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Publication details, including instructions for authors and subscription information:
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Diet and population biology of the invasive crab Charybdis hellerii in southwestern Atlantic waters

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Published online: 04 Jun 2015.

To cite this article: Bruno Sampaio Sant'Anna, Joaquim Olinto Branco, Michel Mattar de Oliveira, Harry Boos & Alexander Turra (2015): Diet and population biology of the invasive crab Charybdis hellerii in southwestern Atlantic waters, Marine Biology Research, DOI: 10.1080/17451000.2015.1024134

To link to this article: http://dx.doi.org/10.1080/17451000.2015.1024134

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Marine Biology Research, 2015
http://dx.doi.org/10.1080/17451000.2015.1024134

ORIGINAL ARTICLE

Diet and population biology of the invasive crab *Charybdis hellerii* in southwestern Atlantic waters

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Abstract

For many species the population structure varies along latitudinal gradients, especially at the extremes of their distributions. This may apply to invasive species, whose ability to grow, reproduce, feed and compete is hypothesized to be lower at higher latitudes. A population of *Charybdis hellerii* was investigated on a rocky shore at Armação do Itapocoroy (Santa Catarina, 26° 40′–26°47′S and 48°36′–48°38′W), Brazil. The study was carried out over two periods to test the hypotheses that: (1) this population differs from other populations that presumably became established earlier and at lower latitudes; (2) the population parameters change over time (number and size of individuals and ovigerous females), progressively showing more indications of establishment; and (3) the diet overlaps with the native crabs. In total, 642 individuals were caught: 544 males, 55 females, and 43 ovigerous females. This population of *C. hellerii* is similar to others presumably established earlier and at lower latitudes on the Atlantic coast, with a predominance of larger males and a male-biased sex ratio. The population is reproducing, but the similarity in the population size and frequency of ovigerous females between periods may indicate that this population is encountering difficulty in increasing in size. The generalist diet was composed mainly of crustaceans, molluscs and algae, thus overlapping with other native crab species. Although the direct and indirect impacts of this invasive species were not assessed, the population parameters indicate that this population of *C. hellerii* is established and may act as a centre of dispersal to higher latitudes.

Key words: *Decapoda, establishment, Portunidae, reproduction, trophic ecology*

Introduction

The introduction of exotic species is among the impacts resulting from human activity; introduced species may modify the native populations and community structures, causing loss of biodiversity, mainly of native and endemic species (Stachowicz et al. 1999). Exotic species may also transmit diseases and even change the function of ecosystems, resulting in significant ecological and economical damage (Morán & Atencio 2006).

The number of invasive species is large and growing in high-diversity environments such as the coastal zone in Brazil (Lopes 2009). In these areas, shipping is the main route of accidental species introductions, via ballast water and fouling on the hulls of vessels (Bax et al. 2003; Lewis et al. 2003).

In the Brazilian marine ecosystem, nine species of decapod crustaceans were recorded by Lopes (2009), with the portunid crab *Charybdis variegata* (Fabricius, 1798) added in 2011 (Sant'Anna et al. 2012a). The first species of *Charybdis* recorded was *C. hellerii* (A. Milne-Edwards, 1867), an Indo-Pacific native occurring in the Mediterranean, East Africa, Red Sea, Persian Gulf, Pakistan, India, Andaman Sea, China, Japan, Malaysia, Singapore, Australia

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Published in collaboration with the Institute of Marine Research, Norway

(Accepted 18 February 2015)

and New Caledonia (Kathirvel & Gopalakrishnan 1974; Wee & Ng 1995). The route of introduction of this crab was probably through larval transport in ballast water (Carqueija & Gouvêa 1996; Dineen et al. 2001; Bezerra & Almeida 2005).

Inspection of the records of *C. hellerii* in the western Atlantic suggests a second hypothesis of introduction, by the Brazil Current, because the species was detected first in 1987 in Cuba (Gómez & Martínez-Iglesias 1990) and then in Venezuela in 1987 (Bolaños et al. 2012). In Brazil *C. hellerii* was first recorded in 1996 in the states of Alagoas, Bahia, Rio de Janeiro and São Paulo (Calado 1996; Carqueija & Gouvêa 1996; Tavares & Mendonça 1996; Negreiros-Fransozo 1996). Southern occurrences were reported in Santa Catarina (SC) in 1998 on the rocky shore of south Caieira da Barra Beach (27°48′S, 48°38′W) in Florianópolis (Mantelatto & Dias 1999), while in 2007 it was recorded at Pinheira Beach (27°51′S, 48°35′W), the southernmost area in the South Atlantic occupied by this crab (Boos et al. 2010).

