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Population dynamics, sex ratio and size at sex change in a protandric simultaneous hermaphrodite, the spiny shrimp *Exhippolysmata oplophoroides*

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Abstract One of the main goals of sex allocation theory is understanding sex ratio evolution. However, theoretical studies predicting sex ratios in species with unusual sexual systems, such as protandric simultaneous (PS) hermaphroditism, are rare. In PS hermaphrodites, juveniles first develop into functional males that mature into simultaneous hermaphrodites later in life. Here, we report on the sex ratio (males/males + hermaphrodites) in the PS hermaphroditic shrimp *Exhippolysmata oplophoroides*. A 2-year study demonstrated that hermaphrodites dominated the population in two different bays. This skewed sex ratio may be explained by limited encounter rates among conspecifics. In agreement with this idea, the density of shrimps was extremely low (≤ 1 shrimp km^{-2}) at the two study sites. Size at sex phase change and sex ratios remained relatively stable through time at the two bays. The stability of these parameters might be explained by the rather steady population structure of this species during the study period. A review of sex ratios in PS hermaphroditic shrimps (*Lysmata* and *Exhippolysmata*) revealed considerable variation; some species have male- and others hermaphrodite-skewed sex ratios. The conditions explaining inter- and intra-specific sex ratio variation in protandric simultaneous hermaphroditic species remain to be addressed.

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Introduction

Sex allocation theory is one of the most robust branches in evolutionary biology (Charnov 1982; West et al. 2000; Munday et al. 2006; Schärer 2009). One of its main goals is predicting the optimal sex ratio of a population in species featuring a wide diversity of sexual systems (Charnov 1982). For instance, for strict sequential hermaphrodites (sex-changing species), the sex ratio is predicted to be skewed toward the first sex. Mathematical modeling demonstrates that the adult sex ratio favors the sex (first sex), experiencing the lower fertility values (Charnov and Bull 1989). This prediction rests on the assumptions that male and female fertility increases with size and that low levels of mortality occur during sexual transition (Charnov and Bull 1989).

Field observations conducted during the last decades have provided partial support for the prediction above. Early studies reported sex ratio skews toward the first sex in various sequential hermaphrodites (Charnov and Bull 1989; Collin 1995). On the other hand, a recent review of sex ratios in 40 species of sequentially hermaphroditic fish and invertebrates from five different phyla demonstrated a large range in sex ratio variation. For instance, in protandric species (male first), sex ratio (males/males + females) varied between 0.11 and 0.89 (Allsop and West 2004). Also, Collin (2006) found that only 8 out of 27 studied populations from 19 species of protandric calyptraeid gastropods featured a male-skewed sex ratio. Clearly, more experimental studies and detailed field data are needed to improve our understanding of sex ratio evolution.

Importantly, sex ratios and other sex allocation parameters might not necessarily be fixed population traits. Instead, sex ratios might vary with changes in population density, resource availability or size-frequency distribution (Charnov 1982; Collin 2006; Baeza 2007). Thus, studies attempting to understand the adaptive value of sex ratios should take into consideration the temporal dimension, population dynamics and environmental conditions.

In contrast to sequentially hermaphroditic species, sex ratio studies in species exhibiting less familiar "mixed" sexual systems are uncommon (for exceptions, St. Mary 1994; Baldwin and Bauer 2003; Baeza 2007; Baeza et al. 2007). During the last decades, several studies have reported species with peculiar "mixed" sexual systems (e.g. males coexisting with simultaneous hermaphrodites in androdioecious clam shrimps—Zucker et al. 1997: bi-directional sex change in goby fishes—St. Mary 1994; Munday et al. 1998; food-dependant sex reversal in caridean shrimps—Zupo and Messina 2007; but see Cobos et al. 2005). One remarkable "mixed" sex allocation pattern is protandric simultaneous hermaphroditism, in which individuals consistently mature and reproduce initially as

males, and later in life, become functional simultaneous hermaphrodites. Protandric simultaneous hermaphroditism has been confirmed in a polychaete worm (Premoli and Sella 1995), in a land snail (*Achatina fulica*—Tomiyama 1996), a tunicate (*Pyura chilensis*—Manríquez and Castilla 2005), and in marine caridean shrimps from the genera *Lysmata* and *Exhippolysmata* (Braga 2006; Baeza 2009).

Formal mathematical models predicting an optimal sex ratio in protandric simultaneous hermaphrodites are lacking. However, theoretical considerations suggest that the sex ratio should be skewed in these species (Charnov 1982; Charnov and Bull 1989; Baeza 2007). A hermaphrodite-skewed sex ratio might be the consequence of males maturing early in life as hermaphrodites if these males experience low male mating opportunities, in turn, driven by low population abundance. In agreement with this notion, experiments have demonstrated that males speed up maturation as hermaphrodites in small compared to large mating groups, because male mating opportunities are lower in the former regime (Baeza 2007).

