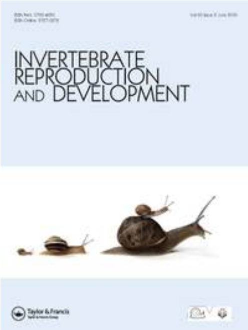

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Reproductive biology of the South American endemic hermit crab *Isocheles sawayai* (Crustacea, Anomura) from the Southern coast of Brazil

Gilson Stanski and Antonio Leão Castilho

NEBECC (Group of Studies on Crustacean Biology, Ecology and Culture), Departamento de Zoologia, Universidade Estadual Paulista, Botucatu, Brazil

ABSTRACT
The goal of this study was to investigate the sex ratio, structure and reproductive biology of *Isocheles sawayai*, a hermit crab captured as bycatch in a non-selective shrimp fishery. The animals were collected from July 2010 to June 2011. Out of the 575 individuals found, the majority were concentrated near the coast with a predominance of silt and clay in the sediment and warmer water. The mean length of males was 7.5 mm, which was larger than that of females (5.5 mm). The sex ratios were male-biased, except in November. The reproductive period was seasonal, with a peak during the spring, mainly in November, when 95% of the total ovigerous females were recorded. Our results suggest different habitat preferences exist according to sex; males prefer coastal regions and females prefer intertidal zones. However, the data demonstrated that both sexes utilised the same coastal regions in the reproductive period, mainly in November. A higher intensity of rainfall was observed in the spring (October, November and December), and early summer, which probably promotes the transport of coastal organic materials, and creates an excellent environment for the reproduction and subsequent larval development of benthic animals such as *I. sawayai*.

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KEYWORDS
Crustacea; Diogenidae; reproduction; mating behaviour

Introduction

Isocheles sawayai (Forest & Saint Laurent 1968) is an endemic hermit crab of the western south Atlantic, and occurs in Brazil, from Ceará (Northeastern Brazil) to Santa Catarina state (Southern Brazil), and Venezuela (Isla Margarita) (Nucci & Melo 2000). It is a benthic suspension feeder, which feeds on particulate matter and has a defence strategy of being partially buried in the sandy bottom (Negreiros-Fransozo et al. 1997).

Isocheles sawayai is captured as a significant bycatch of local shrimp fisheries and after trawling, these individuals and other bycatch species are returned to the sea either dead or moribund, especially in the case of one of the most widely exploited shrimp, *Xiphopenaeus kroyeri* (Heller 1862), which is found at depths greater than two metres (Costa et al. 2003; Branco et al. 2013). A bycatch consists of animals of any size or species captured together with the target species in the fishing trawl (Graça-Lopes 1996). Fishing is critical in southern Brazil; Santa Catarina has about 25,000 artisanal anglers, divided into 186 communities and affiliated with 38 fishing colonies, which represents 23% of the national fishing volume (Epagri/cepa 2010).

This great exploitation of *X. kroyeri* affects *I. sawayai* (Severino-Rodrigues et al. 2002); many animals are captured as bycatch during the reproductive period (ovigerous females) or in the juvenile stage, which represents a considerable loss for future generations and puts the maintenance of the species in the coastal region at risk. From the ecological point of view, *I. sawayai* is an important member of the marine food chain, serving as food for many species of invertebrates and fish (Severino-Rodrigues et al. 2002; Fantucci et al. 2009a).

Considering the ecological importance of the species, no studies exist on the reproductive period or population structure of *I. sawayai* on the southern coast of Brazil. Most studies on this animal are concentrated in São Paulo (Pinheiro et al. 1993; Negreiros-Fransozo et al. 1997; Fantucci et al. 2008, 2009a, 2009b). Therefore, it is necessary to study the reproductive biology, the parameters and important environmental conditions of *I. sawayai* on the south coast of Brazil. For hermit crabs, in addition to food availability, the presence of empty shells suitable for the protection of the soft abdomen is also essential, making this an indispensable resource (Sastry 1983).