Charybdis hellerii has characteristics of a potential invasive species, with a relatively long larval cycle of about 44 days, rapid growth and maturation, a carnivorous diet (Dineen et al. 2001) and multiple spawnings (Sant'Anna et al. 2012b). The wide distribution of localities where *C. hellerii* has invaded has motivated studies about its natural history (Dineen et al. 2001) and population aspects (Mantelatto & Dias 1999; Mantelatto & Garcia 2001; Bolaños et al. 2012) in western Atlantic waters. Recently, a comparative study by Sant'Anna et al. (2012b) that evaluated the abundance of *C. hellerii* and sympatric native species suggested that this invasive crab might cause the decline of populations of the native portunid crab *Cronius ruber* (Lamarck, 1818). However, few studies have discussed the effects of this crab on native species and environments. In addition, in spite of its widening distribution in southwestern Atlantic waters, no study has investigated its diet in an invaded area. The laboratory study of Dineen et al. (2001) indicated that *C. hellerii* is a generalist carnivore and therefore a potential competitor with native species.

Considering that population structure varies along latitudinal gradients, especially at the extremes of a species' distribution, one may suppose that tropical/subtropical invasive species may face greater difficulties in establishing themselves at higher latitudes. A population of *C. hellerii* was investigated close to its southernmost limit of distribution in the western Atlantic (26°47′S), to test the hypotheses that: (1) this population differs in the abundance of individuals, sex ratio, population size and sexual dimorphism from other populations that presumably became established earlier and at lower latitudes; (2) the population parameters, such as number of individuals and frequency of occurrence of ovigerous females, change over time and show more indications of establishment; and (3) this species might compete for food resources with the native crabs.

Material and methods

Animal sampling and population biology analysis

The crabs were caught in the intertidal zone of the rocky shore at Armação do Itapocoroy, SC, Brazil (26°40′–26°47′S and 48°36′–48°38′W). The samples were taken monthly for two years, from September 2006 to August 2007 and from March 2010 to February 2011. Ten traps (ring nets 50 cm in diameter) with a 10 mm mesh were used. During sampling in the second period (2010–2011), the bait (fish) used in the traps was protected with a mesh to prevent the crabs from consuming it (Branco & Verani 1997).

In the laboratory, the crabs were identified (Lemaitre 1995) and sexed. After identification, the carapace width (CW) between the tips of the lateral spines was recorded with calipers (to 0.05 mm). The presence of mutilated or regenerating appendages was also recorded.

In the second period (2010–2011), the fecundity and diet were also studied. A total of 20 egg masses were used to determine the fecundity. Initially the egg mass was weighed wet (0.01 g) and then three subsamples of 0.01 g of the egg mass from each ovigerous female were submerged in water in gridded Petri dishes and counted under a stereomicroscope (Branco & Avilar 1992; Costa & Negreiros-Fransozo 1996). From the mean number of eggs obtained for the three subsamples, the total number of eggs was calculated by the simple rule of three.

Statistical analysis and hypothesis

Population characteristics were described by statistical analysis and compared to literature records. Size-class intervals of 5 mm CW were determined and grouped by season to allow comparisons with the population biology of *Charybdis hellerii* studied in nearby populations (Mantelatto & Garcia 2001; Sant'Anna et al. 2012b). The Komolgorov–Smirnov (KS) test was used to evaluate the normality of the size–frequency distribution of *C. hellerii* for each study period, and their sizes were compared between sexes (males, females and ovigerous females) using the Kruskal–Wallis test, complemented by the Dunn test. Departures from the expected sex ratio of 1:1 (M:F) were evaluated using the chi-square test. The possible differences in the proportion of mutilated crabs among males, females and ovigerous females were also evaluated with the chi-square test. A significance level of $P < 0.05$ was adopted for all tests.

The second hypothesis, that population parameters change over time, progressively showing more indications of establishment such as increases in the number and size of individuals and ovigerous females, was investigated comparing the data sampled in the two study periods: 2006–2007 and 2010–2011.

