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Population biology and breeding cycle of the burrowing shrimp *Callichirus seilacheri* (Decapoda, Callianassidae) from the eastern tropical Pacific

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ABSTRACT

Year-round continuous reproduction in tropical regions is an established paradigm in marine ecology. In this study, we tested this paradigm using the ghost shrimp *Callichirus seilacheri* from the tropical eastern Pacific as a model species. We also examined size-frequency distribution, sex ratio, and recruitment cycle to contribute to the biological knowledge of this species. To this end, a total of 456 individuals of *C. seilacheri* were collected during 12 months of sampling. Population structure was symmetrical for both sexes, and the overall sex ratio did not differ from evenness. Males outnumbered females in smaller size classes, though, revealing a potential sex-dependent mortality in small individuals. The breeding pattern followed the well-marked seasonal regime of the region, with ovigerous females registered during the rainy season. While natural variation in the seawater temperature had no influence on reproduction of this species, changes in water salinity possibly triggered the appearance of egg-bearing females in the population. Recruitment occurred throughout the year but was more intense during the dry season, following the appearance of ovigerous females. The adaptability of the life cycle of *C. seilacheri* to the seasonal climate provides further evidence that reproduction in tropical species is not always continuous.

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Introduction

Continuous (year-round) reproduction in the tropics versus seasonal reproduction in temperate environments has been considered one of a few well-established paradigms in marine ecology (Sastry 1983). This generalization, known as Orton's rule (Orton 1920), has been based on the statement that constant and elevated seawater temperatures characteristic of low latitude regions should favor continuous gonadal development and embryo production in the organisms living in these regions. Thorson (1950) suggested that factors other than constant temperature, such as stable plankton productivity for larval food, should also be considered as possible ultimate factor leading to continuous reproduction in marine organisms. Subsequent revisions of the reproductive biology of marine species have provided support to Orton's rule (e.g. Giese and Pearse 1974; Sastry 1983; Pearse et al. 1991; Clarke 1992; and references therein). There are many exceptions, however, to this model, including various tropical species of invertebrates that do not

exhibit the expected continuous reproductive pattern (e.g. ophiuroids: Hendler 1979; corals: Shlesinger and Loya 1985; sea urchins: Cameron 1986; decapods: Bauer 1992).

Although commonly related to temperate regions, seasonality of environmental factors can also be observed in tropical localities (Asnani 1993; McKnight and Hess 2000). For instance, in the eastern tropical Pacific from El Salvador to northern Panama, a clearly marked seasonal climate has been reported, with a dry tropical season from December to March/April followed by a rainy season from May to October/November (Amador et al. 2006). During the rainy season, the occurrence of intense rainfall decreases the salinity (from 33.1 to 9.8) of estuarine waters along the coast (Cortés 1997; Hernández et al. 2012), while during the dry season, the intensification of trade winds favors coastal upwelling (for details, see Brenes et al. 2003; Kessler 2006). During these upwelling events, occurring mostly from December to March, sea surface temperature drops from about 27–29°C to 20–22°C (Glynn et al. 1983; Jiménez 2001), with a subsequent increase in water salinity and primary production as a consequence of the strong north-east trade winds (Pennington et al. 2006). This suggests

that Orton's rule (1920) might not necessarily apply to all tropical regions, in particular to the Pacific coast of Costa Rica, where the climatic conditions are expected to drive a seasonal reproductive pattern in marine invertebrates instead of a prolonged breeding strategy.

A recent study of the breeding cycle of the intertidal ghost shrimp *Lepidophthalmus bocourti* (A. Milne-Edwards, 1870) has confirmed discontinuous (=seasonal) reproduction of this species from the Pacific coast of Costa Rica, with ovigerous females appearing only during the rainy season (Hernández et al. 2012). This suggests that different environmental factors other than temperature, such as salinity and primary production, may play an important role in determining reproductive activity in tropical environments. Although this is a well-known statement, we still need more studies on the breeding patterns of tropical species to improve our understanding on what conditions may drive the different reproductive strategies in marine invertebrates.

In this study, we are particularly interested in examining the reproductive biology of *Callichirus seilacheri* (Bott, 1955) (Callinassidae), one of the most abundant intertidal ghost shrimp species along the eastern tropical Pacific coast (Hernández et al. 2015). This species is distributed from the southern coast of Mexico to the central Pacific coast of Costa Rica (Ayón-Parente et al. 2014; Hernández et al. 2015), where it forms dense aggregations in the intertidal zone of sandy beaches (Felder 2001) and on tidal flats of estuarine areas (Hernández et al. 2015). Interestingly, in Costa Rica *C. seilacheri* is harvested intensely (up to 1200 shrimps collected per day) by local fishermen and sold as bait for recreational fishing (Hernández and Granda-Rodríguez 2015). This non-traditional fishery has intensified during the last decade due to the lack of employment opportunities for fishermen and the depletion of other traditional resources in the Pacific region of Costa Rica (e.g. penaeid, pandalid shrimps and coastal fish; Instituto Costarricense de Pesca y Acuicultura (Incopesca) 2006; Wehrtmann and Nielsen Muñoz 2009).

Although having considerable economic importance in many coastal communities in Central America, there is no available information about basic aspects of *C. seilacheri* life history, including population structure and reproductive biology, preventing the implementation of any sustainable management program for the conservation of this valuable decapod species. Two previous reports have provided information about the population biology and fecundity of *C. seilacheri* from northern Chile (Hernández and Wehrtmann 2007; Hernández et al. 2008), but a detailed morphological comparison between specimens from the Pacific coast of Central and South America demonstrated that the Chilean populations of *C. seilacheri* actually belong to *Callichirus garthi* (Retamal, 1975) (see Hernández et al. 2015).

