

POPULATION STRUCTURE AND OPERATIONAL SEX RATIO IN THE ROCK SHRIMP *RHYNCHOCINETES TYPUS* (DECAPODA: CARIDEA)

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A B S T R A C T

The ratio of sexually active males to fertilizable females (operational sex ratio, OSR) is the most important parameter determining the direction and intensity of sexual selection. It is widely accepted that the pronounced sexual dimorphism featured by many crustaceans is a consequence of a strongly male-biased OSR. Many studies have contributed to the understanding of function and origin of sexually selected traits, but few attempts have been made to measure the OSR. Using the rock shrimp *Rhynchocinetes typus* as an example, herein we propose a relatively simple method to assess the OSR of natural populations of crustaceans, as follows. The number of individuals willing to mate was estimated by the study of both the population structure (field sampling) and the readiness to mate (laboratory experiments). Field sampling showed that adult sex ratio was balanced during most seasons and that early ontogenetic male stages dominated among the males. Laboratory experiments demonstrated that females became receptive asynchronously, and that males from early ontogenetic stages showed limited readiness to mate. Based on this information, we estimated the OSR under three different scenarios. The results indicate that the OSR is highly male-biased in *R. typus* even in the more conservative scenario supporting the original predictions. Most male mate-competitors are early ontogenetic stages, whereas few are late stages. The results demonstrate the importance of estimating the OSR individually for shrimp categories differing primarily by sex and subsequently by individual conditions (ontogenetic stage, molt stage), which affects the probability of a potential mate to be sexually active. We suggest that this approach provides important information necessary for a better understanding of crustacean mating systems.

The ratio of sexually active males to receptive females, namely operational sex ratio (OSR), is the immediate cause determining the direction and intensity of competition for mates (Emlen and Oring, 1977). Typical sex roles among polygamous species, characterized by male-male competition and female mate choice, are a consequence of a male-biased OSR with males outnumbering females (Andersson, 1994). The main factor causing a male-biased OSR is the higher potential reproductive rate of males compared to females because of sex-specific differences in parental investment (Trivers, 1972; see Kvarnemo and Ahnesjö (1996) for a general discussion about factors affecting the OSR and sex roles). Among the most cited recent proposals to assess potential reproductive rates is the method of empirically estimating the maximum rate of offspring production per sex (Clutton-Brock and Vincent, 1991) or assessing the relative amount of time during which males and females are ready to copulate (Clutton-Brock and Parker, 1992). Although in some cases the determination of the rate of offspring production is suitable and convenient (e.g.,

seahorses—Masonjones and Lewis, 2000), in others it is more practical to investigate when an individual is willing to mate and when not (Clutton-Brock and Parker, 1992). An individual is considered to be in stage “time in” if it is capable of mating when presented with a receptive partner of the opposite sex. “Time in” requires that an organism must be in a proper physiological condition as well as in the correct location in space and time. Conversely, individuals are considered to be in stage “time out” when they cannot mate because they have to undertake parental tasks, recover gamete reservoirs, search for potential mates, or are physiologically incapacitated (e.g., during molting) (Clutton-Brock and Parker, 1992). In this study, we tested a simple method to empirically estimate the relative “time in” of individuals of both sexes and, furthermore, of different ontogenetic stages.

The “adult” sex ratio is another component of the OSR and therefore also contributes to determine the direction and intensity of competition for mates (Kvarnemo and Ahnesjö, 1996). An even sex ratio is probably the most common

pattern among gonochoristic animals (see Conover and VanVoorhees, 1990; Correa and Thiel, in press). Deviations from the ratio 1:1 may arise in different taxa from differential sex ratios at birth or metamorphosis (e.g., Wilson, 1971; Lagomarsino and Conover, 1993; Komdeur *et al.*, 1997). However, even when the sex ratio at birth is balanced, the "adult" sex ratio may become biased later because of sex differences in age/size of sexual maturity in relation to life expectancy (e.g., Sainte-Marie *et al.*, 1996, in Rondeau and Sainte-Marie, 2001; Jann *et al.*, 2000) or because of differential mortality related to sex-roles (e.g., Sudo and Azeta, 1992; Andersson, 1994; Koga *et al.*, 2001). In the case of hermaphroditic species, the timing and cues of sex change also play an important role (e.g., Nakashima, 1987; Gherardi and Calloni, 1993). In some cases, to measure the adult sex ratio precisely is complicated because to identify sexual maturity of individuals, particularly of males, is difficult (see Elnor and Beninger, 1995).