Diet was investigated assessing the items consumed by *C. hellerii* in the second study period, when the bait (fish) used in the traps was protected with a mesh to prevent the crabs from consuming it, preventing any effect on the gut contents. Prey items were identified to the lowest possible taxonomic level, under a stereo microscope. Unidentifiable items in an advanced stage of digestion were designated as non-identified organic matter. The prey items were analysed by the point method and by frequency of occurrence (Hynes 1950; Williams 1981; Wear & Haddon 1987; Haefner 1990), complemented by the feeding index (Kawakami & Vazzoler 1980; Branco & Verani 1997). Sand was not included in the analysis, and the diet was analysed for both sexes together (Wear & Haddon 1987; Branco & Verani 1997). The diet of *C. hellerii* at this beach was compared with published data for native crabs.

Results

Population biology

A total of 642 individuals of *Charybdis hellerii* were caught in the two study periods: 544 males, 55 females and 43 ovigerous females. Following the first hypothesis, that the size of individuals differed between the sexes (H = 138.15; DF = 2; P = 0.0001), males were significantly larger than females (Z = 10.35; $P < 0.05$) and ovigerous females (Z = 6.40; $P < 0.05$) (Table I). Non-ovigerous females were the same size as ovigerous females (Z = 2.22; $P > 0.05$). The overall size–frequency distribution of the population differed from normality in the first (KS(MD) = 0.1104; N = 321; $P < 0.01$) and second periods (KS(MD) = 0.1475; N = 321; $P < 0.01$), with the curve skewed to the left, i.e. a predominance of large adult males (Figure 1). The size–frequency distribution differed from normality in both periods for males (2006–2007: KS(MD) = 0.1213; N = 271; $P < 0.01$; 2010–2011: KS(MD) = 0.1636; N = 273; $P < 0.01$). The size–frequency distributions of females (2006–2007: KS(MD) = 0.1711; N = 27; $P > 0.05$; 2010–2011: KS(MD) = 0.1858; N = 28; $P > 0.05$) and ovigerous females (2006–2007: KS(MD) = 0.0976; N = 23; $P > 0.05$; 2010–2011: KS(MD) = 0.1642; N = 20; $P > 0.05$) did not differ from normality (Figure 1).

The seasonal size–frequency distribution showed the same pattern as the total population, with few juvenile crabs present and larger males more abundant in all seasons (Figure 2). The abundance of crabs

Table I. Number and size (carapace width in mm) of males, females and ovigerous females of *Charybdis hellerii* at Armação do Itapocoroy Beach, state of Santa Catarina, Brazil.

Sex	N	Min	Max	X ± SD
Males	544	22.1	80.9	62.4 ± 10.9
Females	55	10.9	70.9	42.0 ± 11.0
Ovigerous females	43	42.0	65.0	52.9 ± 6.3

N, number of individuals; Min, minimum; Max, maximum; X, mean; SD, standard deviation.