The aim of this study is testing the hypothesis that the sex ratio is skewed in protandric simultaneous hermaphrodites. We used as a model the spiny shrimp *E. oplophoroides* (Holthuis, 1948) from the southeastern Atlantic. We explored the importance of time and locality in explaining natural variation in sex ratio and size at sex-phase change. Also, we described the population dynamic of this species because changes in population structure through time might be relevant in driving sex ratio.

Materials and methods

The studied species and its sexual system

The shrimp *E. oplophoroides* (Caridea: Hippolytidae) mostly inhabits soft bottom environments (up to 45 m depth) on the southeastern Atlantic coast (Holthuis 1980; Chacur and Negreiros-Fransozo 1998; Braga 2006). This species belongs to a monophyletic clade of shrimps (genera *Lysmata* and *Exhippolysmata*) with a peculiar sexual system: simultaneous hermaphroditism with an adolescent male phase (Bauer and Holt 1998; Braga 2006; Braga et al. 2009; Baeza 2009; Baeza et al. 2009). In these protandric simultaneous hermaphrodites (*sensu* Bauer and Holt 1998), juveniles invariably mature first as males bearing typical caridean male characters (i.e. coupling hoods on pleopod 1 and appendix masculina on pleopod 2) only capable of reproducing as males. Later, they acquire female sexual function and become functional simultaneous hermaphrodites (Sukumaran 1973, 1982; Kagwade 1982; Bauer 2000; Laubenheimer and Rhyne 2008; Baeza 2009). After maturation, hermaphrodites resemble females of caridean

gonochoric species brooding embryos under the abdomen. However, hermaphrodites retain testicular tissue, male ducts, and gonopores and reproduce as both male and female (Braga 2006; Braga et al. 2009). After becoming hermaphrodites, individuals probably do not revert to males, and no self-fertilization has been observed (Laubenheimer and Rhyne 2008).

Sampling of *E. oplophoroides*

Individuals of *E. oplophoroides* were collected most commonly once per month, but in a few occasions every 2 or 3 months, from January 1998 to December 1999, at Mar Virado (MV) and Ubatuba (UBA) bays, northeastern coast of Sao Paulo State, Brazil. At each bay, six transects were established between 5 and 20 m depth. A shrimp fishing boat equipped with two double-rig 3.5-m-wide nets (15 and 10 mm mesh diameter at the body and cod end of the net, respectively) was used for trawling. During each sampling, each transect was trawled for 2 km (each trawl lasted 30 min) covering a total area of $18,000$ m^2. Shrimps captured during each trawl were immediately fixed in formaldehyde (10%) and transported to the laboratory.

The rationale for sampling two bays hundreds of kilometers apart from each other was to detect possible short-scale geographical differences in sex ratio and size at sex-phase change in *E. oplophoroides*. Such studies are rare in crustaceans (for exceptions, see Charnov 1982; Anker et al. 2009; Baeza and Piantoni 2010). Sediment is less variable (in terms of grain size distribution) and coarser (larger average grain diameter) at Mar Virado than Ubatuba (Braga 2006). Other parameters such as percentage of organic matter in the sediment and bottom temperature do not vary between the two bays (Braga 2006). Unfortunately, the similarity between bays in the parameters described previously and our scarce knowledge of the biology of *E. oplophoroides* precluded us from formulating predictions about the direction of possible differences in sex ratios between bays.

At each bay, we choose sampling between 5 and 20 m depth because preliminary studies demonstrated that all ontogenetic stages (recruits, juveniles, and adults), sex phases (males and hermaphrodites), and body sizes (4.5 mm < CL < 15 mm) of *E. oplophoroides* live within this depth range. Studies in other marine invertebrates have shown that conspecifics can distribute as unisexual segregations in the environment (Ford 1964). However, our preliminary samplings demonstrated no segregation of shrimps according to sex phase, ontogenetic stage and/or body size at different depths and/or transects. Thus, we are confident that our sampling protocol provides a representative picture of the shrimp population at the two study sites.

We collected a total of 13,846 shrimps during the sampling period. Logistic and time constraints did not permit measuring and sexing of each collected individual from such a large sample. Thus, we followed Wenner et al. (1991) criterion to obtain representative measurements from each sample. We measured and sexed all individuals in samples comprising 80 or fewer shrimps. In samples containing between 80 and 160 shrimps, we measured 80 specimens that were haphazardly selected. Lastly, we measured and sexed 50% or 25% of all shrimps in samples of 160–320 or 321 and more individuals, respectively.

The carapace length of these selected shrimps was measured with a caliper (to the nearest 0.1 mm) as the distance between the orbital angle and the posterior margin of the carapace. Shrimps were classified as male or hermaphrodites according to the degree of development of the appendix masculina on the second pleopods (well developed and bearing spines in males but considerably reduced in hermaphrodites—Braga et al. 2009). Also, the presence or absence of embryos beneath the abdomen of hermaphrodites was recorded.