Another important factor that should be investigated is the *I. sawayai* population structure, which is an important

CONTACT Gilson Stanski bio.gilson@hotmail.com

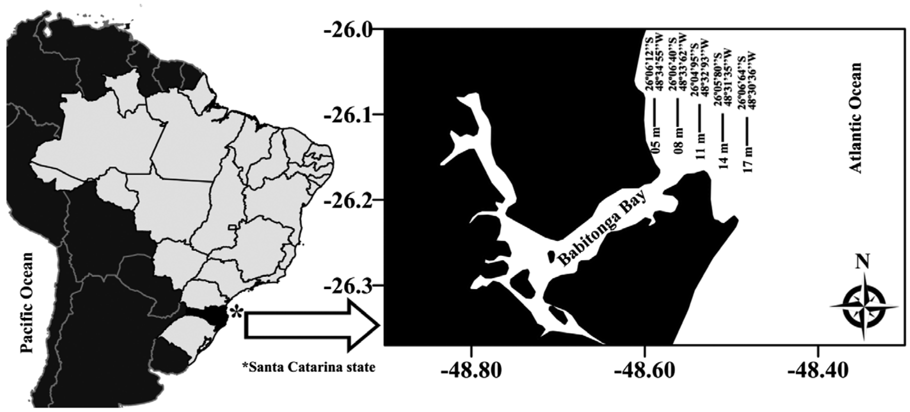

Figure 1. Map of the study area, highlighting the sampled stations in an area adjacent to Babitonga Bay, Southern Brazil (source: Grabowski et al. 2014).

tool in the study of different groups because it reveals the size range achieved by individuals, their frequencies and fluctuations over the different sizes, and therefore, the ecological stability of populations (Begon et al. 1996; Leite et al. 2003).

This study provides information on *I. sawayai* in an infrequently studied geographic region and will enable the observation of biological and ecological standards in this region. Therefore, the objective of this study was to characterise the population structure, sex ratio and reproductive period of the hermit crab *I. sawayai* near the southern limit of its geographic distribution.

Material and methods

In southern Brazil, Babitonga Bay contains an estuarine area surrounded by mangrove forests and an adjacent marine environment with a high conservation priority (MMA 2007), and is a leading candidate for the creation of a sustainable marine protected area (MPA) (Vilar et al. 2011; Grabowski et al. 2014).

Sampling

Hermit crabs and environmental factors were sampled monthly from July 2010 to June 2011 at five sampling sites parallel to the shoreline and at distinct depths (5, 8, 11, 14 and 17 m) in adjacent areas in Babitonga Bay (Figure 1). This bay is located on the northern coast of the state of Santa Catarina, and Joinville, Itapoá and São Francisco do Sul are nearby towns. The area has a rich fauna; previous studies have investigated crustaceans, fish, birds and aquatic mammals (Rodrigues et al. 1998; Grabowski et al. 2014), which were observed during our sampling periods.

Sediment was obtained using a Petersen grab. The samples were packed individually and were frozen, to minimise the loss of organic matter. In the laboratory, the sediment was dried in a 70 °C oven for 72 h. From each sample, a 100-g subsample was ash-weighed to determine the grain-size distribution. Sediments were sieved through 2-mm (gravel), 2.0–1.01-mm (very coarse sand), 1.0–0.51-mm (coarse sand), 0.50–0.26-mm (medium sand), 0.25–0.126-mm (fine sand) and 0.125–0.063-mm (very fine sand) meshes; smaller particles were classified as silt–clay (Suguio 1973; Håkanson & Jansson 1983).

Grain size categories followed the American standard, and fractions were expressed on the phi (φ) scale, i.e. using the formula $\varphi = -\log 2d$, where d = grain diameter (mm) (Tucker 1988), e.g. $-1 = \varphi < 0$ (very coarse sand); $0 = \varphi < 1$ (coarse sand); $1 = \varphi < 2$ (intermediate sand); $2 = \varphi < 3$ (fine sand); $3 = \varphi < 4$ (very fine sand) and $\varphi \geq 4$ (silt + clay). Finally, φ was calculated by plotting cumulative particle-size curves on a computer using the φ scale, with values corresponding to the 16th, 50th, 84th percentiles being used to determine the mean diameter of the sediment using the formula $Md = (\varphi\ 16 + \varphi\ 50 + \varphi\ 84)/3$. The organic matter content (%) was obtained by ash-weighing: three aliquots of 10-g each per station were placed in porcelain crucibles, heated for 3 h at 500 °C, and were then reweighed (Tucker 1988).

Bottom water samples were obtained using a Van Dorn bottle and salinity and temperature were measured using an optical refractometer and a mercury thermometer. Environmental data on rainfall were obtained monthly from Epagri/Ciram/Inmet (Centro de Informações de Recursos Ambientais e de Hidrometereologia de Santa Catarina, Itapoá city).