The OSR is often calculated by assuming that all adult individuals from the same sex are equally likely to be sexually active at a given moment. This assumption is unrealistic for many crustaceans. There is sufficient evidence indicating that the readiness to mate also depends on conditions other than sex (e.g., size/age, ontogenetic stage, phenotype—Thornhill, 1981; Correa *et al.*, 2000; Rondeau and Sainte-Marie, 2001). Herein, we avoid the estimation of the adult sex ratio, but the frequencies of reproducing individuals are accurately considered in the calculation of the OSR.

The distribution of the sexes in time and space also is an important factor affecting the OSR. Temporal clumping of sexually active individuals may play a pivotal role masking effects of differences in reproductive rates (Emlen and Oring, 1977; Grant *et al.*, 1995). In crustaceans, the discussion of reproductive timing has commonly been centered on its adaptive significance in terms of adult and/or larval survival (e.g., Saigusa, 1982; Forward, 1987; Morgan and Christy, 1995). Little attention has been paid to the effects of reproductive timing on the OSR, but observations are provided by Conlan (1989), Orensanz *et al.* (1995), Clark (1997), Moreau and Rigaud (2000), and Rondeau and Sainte-Marie (2001), and for a good discussion on other taxa, see Grant *et al.* (1995) and Thusius *et al.* (2001).

Theoretically, extreme synchronization of the reproductive cycle may lead to a temporal concentration of receptive females, and, therefore, the adult sex ratio approximates the OSR. Conversely, if females become receptive asynchronously, then sex differences in the potential reproductive rates become apparent in the OSR (e.g., amphipod—Conlan, 1989; terrestrial isopod—Moreau and Rigaud, 2000).

The OSR at a local scale may vary when sexually active males and females are spatially separated (Kvarnemo and Ahnesjö, 1996). However even when differences in the spatial distribution of the sexes are minimal, the distribution pattern of the population can affect the OSR. In their simplest model to assess the OSR, Clutton-Brock and Parker (1992) formalized this relationship by introducing the constant β , which represents the minimum expected time for a female to find a mate. Females will take the least time to find a mate (i.e., $\beta \rightarrow 0$) if males are highly mobile, with high detection capabilities, if populations are dense and if the habitat is structurally simple enough to locate conspecifics rapidly. Therefore, encounter probability between potential mates is an important component of the OSR, and it depends both on biotic and abiotic factors.

Crustaceans commonly feature sexual dimorphism in a wide variety of attributes including morphology and behavior, which reflects intense sexual selection (see reviews in Salmon, 1983; Christy, 1987; Conlan, 1989; Jormalainen, 1998; Correa and Thiel, in press). There is a great body of literature dealing with the adaptive value of sexually dimorphic traits and with the mechanisms involved in their evolution (e.g., Knowlton, 1980; Veuille, 1980; Shuster and Wade, 1991; Clark, 1997; Backwell *et al.*, 2000; Jormalainen *et al.*, 2000; Lefebvre *et al.*, 2000; Christy *et al.*, 2002). The widely recognized relationship between the simple OSR concept and the evolutionary process driven by sexual selection, however, contrasts with the limited number of attempts to empirically quantify this parameter in natural populations (for exceptions see Koga, 1995; Orensanz *et al.*, 1995; Jennings *et al.*, 2000; Moreau and Rigaud, 2000). The low number of OSR estimates in crustaceans presumably is due to practical difficulties to incorporate some of the parameters discussed above. The aim of our study, therefore, is to present an assessment of the OSR for a decapod crustacean, simultaneously identifying important parameters in the

calculation of the OSR, and proposing relatively simple measures for their reliable estimation.