Here, we examined the population biology (defined as population structure, sex ratio, breeding and recruitment cycle) of the ghost shrimp *C. seilacheri* from the Pacific coast of Costa Rica. Given the temporal variability in climatic and oceanographic conditions in this region (Amador et al. 2006), we expect a seasonal breeding and recruitment cycle in the *C. seilacheri* population, following the well-marked climatic regime of this tropical area. Additionally, we analyzed the fecundity (number of eggs) of this species and compared with data for other callinassid shrimps to better comprehend the reproductive strategies of these organisms. Therefore, this study provides valuable information about the life history of *C. seilacheri* and will be important to establish the baseline for future conservation protocols to regulate the stock and sustainability use of this valuable crustacean species.

Materials and methods

Study area and shrimp sampling

Specimens of *Callichirus seilacheri* (Figure 1(a)) were collected during monthly sampling from December 2011 to November 2012 in the intertidal zone at 'Mata de Limón' (09°55'12" N, 84°42'37" W), Pacific coast of Costa Rica (Figure 1(b)). The study site is a small and nearly flat area (~4 ha) exposed during low tide and composed primarily of fine sediment mainly originating from the Limón River (Figure 1(c)). We first established six linear transects perpendicular to the shoreline and separated by 80 m along the intertidal zone (Figure 1(c)). Then, we inspected the total area among transects (=4.49 ha = 0.04 km²) in search of burrow openings, from which we collected ghost shrimps using a hand-made 'yabby' pump (diameter = 55 mm, length = 100 cm). This is an efficient method for sampling organisms from intertidal burrows (Rodrigues 1966), and was used to pump each burrow up to five times. To obtain representative sample sizes for each month, we inspected all visible burrow holes in the sampling area since shrimp abundance at this site was relatively low (mean ± SD = 0.6 ± 0.47 burrows/m²) (P. Hernández unpubl. data).

Entrances to the burrows constructed by *C. seilacheri* are easy to identify at the surface of the beach because of their typical volcano shape (Figure 1(a) insert). Shrimp sampling was conducted in the morning when the temperature is milder because during high-temperature periods individuals tend to stay deeper in the burrow and, thus, out of reach of the pumping instrument (Hernández and João in press). Once collected, each shrimp was carefully rinsed with seawater, placed in a plastic bag and preserved in 80% ethanol until further examination at the laboratory. Additionally, the