Reproductive and structural biology

In the laboratory, hermit crabs were identified, counted, carefully removed from their shells and measured (cephalothoracic shield length – CS length, mm). The sex was checked according to the gonopore position (based on

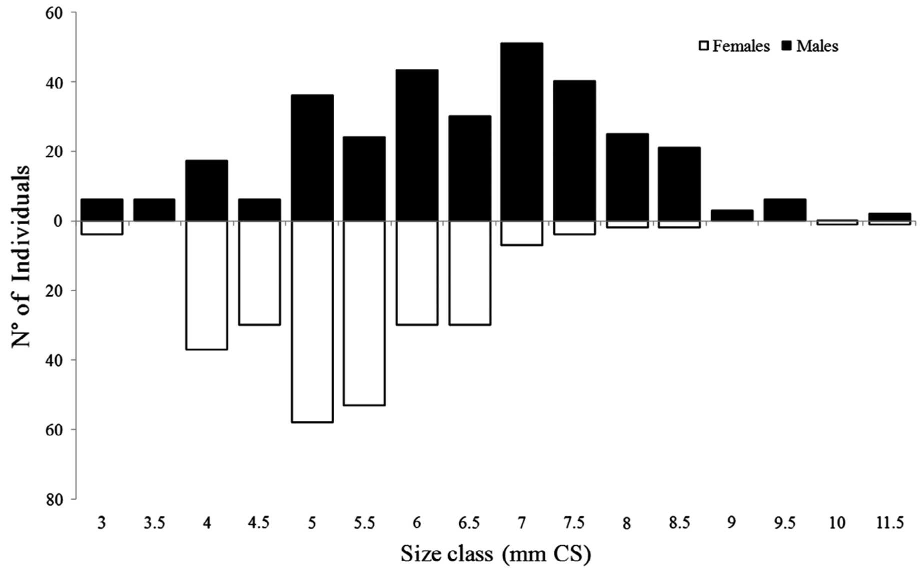

Figure 2. Frequency distribution by size classes of *Isocheles sawayai* collected monthly from July 2010 to June 2011 in an area adjacent to Babitonga Bay, southern Brazil.

the third or fifth pair of pereopods for females and males, respectively) (Melo 1999).

The reproductive period was described based on the frequency of adult females in the population that were incubating embryos (the presence of embryos attached to the pleopods) (Biagi & Mantelatto 2006). The juvenile recruitment was identified according to the period containing a higher frequency of individuals with a CS length less than that of the smallest ovigerous females (Biagi & Mantelatto 2006).

The sex ratio was estimated as the quotient between the number of males and females in samples from each month. Deviations from a 1:1 sex ratio were tested using a binomial test ($\alpha = 0.05$) (Wilson & Hardy 2002; Grabowski et al. 2014).

The normality of the CS length distribution data was checked using the D'Agostino-Pearson test. Sexual dimorphism in size (CS) in the size classes was tested using the Kolmogorov–Smirnov test (null hypothesis: equal distributions) (Zar 1996).

A redundancy analysis (RDA) was used to test the relationship between demographic class (males, females and ovigerous females) and environmental factors (Legendre & Legendre 1998). A previous analysis of the main demographic class showed a linear response in their abundance in relation to the environmental variables used; thus, the use of RDA allows a greater percentage of the variance to be explained regarding the canonical correspondence analysis (CCA), which is more suitable when there is a unimodal response (Gotelli & Elison 2011). The set of environmental variables used in the RDA calculations comprised bottom salinity and bottom temperature, organic matter content and the grain size of sediments. The routine Vegan was used, embedded in the software R (Development Core Team 2009). Tests for homoscedasticity (Levene tests) and normality (Shapiro–Wilk tests) were first performed as pre-requisites for the statistical test. Data were log-transformed prior to analysis (Zar 1996). All data-sets were normally distributed with homogeneous variances.