Sex ratio and size at sex-phase change in *E. oplophoroides*

The sex ratio was estimated as the quotient between the number of males and the number of males plus hermaphrodites in the population. Thus, sex ratio values higher or lower than 0.5 indicate skews toward males or hermaphrodites, respectively, in the population. We have used the number of males as numerator in our calculation to standardize our results with those from previous studies measuring sex ratios in both strict sequential hermaphrodites and protandric simultaneous hermaphrodites (Baeza et al. 2007; Collin 2006).

For each sampling date, we tested for deviations from a 1:1 sex ratio using a binomial test (Wilson and Hardy 2002). We also tested for sex ratio differences between bays and among sampling periods using a repeated-measurements generalized linear model given the sequential sampling of the two bays at regular intervals. The generalized estimating equation analysis was conducted using PROC GENMOD and the statement REPEATED in the software SAS (SAS Institute 2004). The data were distributed as a binomial and transformed by means of a logit-link function.

Lastly, size at sex-phase change (L_{50}) for the different bays and months was estimated as the size at which the probability to be hermaphrodite is 0.5 using logistic regression (Wilson and Hardy 2002).

Abundance of *E. oplophoroides*

Shrimp abundance at each sampling site is represented as catch per unit effort (CPUE). We tested the null hypothesis

of no effect of locality (bay) and time on the abundance of *E. oplophoroides* using one-way repeated measurements ANOVA with CPUE as dependent variable and locality and month as independent and within-subject variables, respectively. The circularity assumption of this test was not violated (Grenhouse–Geisser epsilon = 0.1686). Therefore, we used the univariate *F* statistics to test the effects of the independent and within-subject variables. Lastly, an a posteriori contrasts profile analysis was conducted to compare shrimp abundance among adjacent time periods (months) (SAS Institute 2004).

Population dynamics of *E. oplophoroides*

For each bay, the age and growth of *E. oplophoroides* were determined on the basis of length frequency distributions (LFD's) (Andrade and Pérez 2004). Monthly LFD's were constructed using 0.5-mm CL size intervals, as this scale proved useful for the detection of modes according to preliminary data analyses. Next, the multinomial distribution (Haddon 2001) was used for separating modes of different cohorts present in the LFDs (Zar 1999; Hastings and Peacock 1975). The optimal combination for the *n* distributions comprising a size-frequency distribution was found with the least-squares method that minimizes the difference between observed and expected frequencies.

In this study, cohorts are referred to as modes, because in a normal distribution, the mean for each cohort is equivalent to the mode or median. Also, we assumed that the standard deviation of the mean length of each cohort increased when new age groups were detected (Sullivan et al. 1990) and that the coefficient of variation has a fixed value of 3.5% (Andrade and Pérez 2004).

During the analysis, the different cohorts were separated using the IS index of age class separation (defined in Sparre and Venema 1995). If IS < 2, then it does not become feasible to separate the normal components of the observed frequencies (Sparre and Venema 1995).

After calculation of the parameters described previously for each of the LFD's of all months, we fitted the von Bertalanffy growth curve to our data. This growth curve is a useful expression of growth in shrimps (Silliman 1969; Parrack 1979; García and Le Reste 1987), although crustaceans feature a discontinuous growth pattern. Parameter values from the equation describing the von Bertalanffy growth curve were optimized using the least-squares method and the objective function of Gallucci et al. (1996).

The instantaneous rate of natural mortality (M) was estimated using Alagaraja's equation (Sparre and Venema 1995). Natural mortality was estimated by determining when 99% of a cohort disappeared from the population.

Results

### Sex ratio and size at sex-phase change in *E. oplophoroides*

Throughout the sampling period, sex ratios varied between 0.02 and 0.54 with a mean (±SD) of 0.27 (±0.14) in Ubatuba and between 0.04 and 0.61 with a mean of 0.19 (±0.14) in Mar Virado. Monthly samples with sex ratios skewed in favor of hermaphrodites were observed more frequently than expected by chance alone (35:2 vs. 18.5:18.5, binomial test, $P < 0.0001$; Fig. 1). Thus, the two studied populations are characterized by the predominance of hermaphrodites throughout the year.

The sex ratio was not affected by time (GEE, chi-square test; time: $\chi^2 = 20.14$, $df = 22$, $P = 0.5742$). However, the sex ratio was more hermaphrodite skewed at Mar Virado than at Ubatuba bay (locality: $\chi^2 = 7.99$, $df = 1$, $P = 0.0047$). No significant interaction between locality and month was found (locality × time: $\chi^2 = 11.75$, $df = 13$, $P = 0.5479$).