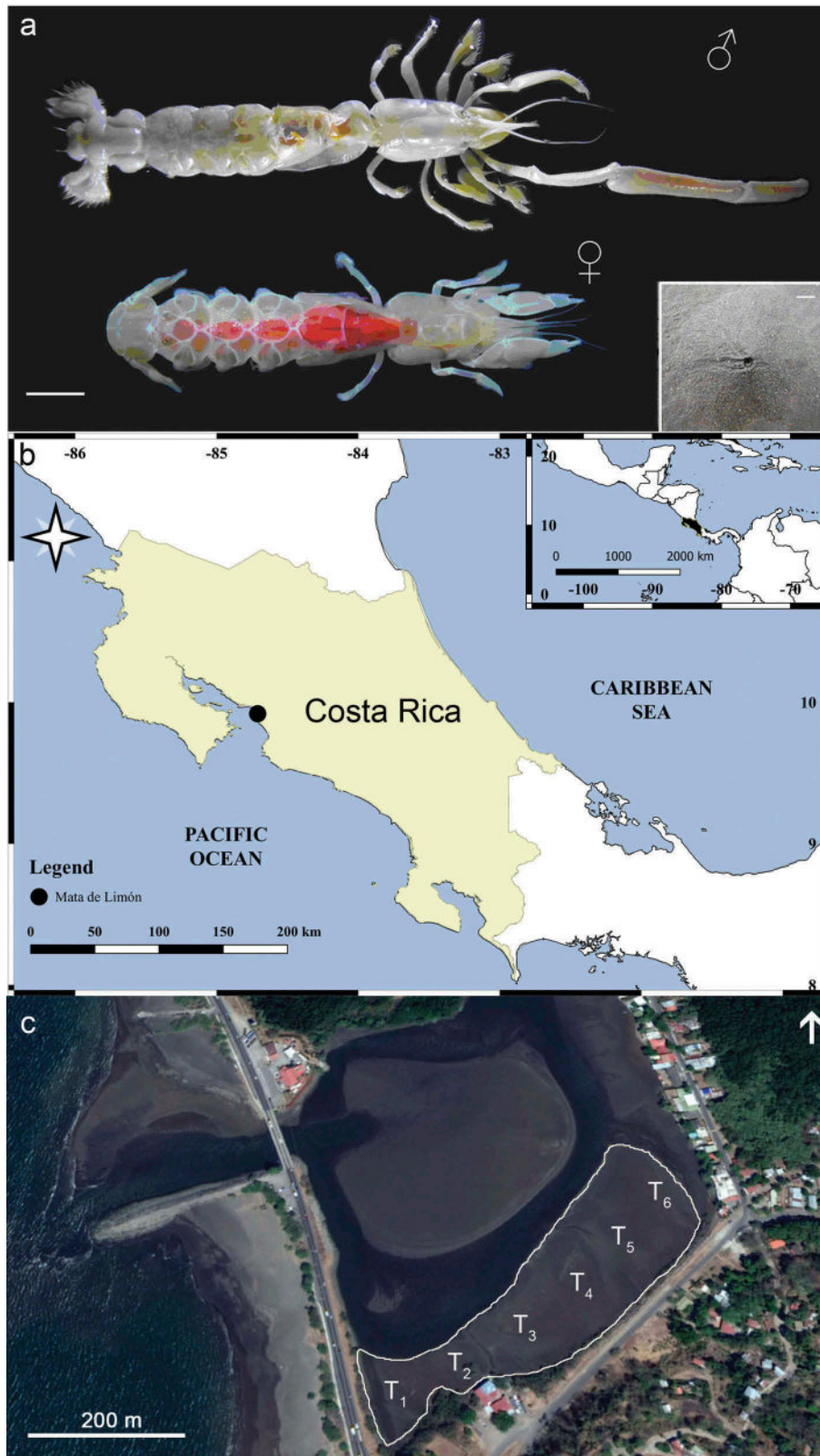


Figure 1. (a) Dorsal view of both male and female *Callichirus seilacheri*, scale bar = 1 cm; (b) geographic position of the study area of the Pacific coast of Costa Rica; (c) white enclosed area showing the intertidal zone at 'Mata de Limón' beach from which specimens of *C. seilacheri* were collected. The indented figure shows a burrow opening of *C. seilacheri* at the sampling site, scale bar = 5 mm.

monthly surface seawater temperature (SWT, $\pm 0.1^\circ\text{C}$) and salinity (Practical Salinity Scale) at the sampling site were recorded by a data logger (HOBO® U24-002-C). Part of the material analyzed in this study was deposited in the Museo de Zoología, Universidad de Costa Rica, Costa Rica (MZUCR 3337–01).

In the laboratory, each shrimp was sexed according to the morphology of the first pair of pleopods; Bi-segmented in males and tri-segmented in females (Hernández et al. 2018). Individuals were also classified as juveniles or adults based on the presence/absence of extremely asymmetric first chelipeds, which become larger and more massive in adult males but not in females or juveniles of both sexes, and the presence of coloured ovaries in adult females (orange or dark red ovaries, depending on the stage of development – Hernández et al. 2015, 2018). Additionally, females were classified as brooding or non-brooding according to the presence or absence of embryos carried beneath the abdomen, respectively. Developing eggs of ovigerous females were classified into three stages: ‘stage I’, characterized by rounded eggs with uniform yolk and no visible eye pigments; ‘stage II’, ovoid eggs with elongated and barely visible eye pigments; ‘stage III’, ovoid eggs carrying embryos with fully developed eyes and free abdomen. We used a stereomicroscope (Olympus® SZ 61) equipped with a graduated ocular micrometer to measure the cephalothorax length (CL, distance from the postorbital margin to the posterior margin of cephalothorax).

Sexual dimorphism, population structure, and sex-ratio

The occurrence of sexual dimorphism in *C. seilacheri* was evaluated by comparing CL values between sexes using a *t*-test, since distribution was normal and variances of the two groups being compared were homogenous. To examine the overall size frequency distribution of the sampled population, we constructed size–frequency histograms based on CL measurements for each sex, using 1 mm size classes and including the frequency of brooding females. The normal components of each histogram were separated by the Bhattacharya method and confirmed by NormSep routine (see FiSAT software – Gayanilo et al. 1996), with the identification of each modal component and the calculation of mean values for each cohort.

Sex ratio along ontogeny was analyzed for *C. seilacheri* to verify whether the ratio between sexes varied according to shrimp size and differed from the natural ratio (1:1) (Wenner 1972). For this purpose, sex ratio was estimated as the number of males divided by the total number of

individuals in each size class (1 mm) and was tested for deviations from an expected 1:1 sex ratio using a binomial test (Wilson and Hardy 2002). For this analysis, we considered 10 or more shrimps in each size class as an adequate sample size to calculate accurate sex-ratios. In case this condition was not fulfilled, shrimps were pooled into a subsequent or preceding size class until attaining the minimal number of individuals to ensure meaningful statistical analysis.

Breeding and recruitment pattern

The climatic regime of the Pacific coast of Costa Rica can be divided into a dry tropical season from December to March/April and rainy season from May to October/November (Amador et al. 2006). Based on this, we first divided the annual cycle into four different periods (‘early dry season’, from December to January; ‘late dry season’, from February to April; ‘early rainy season’, from May to July; and ‘late rainy season’, from August to November) and estimated the proportion of both ovigerous females and recruits of *C. seilacheri* for each period. The proportion of ovigerous females was calculated as the number of females carrying eggs beneath the abdomen relative to the total number of females (excluding those juveniles), whereas the proportion of recruits as the number of shrimps below 7.9 mm CL relative to the total number of shrimps. This threshold value was determined using the 10th percentile obtained from the overall size frequency distribution. Accordingly, the proportion of juveniles and adults in each period was also calculated. All the calculated proportions were compared separately among periods using chi-square tests and the Marascuilo procedure ($\alpha = 0.05$) to verify possible contrasts between and within multinomial proportions (Marascuilo and McSweeney 1977).

The average of seawater temperature and salinity were compared among periods using a one-way ANOVA, since there was a normal distribution and homogeneous variances among groups (Zar 2010). When there was a significant difference ($p < 0.05$), a Tukey ‘a posteriori’ test (Zar 2010) was used to establish the similarity between each pair of periods. The relationship between the surface seawater temperature (SWT) and salinity on the breeding pattern of ghost shrimps (here defined as the number of ovigerous females in each monthly sample) was evaluated through a negative binomial regression analysis, a common type of distribution used to model over-dispersed count data, in which the number of failure events do not tend to be infinite (Cameron and Trivedi 1998). We first performed a negative binomial regression analysis considering

both SWT and salinity as predictor variables. If one of the variables did not contribute significantly to model fitting, we reduced the model using a single predictor variable.