Results

Five hundred and seventy-five individuals were collected, 96% of which were sampled at a depth of 5 m: 156 females (27%), 103 ovigerous females (18%) and 316 males (55%). The animals presented a normal distribution of CS (D'Agostino-Pearson, $p > 0.05$), with the length varying from 3.05 to 11.8 mm in males, 3.2 to 10.2 mm in females, and 4.1 to 11.7 mm in ovigerous females. The mean size of the males was higher in the study area (Kolmogorov–Smirnov test, $p < 0.05$), demonstrating different sizes between the sexes. The mean CS of females and ovigerous females was 5.3 and 5.9 mm, respectively, and that of males was 7.5 mm (Figure 2).

The sex ratio of the population indicated a predominance of males over females (1:0.82, $p < 0.001$), except in November, when an equal ratio was found between the sexes (0.98:1, $p = 0.97$, Figure 3), due to a higher number of ovigerous females (Figure 4).

Ovigerous females were collected only from October to February, when the temperature was between 20 and 26 °C; at 22 °C, 80% of these animals were found, highlighting the seasonality of reproduction (Figures 4 and 5).

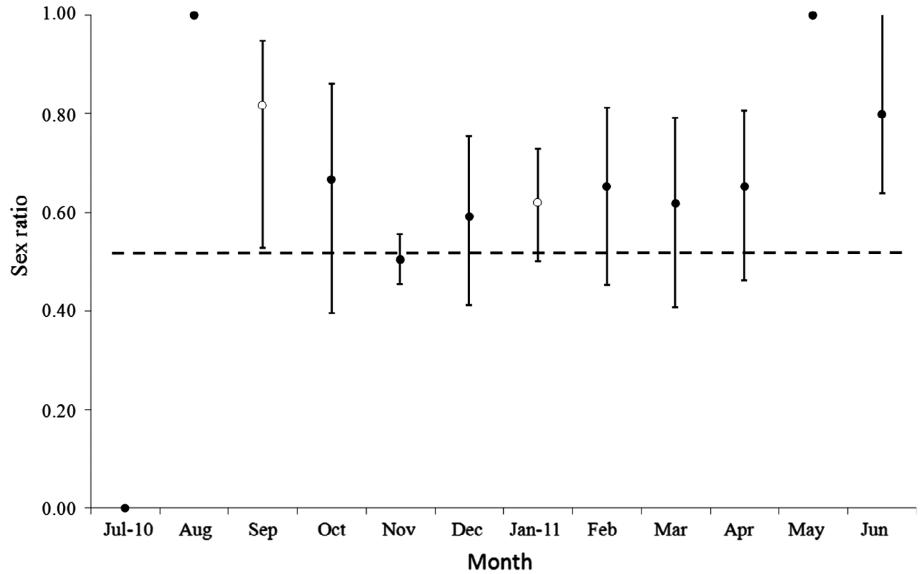

Figure 3. *Isocheles sawayai*. Monthly sex ratio (estimate ± standard error) of animals collected from July 2010 through June 2011 in an area adjacent to Babitonga Bay, southern Brazil. White circles indicate significant deviation from a 1:1 sex ratio (Binomial test, $p < 0.05$).

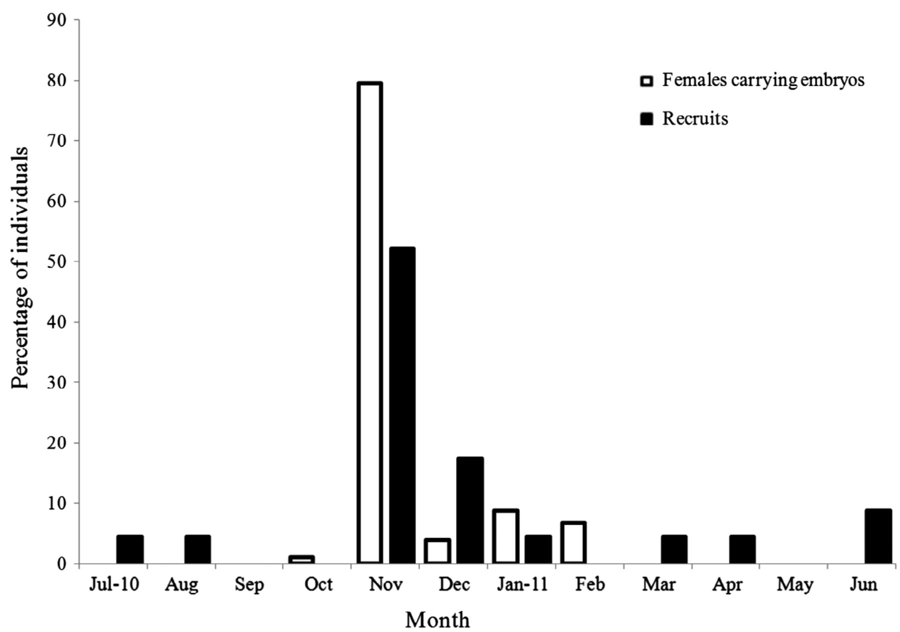

Figure 4. Distribution of ovigerous females and recruits of *Isocheles sawayai* from July 2010 to June 2011 in the region adjacent to the Bay Babitonga – SC.