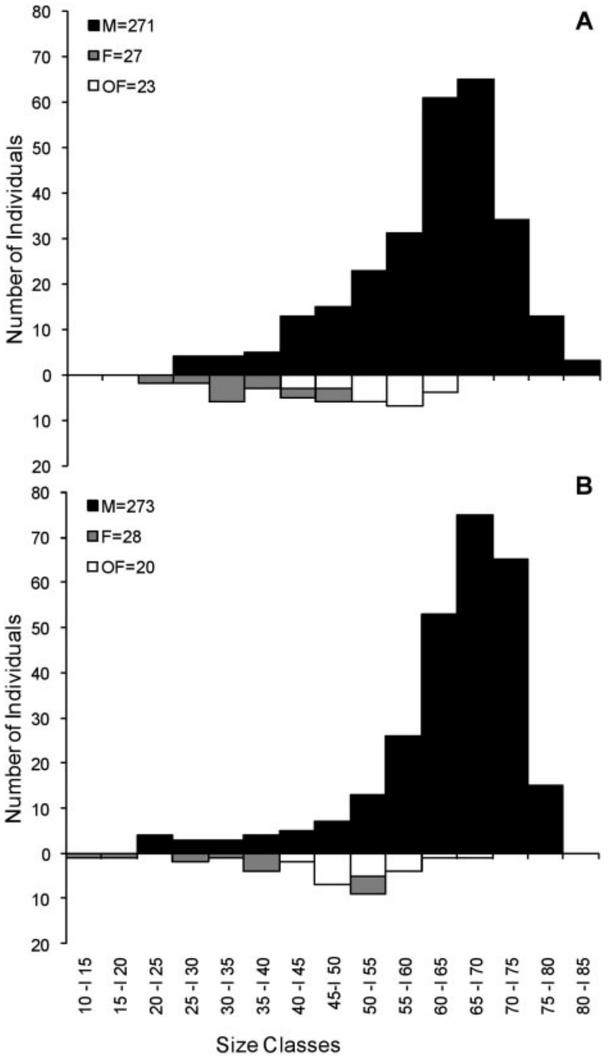

Figure 1. Size–frequency (mm) distribution of males (M), females (F) and ovigerous females (OF) of *Charybdis hellerii* caught at Itapocoroy, Santa Catarina, Brazil, in the first (A, 2006–2007) and second (B, 2010–2011) periods of study.

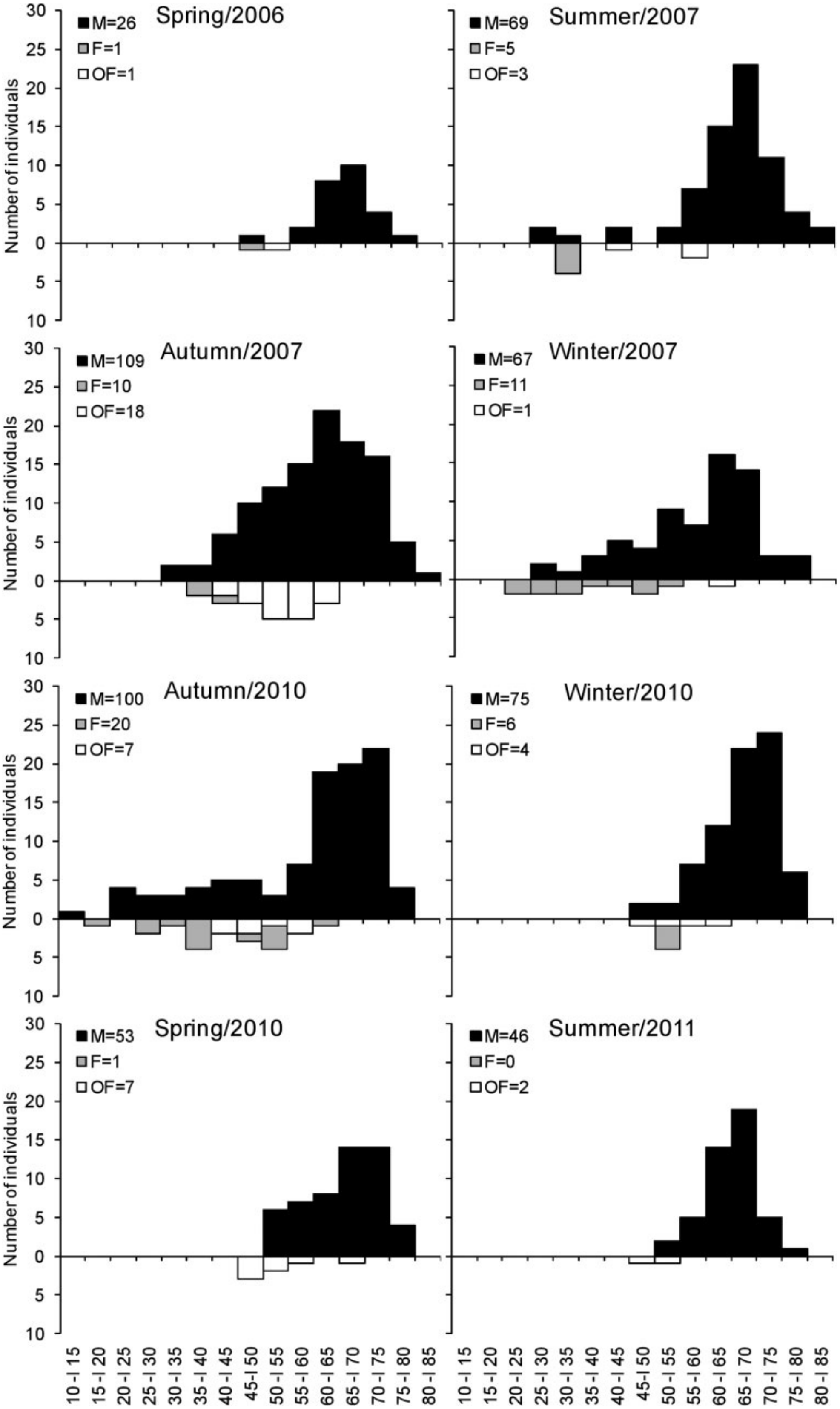

Figure 2. Seasonal size–frequency (mm) distributions of males (M), females (F) and ovigerous females (OF) of *Charybdis hellerii* caught at Itapocoroy, Santa Catarina, Brazil, in the first (2006–2007) and second (2010–2011) periods of study.