Reproductive parameters

A total of 30 egg-bearing females were found during the study period, 24 of which carried embryos in the early stage (stage I), two in Stage II and four in Stage III. Since there is a considerable egg loss during the incubation of embryos in decapods (Kuris 1991), only females carrying embryos in the early stage were used to estimate the size-specific fecundity (NE, number of eggs) relationship in *C. seilacheri*. The total egg mass of brooding females was removed from the pleopods, counted and a random sample of 20 eggs per individual was separated for obtaining measurements of the long and short axis of each egg using a stereomicroscope equipped with a calibrated ocular micrometer. Egg volume (EV) was calculated using the formula proposed by Turner and Lawrence (1979) based on the volume of an ellipsoid: $EV = 1/6(EL*EW*2\pi)$, where EL = egg length and EW = egg width. The relationship between both egg number and egg volume and female size were assessed by regression analysis using a log-transformed version of the power function (allometric model: $\log Y = \log a + b * \log X$, where a is the intercept and b is the slope), with previous outliers removed by Studentized residuals' method. According to Somers (1991), fecundity and body size represent two different dimensions (volumetric vs. linear, respectively) and the theoretical slope of a size-specific fecundity relationship based on an allometric model should be approximately 3. Conversely, when slope values differ from 3, it is assumed that there is a lack of a simple volumetric relationship. Considering the above information, the slopes of the NE x CL and EV x CL relationships were compared with the theoretical value by independent Student's *t*-tests (Zar 2010).

Results

Sexual dimorphism, population structure, and sex-ratio

A total of 456 individuals of *Callichirus seilacheri* were collected during the study period, of which 234 (51.3%) were males and 222 (48.7%) females. Male CL ranged from 2.9 to 17.8 mm (mean \pm SD; 11.1 ± 2.8 mm) and females from 5.2 to 18.4 mm (11.7 ± 2.7 mm). Females, on average, were significantly larger than males ($t = -2.42$, $df = 454$, $p = 0.016$), denoting a slight sexual dimorphism with respect to body size. The size

structure of the overall population was symmetric (mean = median) for both males and females, revealing the presence of three cohorts (Figure 2(a,b)). For males, the average CL for each cohort was 8.7, 10.7, and 13.1 mm, whereas for females the averages were, 9.0, 11.6 and 13.7 mm. Most of the individuals (73% of males and 72% of females) were distributed between the size classes of 8.1 and 14.0 mm CL (Figure 2(a,b)), while the ovigerous females were between 12.2 and 17.2 mm CL (14.6 ± 1.4 mm).

The overall sex ratio did not differ significantly from evenness (males: females = 0.92: 1.00; $\chi^2 = 1.72$, $p > 0.05$). However, males were more abundant than females in the smallest size class (< 5.0 mm) and between 10.1 and 15.0 mm, while in intermediate classes (between 5.1 and 10.0 mm) the sex ratio was female-biased (Figure 2(c)).

Environmental parameters and dynamics of reproduction and recruitment

During the dry season, the surface seawater temperature ranged from $28.1 \pm 0.7^\circ\text{C}$ to $30.9 \pm 0.3^\circ\text{C}$, and salinity between 24.5 ± 1.2 psu and 33.6 ± 0.9 psu in early and late periods, respectively. By contrast, the variation of surface seawater temperature and salinity during both periods of the rainy season ranged from $30.5 \pm 1.1^\circ\text{C}$ and $31.0 \pm 2.1^\circ\text{C}$, and between 13.7 ± 0.96 psu and 23.7 ± 0.88 psu, respectively (Figure 3(a)). No statistically significant differences were detected between the average surface seawater temperature from the different periods (one-way ANOVA: $F = 1.38$, $df = 3$, $p = 0.319$), whereas salinity showed significant differences between periods (one-way ANOVA: $F = 6.65$, $df = 3$, $p = 0.015$) (Figure 3(a)). Salinity reached a greater average value during both periods of the dry season than during the rainy season periods (a posteriori least significant difference, Tukey test, $p < 0.05$) (Figure 3(a)).

Brooding females ($n = 30$) were found exclusively during the rainy season (from May to November), being more common during the late period of the season, when they comprised 23.5% of the adult female population (Marascuilo test: $M = 0.07$, $p > 0.05$, Figure 3(b)). Recruits ($n = 46$, of which 29 were males and 17 females) were found throughout the study period but their proportion was significantly lower during the early period of the rainy season when compared to others (Marascuilo test: $p < 0.05$, Figure 3(c)).