The greatest intensity of recruits into the population was registered during November and January. In contrast, few recruits were collected in September and June (Figure 4). The water temperature began to increase in October, reaching a peak in February and the rainfall began to increase in the region in October (Figure 5).

The relationship between *I. sawayai* abundance and environmental factors shown by RDA is represented by the first and second axes in Figure 6. The first axis of the biplot graphic explains 55% of the total variance in the data, whereas the second axis explains 1.8%. The Monte Carlo test indicated that two canonical axes ($p < 0.05$) were significant: temperature correlated positively, and salinity correlated negatively (Figure 6 and Table 1).

Discussion

Isocheles sawayai is a species that is geographically distributed throughout tropical and subtropical regions and possesses breeding strategies that are adjusted to the regional

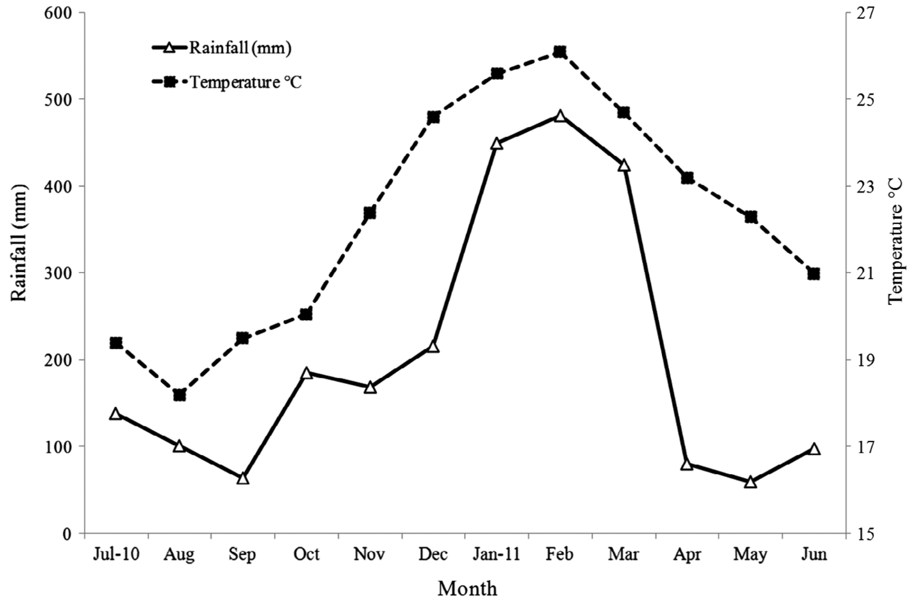

Figure 5. Bottom temperature variation in an area adjacent to Babitonga Bay, southern Brazil and monthly volume of rainfall from July 2010 to June 2011 in Itapoá-SC area. Source; Epagri/Ciram/Inmet.