Table II. Seasonal and overall sex ratios for the population of *Charybdis hellerii* at Itapocoroy, Santa Catarina, Brazil, from September 2006 to August 2007 and March 2010 to February 2011.

Seasons	Males	Females	Total	Sex ratio (M:F)	X^2	P
Spring 2006	26	2	28	13.00	28.00	0.0001*
Summer 2007	69	8	77	8.63	48.32	0.0001*
Autumn 2007	109	28	137	3.89	47.89	0.0001*
Winter 2007	67	12	79	5.58	38.29	0.0001*
Total (2006–07)	271	50	321	5.42	152.15	0.0001*
Autumn 2010	99	28	127	3.53	39.69	0.0001*
Winter 2010	75	10	85	7.50	49.71	0.0001*
Spring 2010	53	8	61	6.63	33.20	0.0001*
Summer 2011	46	2	48	23.00	40.33	0.0001*
Total (2010–11)	273	48	321	5.69	15.71	0.0001*
Total	544	98	642	5.55	309.84	0.0001*

Spring = September, October and November; Summer = December, January and February; Autumn = March, April and May; Winter = June, July and August. *$P < 0.05$.

varied seasonally, peaking in autumn (Table II). The sex ratio (M:F) was always skewed toward males; the overall sex ratio (5.55:1; M:F) differed significantly from 1:1 ($X^2 = 309.838$; $N = 642$; $P = 0.0001$) and followed the same pattern in both periods (Table II). The seasonal percentage of ovigerous females was characteristic of continuous reproduction, with ovigerous females present in all seasons (Figure 3). The fecundity ranged from 32,000 to 215,800, with a mean of 109,132 ± 54,843 eggs, and showed a tendency to increase with female size (Figure 4). The mutilation rates were 15.50% for males, 11.11% for females and 13.04% for ovigerous females, with no significant difference among these groups ($X^2 = 0.4426$; DF = 2; $P > 0.05$).

The population is clearly established; however, the overall abundance of individuals did not increase between study periods ($N = 321$ in 2006–2007 and $N = 321$ in 2010–2011), nor did the abundance of ovigerous females ($N = 50$ in 2006–2007 and $N = 48$ in 2010–2011).

Diet

The analysis of diet and investigation of the third hypothesis were based on 234 stomachs, of which 180 (76.9%) contained food. A total of 16 prey items composed the natural diet of *Charybdis hellerii* (Table III). Excluding organic matter, the most frequent prey were crustaceans ($N = 74$; FO = 24.66%), molluscs ($N = 62$; FO = 20.67%) and macrophytes ($N = 39$; FO = 13%). Based on the point method, the scores for prey items followed the same pattern of frequency of occurrence, with crustaceans, molluscs and macrophytes scoring highest

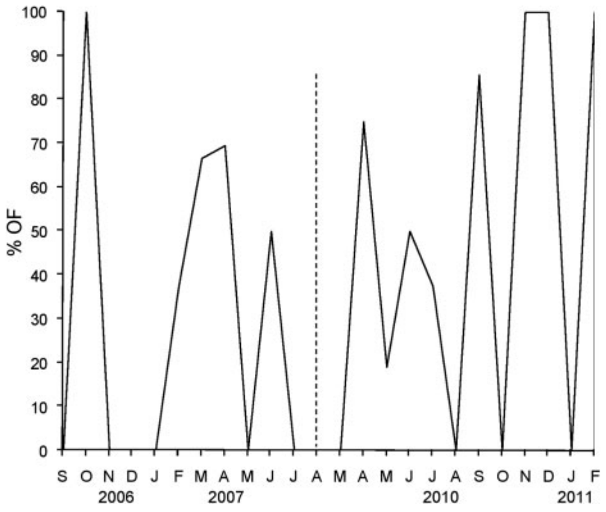

Figure 3. Monthly percentages of ovigerous females (OF) of *Charybdis hellerii* caught at Itapocoroy, Santa Catarina, Brazil, in the first (2006–2007) and second (2010–2011) periods of study.

