shells (Scarratt & Lowe 1972; Reilly 1975). Reilly (1975) reported size increments for 33 field- and 191 laboratory-moulted male and female *C. irroratus*; field pre-moults ranged in size from 1.6 cm to 5.9 cm CW and laboratory pre-moults ranged from 1.2 cm to 6.9 cm CW, with an average size increment from 25 to 42% that was inversely proportional to size. Haefner & Van Engel (1975) reported size increments of 125 laboratory-moulted male *C. irroratus*; pre-moults ranged in size from 5.1 to 11 cm CW, with an average size increment of 21%. Because the pre-moults in our study ranged from 7.3 to 10.2 cm CW, they add further information about the moulting increment of larger *C. irroratus* than that previously documented (Reilly 1975) and showed that the moulting increment percentage is independent of body size in the size range of crabs in the present study. The frequency of moulting varied within the study period from one to three year intervals. Smaller individuals were more likely to moult, indicating a prolonged intermoult phase with age, as seen for other species, such as *C. pagurus* (Bennett 1974), *Neohelice granulata* (Dana, 1851) (Luppi et al. 2004), *Paralithodes camtschaticus* (Nilssen & Sundet 2006) and *Halicarcinus planatus* (Fabricius, 1775) (Diez & Lovrich 2013). Most of the *C. irroratus* that we recaptured after one and two years had not moulted. Generally, male *C. irroratus* moult during winter (Reilly & Saila 1978), which agrees with our results, as newly moulted crabs were rarely observed in the present study (September). According to our data, intermoult periods generally span more than one year for crabs larger than 7.3 cm CW. This suggests that the lifespan of *C. irroratus* could be greater than former studies have reported (Reilly 1975), that is, with longer intermoult periods where moulting occurs every second year on average for larger crabs (>7 cm) instead of annually. The difference in intermoult periods for larger crabs observed in this study is most likely explained by genetic variation, which may also contribute to physiological differences between geographical regions (Darling et al. 2008; Tepolt et al. 2009). A recently developed technique to age crustaceans, which is based on reading growth bands in the gastric mills and eye stalks, is promising (Kilada et al. 2015) and could be used to answer questions about the lifespan of *C. irroratus*. Several species have been reported to have prolonged lifespans at higher latitudes, including the mud crab *Macrophthalmus banzai* Wada & K. Sakai, 1989 (Henmi 1993), the mole crab *Emerita brasiliensis* Schmitt, 1935 (Defeo & Cardoso 2002) and the northern shrimp *Pandalus borealis* Krøyer, 1838 (Koeller 2006; Nilssen & Aschan 2009). Longevity and growth rate might vary among populations within species because of lower temperature and may reflect acclimation or adaptation of the entire life history to different environments (Vogt 2012). The newly settled population of *C. irroratus* in Icelandic waters may provide an opportunity to study evolutionary responses to the habitat in isolation from the conspecifics in North America.

The approach using T-bar tags on *C. irroratus* is a relatively cheap and effective way to estimate its population density and individual growth. *Cancer irroratus* was found in abundances in Icelandic waters that are among the highest compared with those found in its native areas. Whether it is due to favourable environmental conditions, food availability or lack of predators and competitors remains to be seen. How this high population density will affect the Icelandic benthic ecosystem is a concern for further studies.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the University of Iceland Research Fund under grant nos. HI11090118 and HI14090070; Suðurnes Regional Development Fund under grant nos. 31/2011 and 21/2012; and the Icelandic Ministry of Fisheries and Agriculture under grant no. F 12 012-12.

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