Throughout the sampling period, size at sex-phase change varied between 6.47 and 9.19 mm CL with a mean (±SD) of 8.64 (±0.63) in Ubatuba and between 8.24 and 9.14 with a mean of 8.76 (±0.22) in Mar Virado. Visual examination of the data indicated neither major temporal
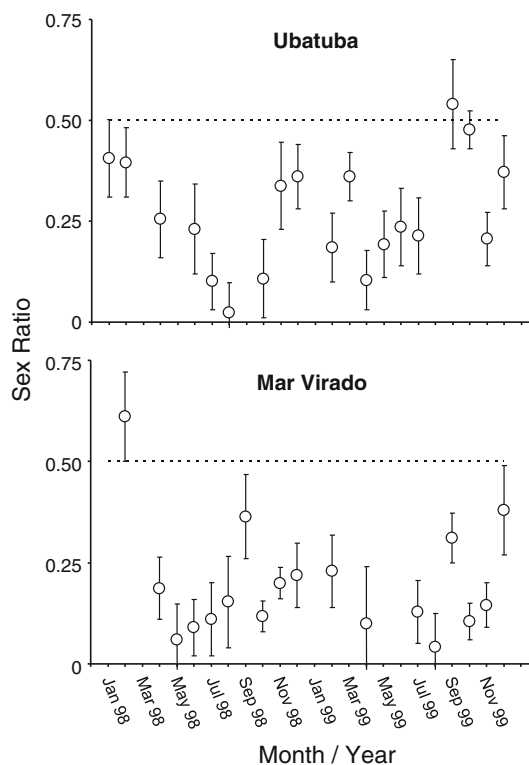
Fig. 1 Sex ratio (mean ± SD) estimated as the quotient between the number of males and the number of males plus hermaphrodites per sample (month) in *Exhippolysmata oplophoroides* (Holthuis, 1948) during the years 1998 and 1999 at Ubatuba and Mar Virado bays, northeastern coast of São Paulo State, Brazil
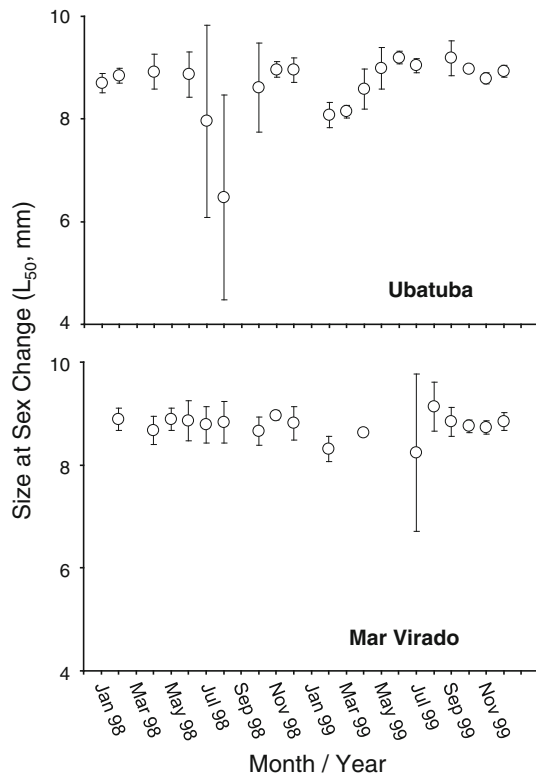
Fig. 2 Size at sex-phase change (estimate ± confidence intervals) in *Exhippolysmata oplophoroides* (Holthuis, 1948) during the years 1998 and 1999 at Ubatuba and Mar Virado bays, northeastern coast of São Paulo State, Brazil
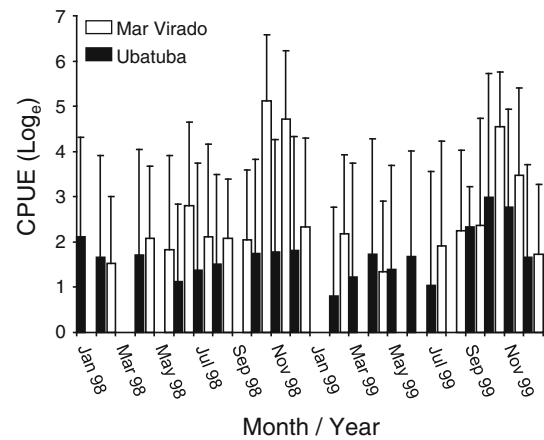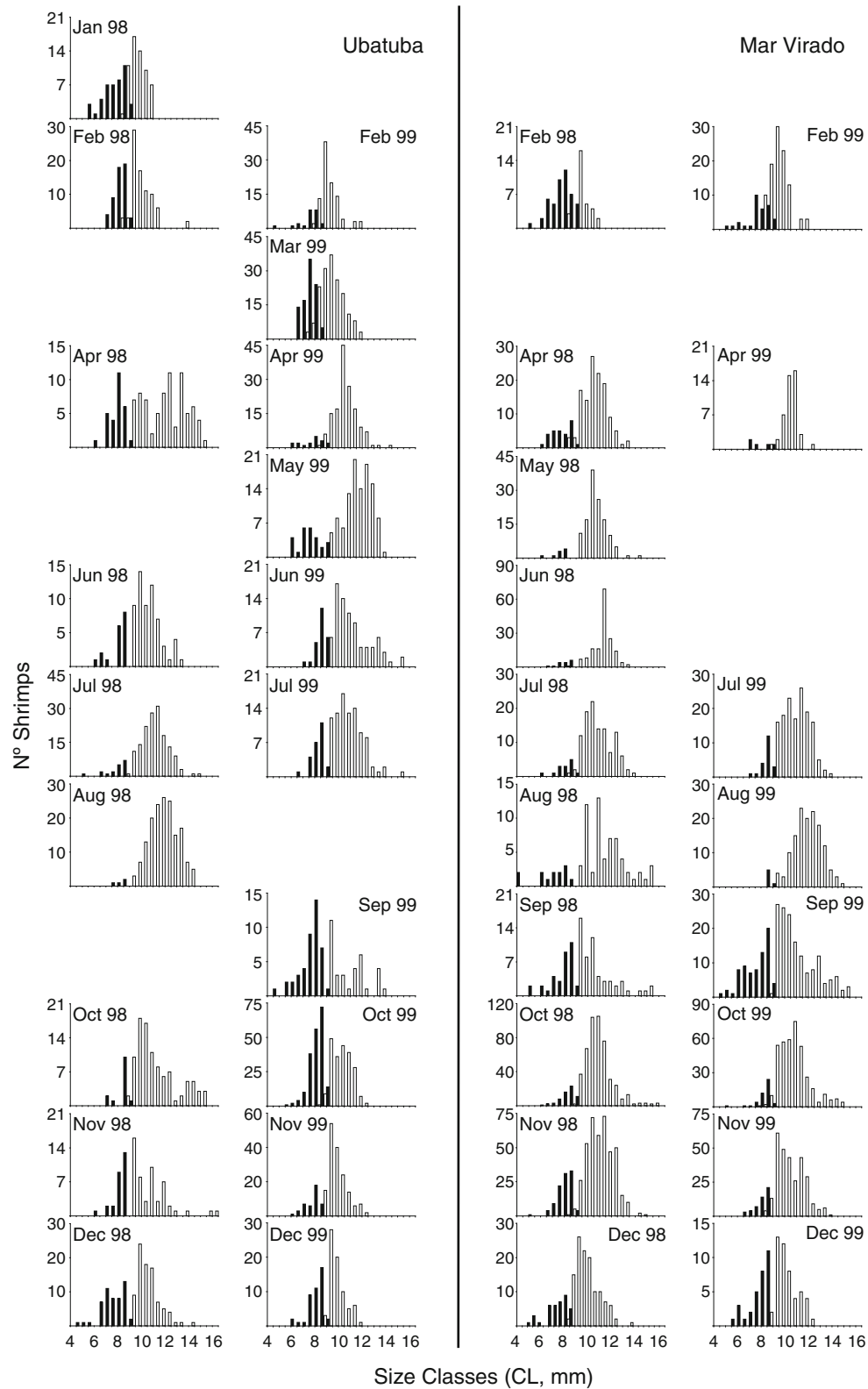