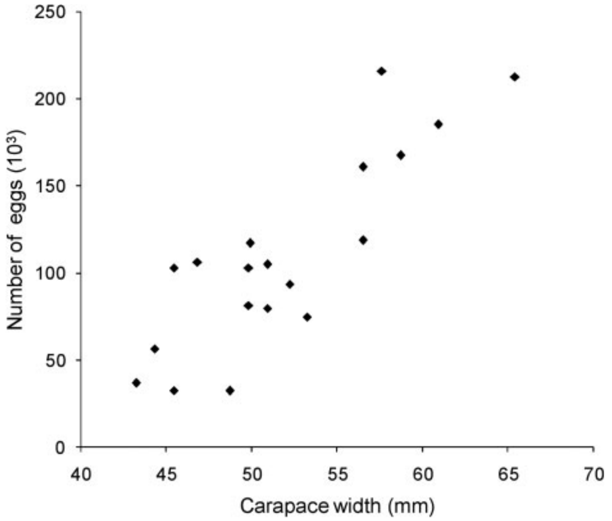

Figure 4. Fecundity of *Charybdis hellerii* caught at Itapocoroy, Santa Catarina, Brazil.

(Table III). In the feeding index (FI), the main prey items were maintained: crustaceans (FI = 0.23), molluscs (FI = 0.16) and macrophytes (FI = 0.12) (Table III).

Discussion

This is the first study to evaluate population aspects and diet of *Charybdis hellerii* on the southern Brazilian coast at a low latitude (27°48′ S), which is close to the southern limit of the distribution of this invasive crab in Atlantic waters. The size range of this population of *C. hellerii* is similar to those observed in other parts of the world (see Table IV), with a predominance of larger adult males and a male-biased sex ratio. This pattern was observed in other studies in Brazil (Sant'Anna et al. 2012b) and Venezuela (Morán & Atencio 2006), but differs from populations studied in Venezuela (Bolaños et al. 2012) and the USA (Dineen et al. 2001) where the sex ratio did not differ from the expected 1:1 proportion. As suggested by Sant'Anna et al. (2012a), the skewed sex ratio may be a sampling artefact because females tend to be cryptic and less active than males and, also, females may occur in different microhabitats than males. Small-sized and immature individuals, sampled in low abundance in the present study, may also prefer different microhabitats, as also suggested by Bolaños et al. (2012).

According to Fisher's theory, the expected sex ratio is 1:1 (males to females) (Fisher 1930). In many cases, Fisher's model is sufficient to explain the population sex ratio, but there are many exceptions to equal investment that are explained by other models in sex-allocation theory (Bull & Charnov 1988). A biased sex ratio may alter both male–male competition and female mate choice (Jirotkul 1999), as males tend to compete more intensively for mates because they have more potential competitors. Assuming that this male-biased sex ratio occurs in nature, it would explain the mutilation rate observed in this population (15%) and in other populations studied by Sant'Anna et al. (2012b), who observed that about 53% of males and 28% of females were mutilated, and by Morán & Antencio (2006), who found 47% mutilated individuals. This mutilation rate may also be due to competition for space and food, and for other reasons with native species.

In Portunidae, sexual dimorphism with males larger than females is common (Williams 1974; Pinheiro & Fransozo 1999; Araújo et al. 2012). This pattern was observed for *C. hellerii* both in the present study and in other populations (Morán & Atencio 2006; Sant'Anna et al. 2012b). The larger size of males is associated with the puberty moult, when metabolic energy is directed to somatic growth in males and to ovary development and growth in females (Hartnoll 1985). The larger size of males facilitates manipulation of the female during copulation (Santos et al. 1995) and protection of the female after copulation while the carapace is soft.

The seasonal size–frequency distribution pattern of *C. hellerii* was consistent in both periods, with higher abundances in autumn. The same pattern was observed in the population of *C. hellerii* studied in São Paulo by Sant'Anna et al. (2012b). The native crab *Callinectes danae* Smith, 1869 has an inverse pattern, with higher abundances in warmer seasons

Table III. Prey items of the invasive crab *Charybdis hellerii* at Itapocoroy, Santa Catarina, Brazil.