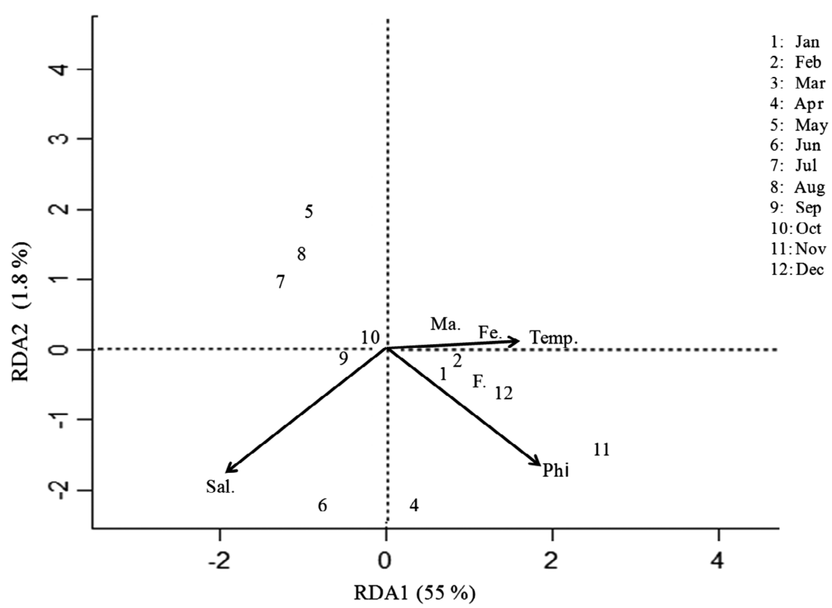

Figure 6. Redundancy Analysis (RDA), biplots illustrating the relationship between significant environmental variables and *Isocheles sawayai* (females = F, ovigerous females = Fe, males = Ma. and environmental factors, water temperature = Temp., sediment texture (ϕ) = Phi and water Salinity = Sal), collected in an area adjacent to Babitonga Bay, southern Brazil, from July 2010 to June 2011.

Table 1. Summary and results of the redundancy analysis of Isocheles sawayai (males, females and ovigerous females) and environmental variables collected from July 2010 to June 2011 in the region adjacent Babitonga Bay-SC (ϕ: Mean grain size). Significance was inferred using alpha ($p < 0.05$): 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1, p-values are based on 9999 permutations.

	RDA1	RDA2	R^2	*P*
Proportion explained	0.550	0.018		
Bottom temperature	0.655	0.028	0.325	0.045*
ϕ	0.682	−0.722	0.491	0.169
Bottom salinity	−0.614	−0.767	0.516	0.034*

environmental conditions, particularly water temperature, an important factor for the maintenance of gametogenesis, which varies considerably throughout the year in the subtropical region (Orton 1920; Thorson 1950). Thus, the population structure and reproductive periodicity of the species in subtropical regions differs from that observed in tropical ones.

Population structure

The size of *Isocheles sawayai* differed between the sexes, with males being larger, which is a common pattern found in hermit crabs (Negreiros-Fransozo & Fransozo 1992; Pinheiro et al. 1993; Garcia & Mantelatto 2001; Fransozo et al. 2002; Bertini et al. 2004; Galindo et al. 2008; Fantucci et al. 2009a).

The differential size between hermit crab sexes occurs primarily because they display different growth rates; males canalise all their energy exclusively into somatic body growth, whereas females direct part of their energy towards the production of eggs, which causes them to be smaller (Bertness 1981a; Abrams 1988; Sampaio et al. 2009).

Differences in body size might also be related to sexual selection; larger males are more successful in fighting for mates and in mating. In laboratory experiments with the hermit crab, *Diogenes nitidimanus* Terao (1913), larger males showed a greater reproductive success when mating with females. In addition to the body size, the size of the chelae also determines the hierarchy of these animals, and suggests that selection pressure leads to males being larger, which provides a greater possibility of success to offspring (Asakura 1987; Ayres-Peres & Mantelatto 2008).

According to Sant'Anna et al. (2008), male *Clibanarius vittatus* (Bosc 1802) hermit crabs are larger because they initiate growth approximately five months before the females. This can also occur for *I. sawayai* in this study, which explains why the intermediate classes contain more females than males; the constant low growth of females might be a result of the use of relatively small shells in nature (Litulo 2005).

The different size of the sexes can be beneficial for the population because it reduces competition for appropriate shells and consequently, avoids intraspecific competition and reduces the risk of death, since an animal without a shelter is much more susceptible to attack from predators (Abrams 1988).

As females select shells differently to males, they can exploit this feature for a longer time; they begin reproductive activity when they are still relatively young, as found in this study, when ovigerous females have a CS length of 4.1 mm. In contrast, females have a higher physical stress during the prolonged incubation of embryos in the same shell, as it is a risk to expose their offspring to predators when exchanging shelters. Thus, hermit crabs that use the same shell for a long time tend to show retarded body growth (Hazlett 1981).