The abundance of ovigerous females in the population was negatively correlated with the annual oscillation of salinity (model containing only salinity as predictor variable: $r^2 = 0.510$, $p = 0.001$), but not with

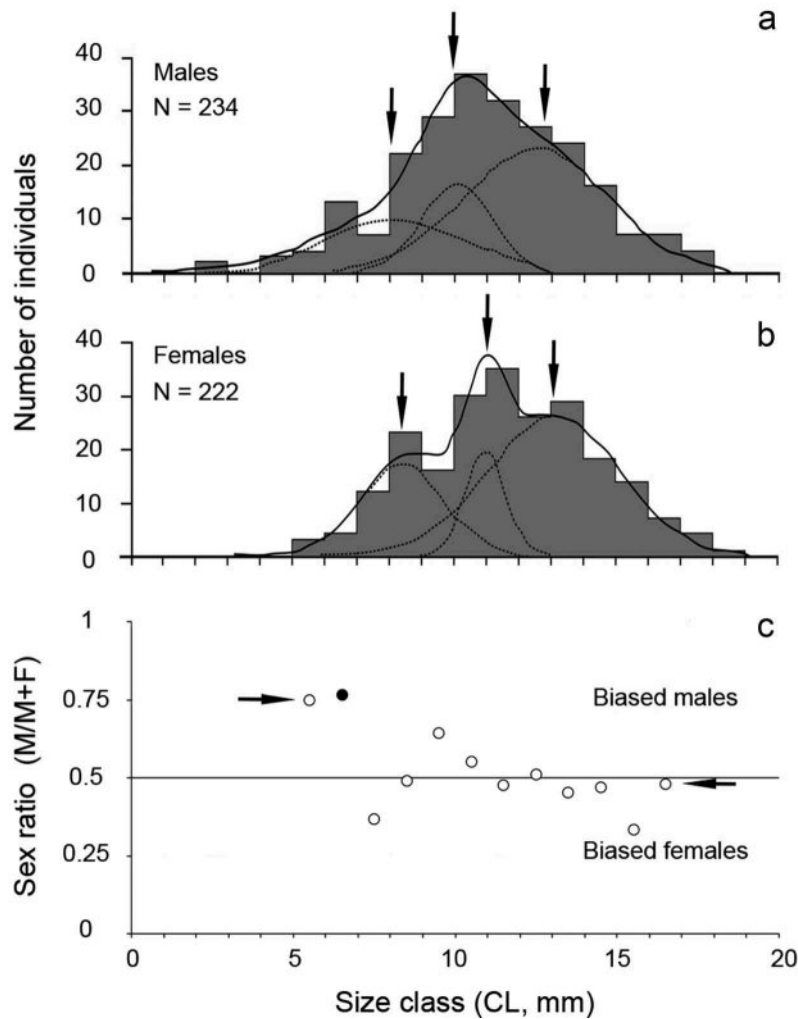


Figure 2. Size-frequency distribution for males (a) and females (b) of the intertidal ghost shrimp *Callichirus seilacheri* with the identification of each modal component. The sample size for both sexes is shown in each histogram. Sex ratio as a function of size of the sampled population at 'Mata de Limón' (c), Pacific coast of Costa Rica. In (c), the black circle indicates a deviation from a 1:1 sex ratio.

surface seawater temperature ($p = 0.98$) (Figure 4). Brooding females appeared in the population when the salinity of seawater dropped during the rainy season, being totally absent when salinity reached a value >24 (Figure 4).

Reproductive parameters

Fecundity in *C. seilacheri* varied between 336 and 7725 eggs (mean \pm SD; 2387 ± 1620 eggs) and was positively correlated with female size ($r = 0.78$, $p < 0.001$). Female CL explained 90% of the observed variation in *C. seilacheri* fecundity (Figure 5(a)). The estimated slope for the log-transformed size-specific fecundity values indicated positive allometry, being significantly different from three ($b = 7.77$, $t = 7.41$, $p < 0.001$) and emphasizing the absence of a simple volumetric relationship between

the number of eggs and cephalothorax length. The length of eggs in the first developmental stage (stage I) ranged from 0.54 to 0.97 mm (0.71 ± 0.098 mm), and its volume between 0.099 and 0.194 (0.148 ± 0.028 mm³). Egg volume was positively correlated with female size ($r = 0.76$, $p < 0.01$) and female CL explained 58% of the observed variability in egg volume (Figure 5(b)). The estimated slope for the relationship between the egg volume and female size indicated negative allometry, being significantly different from the theoretical value of 3.0 ($b = 1.31$, $t = -6.90$, $p < 0.001$), which confirms that female size did not limit the increase of egg volume.

Discussion

Female *Callichirus seilacheri* attained, on average, a larger body size than males, which confirms the

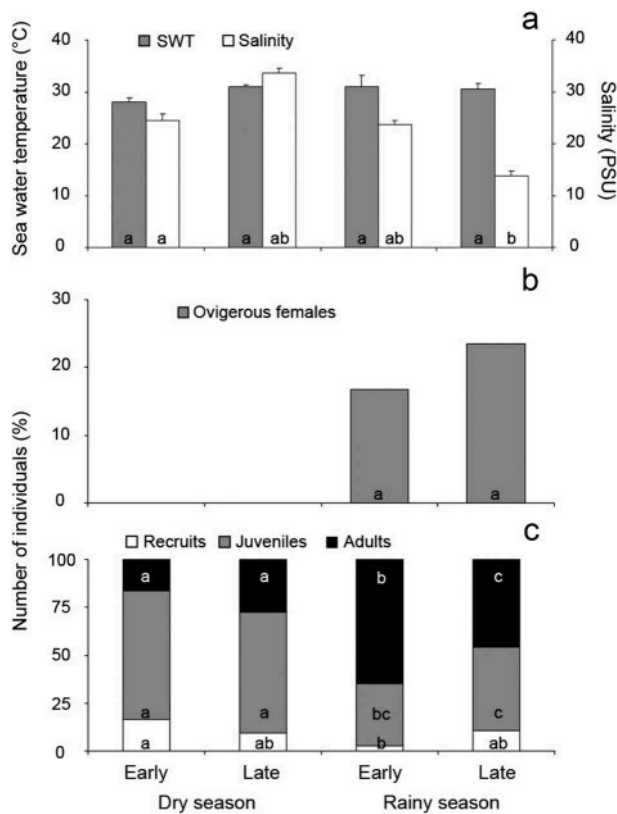


Figure 3. Seasonal variation in the (a) mean (\pm SD) seawater surface temperature (SWT) and salinity; (b) the percentage of ovigerous females, and (c) the percentage of recruits, juveniles and adults of the ghost shrimp *Callinectes seilacheri* at 'Mata de Limón' during dry and rainy seasons.