Fig. 3 Abundance (capture per unit of effort, CPUE) of *Exhippolysmata oplophoroides* (Holthuis, 1948) during the years 1998 and 1999 at Ubatuba and Mar Virado bays, northeastern coast of São Paulo State, Brazil

variation in size at sex change within bays nor differences between bays (Fig. 2).

Abundance of *E. oplophoroides*

A total of 8,176 shrimps were measured and sexed during the present study. In general, the density of *E. oplophoroides* at the study sites throughout the study period was low, with less than 1 shrimp per 1,000 m^{-2}. The abundance of *E. oplophoroides* did not differ between bays ($F = 1.77$, $df = 1,10$, $P = 0.2134$) but varied throughout the sampling period ($F = 2.66$, $df = 23,230$, $P = 0.0001$). The profile analysis confirmed that shrimp abundance varied through time. Shrimp abundance was particularly greater in September and October compared to August and November 1998 ($P < 0.05$ in both cases). No significant interaction between sampling locality and month was found (locality × time: $F = 1.48$, $df = 23,230$, $P = 0.0768$; Fig. 3).

Population dynamics of *E. oplophoroides*

A total of 52 and 71 cohorts, present in at least two contiguous months, were detected at Mar Virado and Ubatuba, respectively (Table S1). Hermaphrodites, both small and

large, were found year-round at both localities (Fig. 4). At Mar Virado, cohorts composed solely of hermaphrodites, on average, of 15 mm CL, were detected in August and September 1998. Thus, growth had already ceased at that body size ($\Delta L/\Delta t = 0$; Fig. 5). This estimation was confirmed by fitting growth parameters to the von Bertalanffy equation ($L_t = 15.3\ (1 - \exp^{-0.16(t+0.26)})$ and $L_t = 16.6\ (1 - \exp^{-0.08(t+2.53)})$ for Mar Virado and Ubatuba, respectively). According to these equations, *E. oplophoroides* reaches a maximum body size of approximately 15–17 mm CL (15.3 and 16.6 mm CL at Mar Virado and Ubatuba, respectively), grows quickly ($K = 0.16$ month^{-1} and 0.08 month^{-1} at Mar Virado and Ubatuba, respectively), and has a larval period of approximately 76 days ($t_0 = -2.53$) at both localities.