Sex ratio

The predominance of males in the population of *I. sawayai* might be because a differential depth distribution exists between the sexes. In samples from shallow waters 5 m deep, the sex ratio of *I. sawayai* favoured males (the present study; Masunari et al. 2008; Fantucci et al. 2009a), whereas in intertidal samples in the Ubatuba region and in Venezuela, females were more abundant than males (Pinheiro et al. 1993; Galindo et al. 2008). However, during the reproductive period, the sex ratio approached 1:1. This balance in the sex ratio might be related to two factors. Firstly, where males and females share the same habitat, it might represent a strategy to increase the efficiency of reproduction. Secondly, the presence of the greatest number of females in November is related to a set of favourable environmental conditions, which include the availability of empty shells provided by marine currents or by the continent's water supply, as males demonstrate competitive predominance over females in obtaining shells (Bertness 1981b). Therefore, sharing of the same habitat only occurs when this resource is abundant. Furthermore, females are less active than males mainly in the breeding season, and an extremely thin substrate in this period as found in 5 m, encourages the burrowing of these animals (Negreiros-Fransozo et al. 1997), which reduces the risk of ovigerous females being preyed upon.

Reproductive periodicity

According to Fantucci et al. (2009a), the distribution limits and life stages of a species are determined by abiotic factors in the environment. However, some factors fluctuate more widely than others and consequently, more strongly influence the animal's life habits, such as reproduction, which in *I. sawayai* is directly related to water temperature and food availability. *Isocheles sawayai* clearly demonstrated features of a population with seasonal reproduction, with the presence of embryo-carrying females in spring (84%) and early summer. A seasonal reproduction pattern was also found by Fantucci et al. (2009a) for *I. sawayai* in Caraguatatuba (23° S, Brazil). However, the periodicity was higher than that in the present study, i.e. during the spring–summer and in the latter winter months. Thus, at a higher latitude (present study), a shorter reproductive period was observed, which is expected in subtropical regions that experience expressive variations in environmental parameters throughout the year (Thorson 1950).

Temperature plays several roles in the lives of hermit crabs, and can act as a metabolic, biochemical and hormonal modulator, triggering moulting and mating, and accelerating the development of the gonads. It also influences the duration of the larval stages (from birth to Megalopa), as observed in laboratory experiments with some species of hermit crabs of the genus *Pagurus*. At temperatures about 25 °C, complete larval development occurred within two weeks, whereas at 6 °C, development was prolonged for two months (Oba & Goshima 2004).

Shorter cycles of larval development in warmer periods of the year might explain the considerable presence of ovigerous females at temperatures around 22 °C in this study; a short development cycle decreases the exposure of larvae to predators and increases reproductive success. According to Negreiros-Fransozo and Hebling (1983), *I. sawayai* has a larval development cycle of about 28 days. Temperature also indirectly influences the availability of food, because warmer months tend to result in a higher primary productivity, which provides more suitable conditions for the development of larvae.

Crustacean females synchronise their reproductive period with the availability of food for their larvae in warmer seasons such as summer. During this period, nutrients in the waters are greatly enriched, mainly due to the transport of organic materials from the mainland to the coastal marine area by rain, which provides ideal conditions for primary production. Due to an increase in the population of phytoplankton, the zooplankton herbivore biomass rises and creates better conditions for the survival of the larvae of many benthic animals, which are ecologically favourable for the development of a new population (Asakura & Kikuchi 1984; Negreiros-Fransozo & Fransozo 1992; Pires-Vanin & Matsuura 1993; Meireles et al. 2006; Sant'Anna et al. 2009).

We found a large number of adult *I. sawayai* animals and few juveniles in the population. Thus, we propose that the larval settlement area and the initial juvenile stages of *I. sawayai* differ from that inhabited in adulthood. To develop to the Megalopa stage, hermit crabs seek protected areas with available food resources and mainly small empty shells, because it reduces the intraspecific competition for resources (Asakura 1991; Wada et al. 2000).

This hypothesis is supported by Fantucci et al. (2008), who studied *I. sawayai*, Fransozo and Mantelatto (1998), who studied *Calcinus tibicen* (Herbst 1791), and Turra and Leite (2000), who studied species of the genus *Clibanarius*, All authors also found few juvenile animals and attributed their low abundance to the migration of larvae after hatching to other local sites to complete their development.

The present study found that *I. sawayai* reproduces in periods that offer suitable conditions for the development of embryos, especially when the temperature of the environment is high – a factor that accelerates crustacean metamorphosis in the early stages and provides greater food availability, which is an essential condition for success after hatching.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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