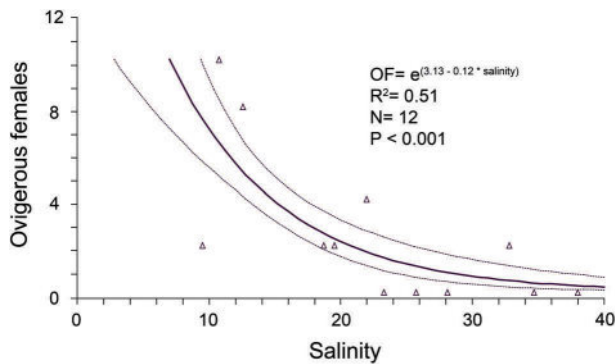


Figure 4. Relationship between ovigerous females of *Callinectes seilacheri* at 'Mata de Limón' and water salinity. The black curve was fitted through negative binomial regression analysis considering the monthly count of brooding females and salinity as dependent and independent variables, respectively. The grey curves indicate the 95% confidence interval around the adjustment.

trend reported for other callinassid shrimps (e.g. *Biffarius filholi* [A. Milne-Edwards, 1878]; Berkenbusch and Rowden 2000; *Callinectes major* [Say, 1818]; Botter-Carvalho et al. 2007; *Lepidophthalmus siriboia* Felder

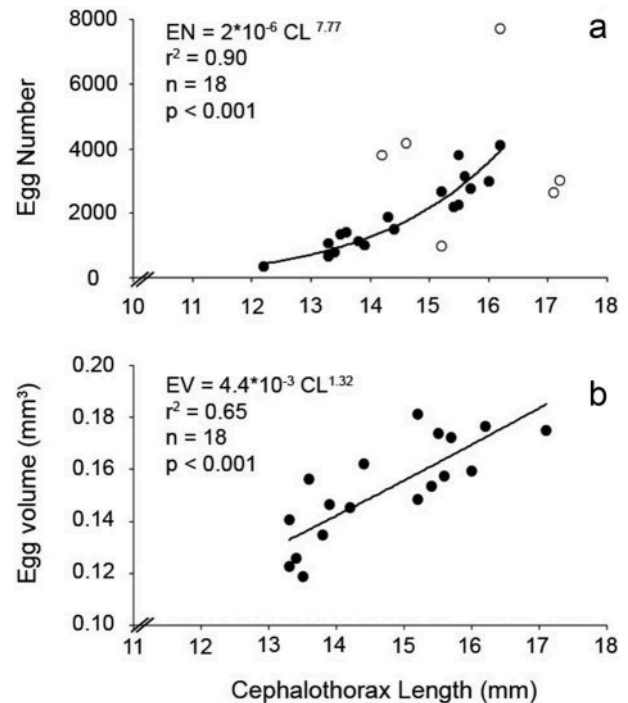


Figure 5. Size-specific fecundity relationships using either the number of eggs (a) or their volume (b), based on 24 ovigerous females of the ghost shrimp *Callinectes seilacheri* at 'Mata de Limón'. The cephalothorax length of each female was used as a proxy of size. In (a), outliers (open circles) are included in the graph but not considered in regression analysis. In (b), the linear regression equation was obtained by previously log-transforming both variables.

and Rodrigues 1993; Rosa Filho et al. 2013). The sexual dimorphism observed in *C. seilacheri* might be related to: (i) the predominance of a particular mating system within the Callinassidae in which there is no mate guarding of females by males before or after copula; and/or (ii) the existence of sexual differences in the amount of energy invested in body growth. Many studies have described the existence of a close relationship between sexual dimorphism and the mating system in caridean shrimps (see Correa and Thiel 2003; Bauer 2004), but such information is virtually non-existent for callinassid shrimps. In many caridean shrimp species in which males are smaller than their female partner, copulatory behavior is brief because the male cannot monopolize the female during mating. In Callinassidae, there is a single study presenting experimental evidence of an extremely brief (i.e. extending no more than two minutes) pre and post-copulatory behavior in *Nihonotrypaea harmandi* (Bouvier, 1901), a species in which females are larger than males (Tamaki et al. 1997). In addition, in many decapods, females appear to invest more energy into somatic growth than males to ensure high offspring production

(Andersson 1994). This assumption is supported by our results and also by the fact that female body size meaningfully explains brood size in most decapod groups (e.g. Corey and Reid 1991; Hines 1991; Reid and Corey 1991; Hernáez and Palma 2003). Finally, males of callinassids are usually smaller than females probably because they invest heavily in hypertrophied chelipeds, which are used as armament against other potential competitors during mating (Shimoda et al. 2005) or to defend their territory (Rodrigues and Höld 1990). Unfortunately, our observations do not allow further conclusions about what reasons could explain the observed sexual dimorphism in *C. seilacheri* and only additional experiments about the mating strategies used by shrimps would clarify such points.