Exhippolysmata oplophoroides takes longer to attain its maximum body size at Ubatuba (∼59 months) than at Mar Virado (∼23 months) (Fig. 5c). The relationship between CL and monthly increase in CL was negative (Fig. 5a, b). Natural mortality was estimated to be 0.28 and 0.13 month^{-1} at Mar Virado and Ubatuba, respectively. Thus, ∼72 and ∼87% of shrimps in the population survive every month at Mar Virado and Ubatuba, respectively.

The percentage of brooding hermaphrodites was relatively high (>50%) during the sampling period at both localities (Fig. 6). No evident reproductive seasonality was observed. Thus, *E. oplophoroides* reproduces continuously and with similar intensity during the year at the two studied localities.

Small males (<6.0 mm CL) were intermittently found during the year at both localities (Fig. 4). However, they were more frequently observed from December to February during both years and also during September. Thus, recruitment in *E. oplophoroides* is intermittent but somehow restricted to the austral summer and during a short time

Fig. 4 Population dynamics of *Exhippolysmata oplophoroides* (Holthuis, 1948) during the years 1998 and 1999 at Ubatuba and Mar Virado bays, northeastern coast of São Paulo State, Brazil. The mean and standard deviation of the different modes detected in our analysis are shown in Table S1. *Black* and *white bars* represent males and hermaphrodites, respectively
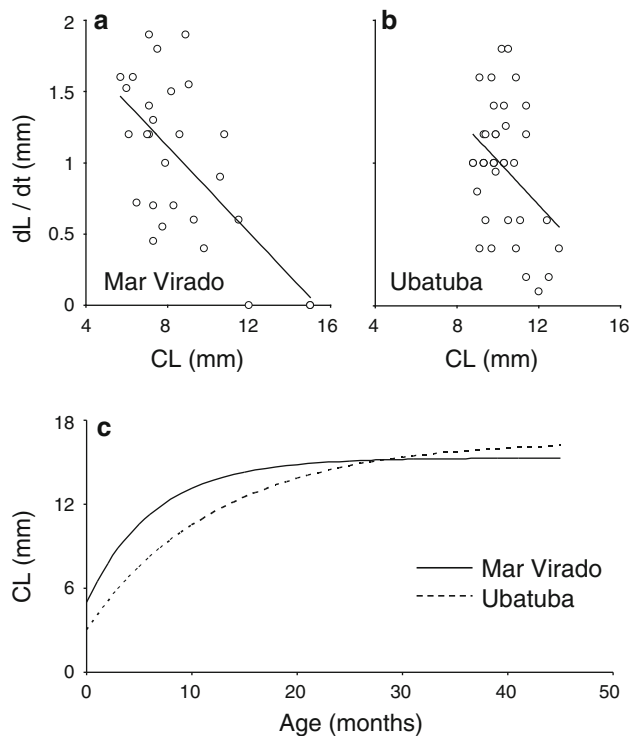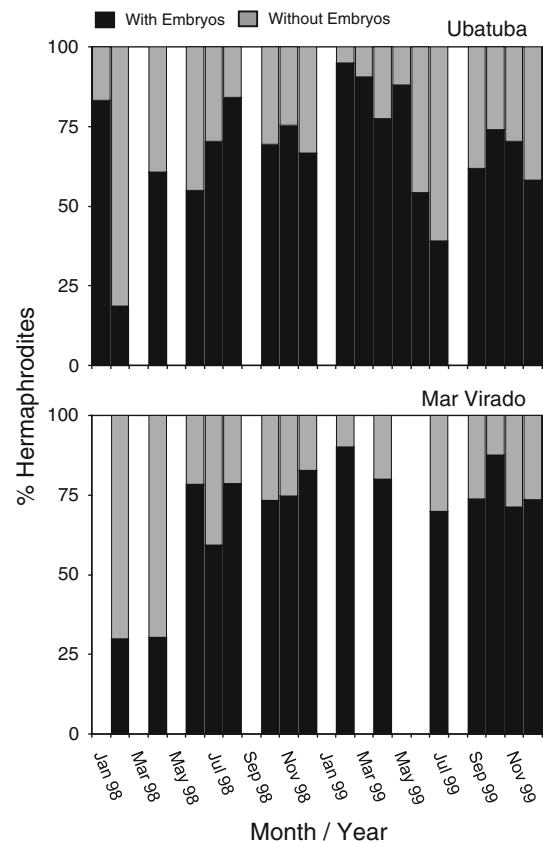
Fig. 5 Populations parameters of *Exhippolysmata oplophoroides* (Holthuis, 1948) at the Mar Virado and Ubatuba Bay. The *upper parameter* shows the instantaneous mortality rate (dL/dt) of the species as a function of body size at Mar Virado (**a**) and Ubatuba bays (**b**). The *lower parameter* shows the growth curve calculated for *E. oplophoroides* at the Mar Virado and Ubatuba bays (**c**)

Fig. 6 Frequency of occurrence of brooding hermaphrodites of *Exhippolysmata oplophoroides* (Holthuis, 1948) during the years 1998 and 1999 at Ubatuba and Mar Virado bays, northeastern coast of São Paulo State, Brazil

period during the end/start of the austral fall/spring (September).