Prey items	*N*	FO (%)	PM	%	FO (%) × PM (%)	Feeding index
Macrophytes	39	13.00	593	13.28	172.62	0.122924
Foraminiferans	1	0.33	6	0.13	0.04	0.000032
Poriferans	2	0.67	3	0.07	0.04	0.000032
Cnidarians	2	0.67	55	1.23	0.82	0.000585
Molluscs						
Gastropods	37	12.33	620	13.88	171.22	0.121930
Bivalves	25	8.33	321	7.19	59.90	0.042654
Polychaetes	14	4.67	515	11.53	53.81	0.038322
Crustaceans						
Penaeids	1	0.33	45	1.01	0.34	0.000239
Carideans	1	0.33	20	0.45	0.15	0.000106
Portunids	1	0.33	85	1.90	0.63	0.000452
Xanthids	7	2.33	221	4.95	11.55	0.008223
Brachyurans (unidentified)	60	20.00	714	15.99	319.75	0.227702
Amphipods	1	0.33	80	1.79	0.60	0.000425
Eggs	3	1.00	11	0.25	0.25	0.000175
Fish (Actinopterygii)	19	6.33	299	6.70	42.40	0.030195
Organic matter	87	29.00	878	19.66	570.13	0.406004
Total	300	100.00	4466	100.00	1404.246903	1.0000

N, number; FO, frequency of occurrence; PM, point methods.

Table IV. Size (carapace width in mm) of *Charybdis hellerii*, according to latitude, in invaded areas of the Atlantic Ocean.

Country	Approximate latitude	Males		Females		Author
		X	MS	*X*	MS	
USA	27°51′N and 26°46′N	–	79.0	–	77.0	Dineen et al. (2001)
Colombia	11°19′N and 12°13′N	68.4	74.2	–	55.6	Campos & Turkay (1989)[c]
Venezuela	11°35′N and 12°15′N	71.2	83.2	65.6	67.6	Morán & Atencio (2006)[a]
Brazil	22°54′S and 23°01′S	75.0	–	62.0	–	Tavares & Mendonça (1996)
Brazil	23°23′S	45.4	64.9	35.5	51.6	Mantelatto & Dias (1999)
Brazil	23°23′S and 23°31′S	40.8	64.7	29.9	50.3	Mantelatto & Garcia (2001)
Brazil	23°58′S	56.4	72.7	45.7	63.1	Sant'Anna et al. (2012a)
Brazil	25°50′S	40.54	56.54	–	–	Frigotto & Serafim-Junior (2007)[d]
Brazil	26°40′S	62.4	80.9	42.0	70.9	Present study
Brazil	27°48′S	63.3	72.2	–	–	Mantelatto & Dias (1999)[b]
Brazil	26°46′S and 27°51′S	65.0	80.2	47.4	51.0	Boss et al. (2010)

X, mean; MS, maximum size.[a]Only three adult crabs were investigated; [b]excluding lateral spines; [c]only six males were investigated; [d]only four males were caught.

(Chacur & Negreiros-Fransozo 2001; Sant'Anna et al. 2012c). Probably the abundance of native portunid species in warmer seasons increases competition with the introduced crab *C. hellerii*, which reduces its activity at this time of year and is not attracted by bait.

In populations of *C. hellerii* studied by Mantelatto & Garcia (2001) and Sant'Anna et al. (2012b), reproduction continued year-round, with a higher incidence of ovigerous females in the winter and spring, the inverse period of reproduction of the native portunid crabs. As observed by Bolaños et al. (2012) in the Caribbean Sea, and in the present study, the reproduction of *C. hellerii* was continuous, with very low intensity during the year. Thus, this invasive crab seems to adapt its reproductive cycle to local conditions, suggesting that it is not completely subjected to an endogenous control, differently from other swimming crabs (Sant'Anna et al. 2012c). Although ovigerous females occurred throughout the year, recruitment was very low during the study period. As suggested by Bolaños et al. (2012), the location of larval settlement may differ from the preferential habitat of larger juveniles and adult crabs, or the low occurrence of juveniles may also be due to the specificities of the sampling method.