The population of *C. seilacheri* at Mata de Limón during the study period consisted mainly of juveniles (55%) and adults (34%), with few recruits (11%). Juveniles were especially abundant during both dry season sub-periods, whereas adults predominated during the two subsequent rainy periods, suggesting high seasonality in the structure of the sampled population. This can be explained probably by: (i) the entry of new individuals into the population mainly during the dry season, which corresponds to the larvae produced during the breeding period occurring in the previous season; and/or (ii) be related to temporal changes in the vertical distribution of shrimps within the gallery (mainly adult shrimps), which would make capture by our sampling pump difficult because individuals are located deeper in the burrow (for further discussion on this see Hernáez et al. 2008; Dworschak 2015).

In Mata de Limón, the overall population of *C. seilacheri* had an unbiased sex ratio, without statistical differences between the frequency of males and females. This result agrees with the expected pattern under Fisher's theory where natural selection favours an equal frequency of males and females (Fisher 1930). However, despite the absence of a significant difference in sex ratio, males outnumbered females during the study period. This finding contradicts the general trend of female-biased sex ratio observed in many ghost shrimp species (*Lepidophthalmus louisianensis* [Schmitt, 1935]: Felder and Lovett 1989; *Sergio mirim* [Rodrigues 1966]: Pezzuto 1998; *Lepidophthalmus sinuensis* Lemaitre and Rodrigues, 1991; Nates and Felder 1999; *Callichirus garthi*: Hernáez and Wehrtmann 2007; *Trypaea australiensis* Dana, 1852: Butler et al. 2009). We speculate that the unbiased sex ratio observed in our study may be associated with the absence of sex-specific differences in mortality rates along the lifespan of *C. seilacheri* individuals. This suggests that shrimp mortality by fishing does not specifically affect one of the sexes, which

indirectly will facilitate the management of *C. seilacheri* as a bait resource.

Many different authors have provided support for Orton's rule (Orton 1920) showing for many invertebrates that the constant and high seawater temperatures of tropical regions favor embryo production throughout the year (e.g. Thorson 1950; Giese and Pearse 1974; Sastry 1983; Pearse et al. 1991; Clarke 1992 and references therein). Some studies on tropical decapods have corroborated this rule, showing that most of them breed continuously throughout the year or exhibit extended breeding seasons (e.g. Caridea: Bauer 1989; Anomura: Martinelli et al. 2002; Penaeoidea: Costa and Fransozo 2004; Brachyura: Litulo et al. 2005) compared to species from higher latitudes in which reproduction is restricted to short periods of time (e.g. Brachyura: Antezana et al. 1965; Penaeoidea: Crocos and van der Velde 1995; Caridea: Company and Sardà 1997; Anomura: Palma and Arana 1997). Nevertheless, contrary to Orton's rule, our results provide evidence that reproduction in tropical species is not always continuous. The emergence of egg bearing-females in the *C. seilacheri* population only during the rainy season clearly indicates that reproductive periodicity in this species is seasonal and strongly correlated with the climatic conditions of the eastern tropical Pacific, as mentioned in other recent studies conducted in the same region (Hernáez et al. 2012; Hernáez and Wehrtmann 2014). Most importantly, the relative stability of the seawater temperature in the region did not induce constant egg production in this species, which undoubtedly changes the importance of this parameter as being the main driving factor regulating the reproduction of marine invertebrates in tropical regions. In fact, our results suggest that oscillations in the seawater salinity may play an important role in the activation of reproduction in *C. seilacheri*.

For species breeding seasonally, reproduction is usually triggered by an abrupt change in some environmental factor (Sastry 1983). For instance, the onset of the reproductive period in many species inhabiting temperate waters from the Chilean coast occurred when the temperature of seawater declines during winter (e.g. Antezana et al. 1965; Arana and Tiffou 1970; Bahamonde et al. 1986; Wolff and Cerda 1992; Lardies et al. 2004). Conversely, on the Pacific coast of Central America reproduction of two tropical decapods is activated when seawater salinity (Hernáez et al. 2012) or temperature (Hernáez and Wehrtmann 2014) declines dramatically. In Mata de Limón, the seawater surface temperature was relatively stable throughout the year (coefficient of variation = 6.2%), which, in our view, indicates that temperature should not be considered

the unique triggering factor of reproduction in *C. seilacheri*. However, salinity showed a marked seasonal change (coefficient of variation = 40.7%) and was correlated with the appearance of brooding females ($r = -0.67$). Therefore, salinity may be a critical factor for the onset of reproduction in *C. seilacheri*, although additional studies are necessary to test the importance of other factors possibly regulating the reproduction of this species.

Several past studies underline the difficulty of sampling large numbers of ovigerous females of callianassid species. In fact, the reported percentage of ovigerous females for callianassids in the literature varies between 6 and 27% (calculated over all sampled individuals), which is consistent with our findings for *C. seilacheri* (Table 1). Several researchers have pointed out that ovigerous females of Callianassidae tend to be located closer to the entrance of the burrows to ventilate their eggs and optimize offspring release, which would facilitate their capture by suction pumps (Rowden and Jones 1994; Nates and Felder 1999; Rosa Filho et al. 2013). This suggests that the small proportion of ovigerous females reported by us and many other authors is not an outcome of the sampling method but might be related to a low probability of encounters between sexual partners due to the cryptic and solitary lifestyle of most callianassid species, including *C. seilacheri*, whose individuals solitarily inhabit their galleries (Hernández and Granda-Rodríguez 2015).