Discussion

Sex ratio and size at sex-phase change in *E. oplophoroides*

In *E. oplophoroides*, the sex ratio was skewed toward hermaphrodites during our 2-year study period at two different bays. Taking into account the area covered by each transect (18,000 m^2) and the average number of shrimps retrieved per trawl, the density of *E. oplophoroides* at the study sites was approximately one shrimp per 1,000 m^{-2} during the sampling period. Encounter rates among conspecifics are expected to be rare in low-density species (Charnov 1982). Thus, we interpret low density in *E. oplophoroides* as an indication of shrimps having scarce mating opportunities in the field. Young males facing infrequent male mating opportunities should turn into hermaphrodites early in life so as to assure reproduction via the male and/or female function whenever mating opportunities arise. This result agrees with the notion that species and/or populations of

protandric simultaneous hermaphrodites with low natural densities feature sex ratios skewed toward hermaphrodites.

In *E. oplophoroides*, the sex ratio was more skewed toward hermaphrodites at Mar Virado than at Ubatuba. Differences in the speed of sex-phase change, in turn driven by differing local abundances, might explain the observed differences in sex ratios between bays. However, abundance did not differ between the two bays in disagreement with our theoretical argument. Alternatively, sex ratio differences between the studied bays might be explained by conditions other than dissimilar shrimp abundance, such as differing resource (food) availability, inter-specific competition intensity and/or predation pressure, between bays. Clearly, much detailed information on community composition from the two bays, including potential food items, predators and competitors, is needed before determining what conditions drive sex ratio differences between bays in *E. oplophoroides*.

We have reviewed sex ratios in protandric simultaneous hermaphroditic shrimps (genus *Lysmata* and *Exhippolysmata*) and found variability in this parameter both at the inter- and intra-specific level (as shown here for *E. oplophoroides*) (Table 1). In some species, the sex ratio is extremely skewed toward males; more than 90%

Table 1 Sex ratios (SR) in different species of protandric simultaneous hermaphroditic shrimps, with information on the number of populations (*P*) on which the measurements were based, the latitude and the socioecology of the different species

Species	SR	*P*	Latitude	Socioecology	Authority
E. oplophoroides	0.27	2	Subtropical	Crowd	This study
L. boggessi	0.84	1	Subtropical	Groups	Baeza (2009)
L. californica[a]	Biased	4	Temperate	Crowd	Bauer and Newman (2004)
L. galapagensis	0.98	1	Tropical	Crowd	Baeza (2009)
L. hochi	0.23	1	Tropical	Groups	Baeza and Anker (2008)
L. holthuisi[b]	0.61	4	Tropical	Crowd	Anker et al. (2009)
L. nayaritensis[c]	0.92	1	Tropical	Crowd	Baeza et al. (2007)
L. wurdemanni[d]	0.14–0.88	1	Temperate	Crowd	Baldwin and Bauer (2003), Baeza (2007)

[a] *L. californica*, no quantitative estimates, but sex-phase ratio was biased toward males in four samples and toward hermaphrodites in one sample. Samples were obtained from four different localities during five different times

[b] *L. holthuisi* estimates based on four different populations taken during four different months

[c] *L. nayaritensis* single sex-phase ratio estimate based on samples taken during a 3-month period

[d] *L. wurdemanni* variation in sex-phase ratio during one reproductive season

of the population is comprised by males in *L. galapagensis* (Baeza 2009). In others, hermaphrodites outnumbered males (e.g., *L. hochi*—Baeza and Anker 2008). Also, the magnitude of the variation in sex ratio with time differs among species. In *E. oplophoroides*, hermaphrodites dominate the population almost during the whole year and sex ratios remain rather stable through time (this study). In turn, in *L. wurdemanni*, sex ratios vary considerably during a single reproductive season (Bauer 2002; Baldwin and Bauer 2003; Baeza 2007; Table 1). No evident correlation between lifestyle or latitude and sex ratio skews is evident from our review. Studies exploring the conditions explaining such variability are warranted as they might provide insights into the evolution and stability of sex ratios in species with mixed sexual systems.

Do population dynamics affect the sex ratio and size at sex-phase change?