Sympatric native portunid crabs from the Brazilian coast such as *C. danae* and *Callinectes ornatus* Ordway, 1863 have a high reproductive potential, with fecundity measured at 598,885, 826,638 and 811,267 eggs for *C. danae*, respectively (Branco & Avilar 1992; Costa & Negreiros-Fransozo 1996; Pereira et al. 2009) and 379,815 eggs for *C. ornatus* (Mantelatto & Fransozo 1997). The menippid crab *Menippe nodifrons* Stimpson, 1859 lives on Brazilian rocky shores in sympatry with *C. hellerii*, and its fecundity reached 212,00 and 348,442 eggs in two populations investigated (Oshiro 1999; Oliveira et al. 2005). Although *C. hellerii* has a lower reproductive potential than have native crabs, the fecundity observed in the present population is similar to that observed in its native location by Siddiqui & Ahmed (1992), indicating that in invaded areas, it has a high potential to colonize new areas and expand its distribution and population density.

Investigating the population of *C. hellerii* in the two periods 2006–2007 and 2010–2011, we hypothesized that the population would be more established in the second period. However, the abundance of individuals and ovigerous females remained the same between periods, suggesting that this population of *C. hellerii* has encountered some difficulties in growing. Invasion success can be facilitated when the native species' diversity is reduced (Lyons & Schwartz 2001); in other words, higher diversity in ecosystems increases the resistance of communities to invasive species, as stated in Elton's hypothesis (Elton 1958). The study of Stachowicz et al. (2002) demonstrated that this could occur because species differ in their temporal patterns of spatial occupation, and the presence of more species optimizes the use of the limiting resource of space. The difficulty of the invasive crab *C. hellerii* in increasing its population may be explained by competition with native species for space and natural resources (i.e. food) and by the capacity of the environment to support it, among other factors. In order to fully explain the success of an invasion, it is necessary to investigate the seasonal structure and diversity of the native community and the environmental characteristics associated with the invasive species, in this case *C. hellerii*.

The natural diet of *C. hellerii* in its native range is omnivorous (Williams 1979), but in invaded areas the diet has not been studied. The only information about the feeding of these crabs was obtained in the

Table V. Most frequent prey items in the diet of crab species that live in the same habitats as *Charybdis hellerii* on the Brazilian coast.

Species	Prey item							Author
	Crustacea	Fish	Mollusca	Polychaeta	Echinodermata	Algae	Porifera	
Callinectes ornatus Ordway, 1863	1	2	3	4	5	6	–	Branco et al. (2002)
Callinectes ornatus Ordway, 1863	1	4	2	6	3	5	–	Mantelatto & Christofoletti (2001)
Callinectes danae Smith, 1869	2	3	4	1	–	5	–	Branco & Verani (1997)
Menippe nodifrons Stimpson, 1859	2	8	1	3	6	4	5	Madambashi et al. (2005)
Charybdis hellerii (A. Milne-Edwards, 1867)	1	4	2	5	–	3	6	Present study

Numbers indicate the order of importance for each crab species.

laboratory, by Dineen et al. (2001), who found that *C. hellerii* is carnivorous if animal food is available. In the present study, excluding sand and non-identified organic matter, the diet of *C. hellerii* was composed principally of crustaceans, molluscs and algae, and smaller proportions of polychaetes and fish, i.e. an omnivorous diet. This omnivorous diet confers an advantage in colonizing new areas and indicates that this invasive crab can cause serious impacts on the native biota, principally in locations where it is increasing in abundance compared to native species. The diet of *C. hellerii* is similar to other sympatric native portunid crabs such as *C. ornatus*, *C. danae* and the rocky shore crab *Menippe nodifrons*, which feed on crustaceans, molluscs, polychaetes and algae, among others (see Table V).

The reproductive population recorded here indicates that *C. hellerii* has become established in this area. Its generalist diet is a matter for concern, considering the trophic-niche overlap with native species, which may cause direct and indirect impacts on species populations or the community. Considering that in some locations *C. hellerii* is more abundant than the native species (Sant'Anna et al. 2012b), these effects are ongoing and investigations of this invasive crab's impacts should be a priority.

Acknowledgements

We thank Dr Janet W. Reid (JWR Associates) for revising the English text.

Funding

The authors thank the National Council of Technological and Scientific Development (CNPq) (grants no. 308390/2012-1; 305799/2012-6) (AT and JOB, respectively), and the Centro Nacional de Pesquisa e Conservação da Biodiversidade Marinha do Sudeste e Sul, for support during sampling. This paper was partially supported by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (Ibama) (Project 'Biologia reprodutiva da espécie exótica invasora Charybdis hellerii na Enseada de Itapocoroi, SC') and the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

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Editorial responsibility: Ingo Wehrtmann