Fecundity increased with body size in *C. seilacheri* as reported for other species of ghost shrimps (Hanekom and Erasmus 1989; Souza et al. 1998; Berkenbusch and Rowden 2000; Botter-Carvalho et al. 2007; Hernáez et al. 2008; for an exception, see, 2012). This species produced a smaller number of eggs than other *Callichirus* species (Table 2), which might be explained by the smaller body size of *C. seilacheri* individuals when compared to other larger callianassids, which brood a substantially greater number of eggs. For instance, an average-sized *C. seilacheri* female roughly carries seven times fewer eggs than an average-sized female of *C. garthi*, a species with a CL 1.5 times larger than *C. seilacheri* (Table 2). These differences together with the absence of a volumetric relationship between the number of eggs and cephalothorax length for *C. seilacheri* support the main generalization that female size is the major constraint for egg brooding in decapods (e.g. Corey and Reid 1991; Hines 1991; Reid and Corey 1991; Hernáez and Palma 2003, among others). In addition, although the size of the eggs carried by *C. seilacheri* increases with female size, this relationship is negatively allometric because egg size is not linearly related to cephalothorax length. Instead, egg size increases as the physical space available to the embryo inside the egg also increases during embryogenesis.

In conclusion, our findings confirm the observed pattern for other related species of Callianassidae in that females are often larger in body size than males. Also, the homogeneous structure of the sampled *C. seilacheri* population, characterized by a similar number of males

Table 1. Population dynamics of ghost shrimps in natural environments. Comparison of the sampling period (in months), sex ratio, and the percentage of ovigerous females (OF) from populations of six different ghost shrimp species studied between 1998 and 2018. n.a. = the information is not indicated in the referred publication.

Species	Sampling period (months)	Sample size M: F = total	OF (%)	Reference
<i>Callichirus garthi</i>	12	267: 313 = 580	16.9	Hernáez and Wehrmann (2007)
<i>C. major</i>	14	707: 720 = 1427	21.8	Botter-Carvalho et al. (2007)
<i>C. seilacheri</i>	12	234: 222 = 456	13.5	Present study
<i>Lepidophthalmus bocourti</i>	12	227: 272 = 499	6.3	Hernáez et al. (2012)
<i>L. siriboia</i>	12	753: 515 = 1268	27.0	Rosa Filho et al. (2013)
<i>Sergio mirim</i>	54	739: 1020 = 1759	n.a.	Pezuto (1998)

Table 2. Reproductive aspects of American ghost shrimps. Ovigerous female size (CL, cephalothoracic length), number of eggs (NE), egg length (EL), and the number of larval stages of eight callianassid shrimp species from the Americas. When possible, reproductive parameters were based on females with recently extruded eggs. n.a. = Information is not available in publication.

Species	CL(mm)	NE(eggs)	EL(mm)	Number of larval stages
<i>Callichirus garthi</i>	21.7 ^A	17450 ^A	0.89 ^A	5 ^B
<i>C. major</i>	13.0 ^C	4565 ^C	0.79 ^C	4-5 ^D
<i>C. seilacheri</i>	14.6 ^E	2387 ^E	0.71 ^E	n.a.
<i>Lepidophthalmus bocourti</i>	15.3 ^F	2002 ^F	0.87 ^F	>2 ^F
<i>L. louisianensis</i>	n.a.	598 ^G	1.01 ^H	2 ^G
<i>L. sinuensis</i>	n.a.	258 ^G	1.22 ^I	2 ^G
<i>L. siriboia</i>	n.a.	825 ^J	1.08 ^H	4 ^K
<i>Neotrypaea californiensis</i>	14 ^L	3900 ^L	0.62 ^L	5 ^M

A: Hernáez [date unknown]; B: Aste and Retamal (1983); C: Peiró et al. (2014); D: Strasser and Felder (2000); E: present study; F: Hernáez et al. (2012); G: Nates et al. (1997); H: Felder and Rodrigues (1993); I: Nates and Felder (1999); J: Rosa Filho et al. (2013); K: Abrunhosa et al. (2005); L: Dumbauld et al. (1996); M: Buncic (2010).

and females, suggests that the mortality of ghost shrimps for fishing, as a result of constant removal of individuals from the population by bait gatherers has not been strong enough to affect both reproduction and recruitment of the species at this site. More importantly, our outcomes provide further evidence for the predominance of a seasonal breeding pattern in marine invertebrates from the tropical eastern Pacific. In fact, our evidence constitutes the third case of seasonal reproduction for a decapod species from the same tropical region. The breeding cycle in *C. seilacheri* seems to be adapted to the superimposition of a dry/wet season where low salinity is a proximate factor of reproduction, and seasonal productivity induced by rainy season nutrient input is an ultimate factor for larval development. This suggests to us that *C. seilacheri* also synchronizes their breeding cycle with the seasonal climate of the Pacific coast because environmental conditions during the wet season are more advantageous for larval release, given flooding of the river system with large amounts of freshwater may favor larval dispersal more effectively than in the dry season. This assumption is supported by the fact that many estuarine species export their larvae to adjacent coastal or offshore marine areas, where the conditions for larval development are more favorable (Strathmann 1982). Therefore, the well-known paradigm about continuous reproduction in tropical species should be reformulated, since there are many exceptions to this model (Bauer 2004), for marine species and decapod crustaceans, including this work. In addition, future studies should answer whether the observed reproductive pattern of *C. seilacheri* is correlated with other environmental factors varying with latitude or is it a phylogenetically based trait, inherited from a common ancestor. Such information will be essential for improving our knowledge about the different breeding patterns occurring in invertebrates from tropical regions.

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