In *E. oplophoroides*, sex ratios exhibited no considerable variation during our 2-year study period at two different bays. Also, size at sex-phase change did not vary considerably between and within bays with time. Importantly, the population structure of this species was steady during the sampling period. Recruitment, although somehow restricted to one particular season, was never intense and large individuals disappeared from the population rather constantly and slowly during the year. Thus, the absence of abrupt changes in sex ratio with time in *E. oplophoroides* might be due to the relatively stable population structure, in turn, driven by stable environmental conditions at the two studied bays.

In contrast to our observations of no abrupt changes in the population structure of *E. oplophoroides*, population structure, sex ratio, and size at sex-phase change of another protandric simultaneous hermaphrodite, *L. wurdemanni*, varies considerably during the year (Bauer 2002; Baldwin and Bauer 2003; Baeza 2007). In *L. wurdemannni*, hermaphrodites dominate the population at the start of the breeding season but sex ratios turn highly male skewed toward the end of the season (Baldwin and Bauer 2003). Concomitantly, with these changes in sex ratio, shrimp abundance and water temperature increases throughout the breeding season. In fact, the environment of *L. wurdemannni* is highly seasonal (Baldwin and Bauer 2003), in contrast to that of *E. oplophoroides*. Manipulative experiments have demonstrated that temperature and photoperiod affect the timing of sex phase change in *L. wurdemanni* (Bauer 2002; Baldwin and Bauer 2003). Also, the social environment is most relevant in determining the timing of sex-phase change in *L. wurdemanni* (Baeza and Bauer 2004; Baeza 2007). In general, the observed shifts in sex ratio reported for *L. wurdemanni* in the field are consistent with the effect of both social and abiotic conditions in the timing of sex-phase change (Baldwin and Bauer 2003).

We argue in favor of additional studies to understand the role of population dynamics and other environmental conditions (both biotic [social] and abiotic) in explaining sex ratio and size at sex-phase variability in natural populations of protandric simultaneous hermaphrodites. Overall, we should expect variation in sex ratios in natural populations of these species whenever population structure is not stable due to, e.g., changes on recruitment intensity, availability of hermaphrodites, and density.

Reproductive biology of *E. oplophoroides*

Reproductive biology in *E. oplophoroides*, both at Mar Virado and Ubatuba, displays a "mixed" pattern between those reported for tropical and temperate crustaceans, including other caridean shrimps. On the one hand, a large proportion of hermaphrodites brooded embryos continuously during the year, as reported for other shrimps from the same subtropical locality and other tropical (Caribbean)/subtropical localities (Felder 1982; Bauer 1985, 1989). In contrast, reproduction in species from temperate latitudes is usually restricted to the fall and or spring/summer months (Allen 1966; Oh and Hartnoll 2004). In terms of reproductive periodicity, *E. oplophoroides* resembles tropical rather than temperate species. On the other hand, recruitment of juveniles of *E. oplophoroides* to the benthic population, albeit intermittent, was somehow limited to summer months. This seasonality in recruitment is characteristic of species from temperate latitudes (Allen 1966; Antezana et al. 1965; Baeza and Thiel 2000). Temperature and primary productivity are considered important conditions driving both reproductive periodicity and recruitment in shrimps and other crustaceans (Sastry 1983; Bauer 1985, 1989, 1992). The shrimp *E. oplophoroides* can be used as an example to understand the conditions favoring "mixed" reproductive patterns in subtropical environments.

Exhippolysmata oplophoroides attained smaller body size, grew quickly, and suffered lower mortality at Mar Virado than at Ubatuba. Also, shrimps took longer to attain their maximum body size at Ubatuba than at Mar Virado. Physical differences between Ubatuba and Mar Virado could explain dissimilar life history schedules of *E. oplophoroides* between bays. Sediment is less variable and coarser at Mar Virado than Ubatuba (see "Materials and methods"). Other parameters such as percentage of organic matter in the sediment and bottom temperature do not vary between the two bays (Braga 2006). These few differences in sediment characteristics might be driving differences in food availability and community structure (including presence/absence of predators) between bays that, in turn, might explain the differences in sex ratio and other life history parameters of *E. oplophoroides*. Unfortunately, nothing is known about the diet and natural predators of *E. oplophoroides*. Future studies are needed to reveal the food habits and predators to understand variation in the life history schedule of *E. oplophoroides* at short spatial scales (10–100 km apart).

Outline

This study demonstrated that the sex ratio in one protandric simultaneous hermaphroditic shrimp is skewed toward hermaphrodites, in agreement with theoretical considerations.

On the other hand, our review of sex ratios of protandric simultaneous hermaphrodites demonstrated considerable sex ratio variability at the inter-specific level (Table 1). *Exhippolysmata oplophoroides* belongs to a peculiar monophyletic clade of shrimps recognized for their diverse socioecology and unusual sexual system (Baeza 2009, 2010). The present and future descriptive studies on the socioecology of other species of *Exhippolysmata* and *Lysmata* will set the stage for comparative studies that will allow understanding the role of population dynamics, mating systems, and environmental conditions in driving the optimal sex allocation, including sex ratio, of protandric simultaneous hermaphrodites.

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