The common rock shrimp *Rhynchocinetes typus* Milne Edwards, 1837 (Decapoda: Caridea) from the central-northern coast of Chile is our model species. Densities of *R. typus* are high on shallow subtidal hard-bottoms (Miranda and Kong, 1970; Caillaux and Stotz, 2003; own observations), which in combination with high mobility of these shrimp facilitates encounters between mates. Females carry their offspring beneath their abdomen during embryonic development, which may last 21–52 d (Dupré *et al.*, 1992). Following release of larvae, females molt and some hours later become receptive for mating (see Correa *et al.*, 2000), similar to other carideans (Correa and Thiel, in press). During preliminary field samplings, we found females carrying embryos of different developmental stages (personal observations), suggesting that reproductive cycles are not synchronized. The reproductive rate of adult males appears to be higher than that of females because males are capable of fertilizing multiple females over consecutive days (Hinojosa and Thiel, 2003). Sex differences in reproductive rates, and the eventual absence of temporal clumping of receptive females, would result in a male-biased OSR and thereby cause intense male sexual competition. Intense male-male competition has probably led to the evolution of extreme sexual dimorphism in *R. typus*. Males feature pronounced morphotypic differentiation of fighting structures (3rd maxillipeds and 1st pereopods) after the onset of sexual maturity (see Correa *et al.*, 2000). Additionally they perform alternative mating tactics depending on their ontogenetic stage and on the social environment (Correa *et al.*, 2003). In competitive situations, subordinate males seize a receptive female when this becomes available and rapidly transfer spermatophores to the female (Correa *et al.*, 2003). Females, in contrast, apparently present neither morphological nor behavioral adaptations for mate competition, but they may have preferences for certain males (Hinojosa, 2001; Díaz, 2002). Here, we examine whether the OSR is skewed toward male shrimp, as has also been suggested for many other sexually dimorphic crustaceans.

A seasonal study of a natural population of *R. typus* was conducted, focusing on the relative abundance of females of different reproductive status and of males of different ontogenetic stages. The results are used to determine

population structure, to document the reproductive season, and (in combination with experiments) to calculate the OSR.

MATERIALS AND METHODS

Field Sampling of Rock Shrimp

Seasonal samples were taken in La Herradura Bay in Coquimbo, Chile (Fig. 1) during the months October (austral spring 1999), January (summer), April (autumn), and August (winter 2000). Samples were taken by the same person using a specially designed "airlift sampler" (device based on models from Benson (1989) and A. Palma, personal communication; Fig. 1). Each seasonal sampling consisted of five consecutive dives conducted over a period ≤ 10 days; shrimp from subsequent dives were pooled for each seasonal sample. Samples were taken at a water depth of 3–9 m on hard-bottom substrata typically inhabited by *R. typus*. The diver with the airlift sampler examined the habitat, searching for cracks, rock-joints, or cavities inhabited by shrimp and appropriate for a good performance of the airlift. After locating a suitable spot, the diver placed the mouth of the airlift in the escape route of a group of shrimp, opened the air valve, starting suction, and then herded the shrimps toward the airlift's mouth. This sampling method was used because it minimizes selective capture of a particular size class, sex, or ontogenetic stage of rock shrimp.

All captured individuals were transferred alive to the flowing seawater laboratory where they were maintained in large holding tanks. Within two days of capture, all shrimp were sexed, sized, and assigned to one of the categories described below. Their cephalothorax length (CL) was measured with a caliper to the nearest 0.1 mm (from the postorbital margin to the medium posterior border of the carapace). Immature individuals (CL < 6 mm) were not sexed because they present no cues that can be used to discriminate between the sexes—because they do not contribute to the OSR, they are disregarded herein.

Criteria for Different Categories of Males and Females

Among males, we distinguished three different ontogenetic stages based on morphological characters (see Correa *et al.*, 2000, 2003, for illustrations):

Typus male (=T): The morphological stage in which males reach sexual maturity; morphologically similar to females.

Propodus and dactylus of 1st chela (1st pereopod) without or with only few fine, short hairs scattered over the appendix, and four teeth on distal tip of both segments. Last segment (carpus) of 3rd maxilliped is straight, with scattered hairs and with seven spines on distal tip.

Intermedius male (=I): Males in transition between typus and robustus stage; including males with ongoing morphological differentiation of the 1st chela and 3rd maxilliped. Propodus and dactylus of 1st chela with one dense patch of many fine hairs located on the dorsal surface near the junction of both segments. On early intermedius stages, the hairs are short and the patch is small, whereas in later stages, the hairs are longer and the patch is larger, conspicuous, and colored white and ochre when recently molted and brown later when dirty. Similar to typus, both segments feature four teeth on distal tip. Carpus of 3rd maxilliped is straight, with few scattered hairs in early stages and hairless on later instars and with seven spines on distal tip.

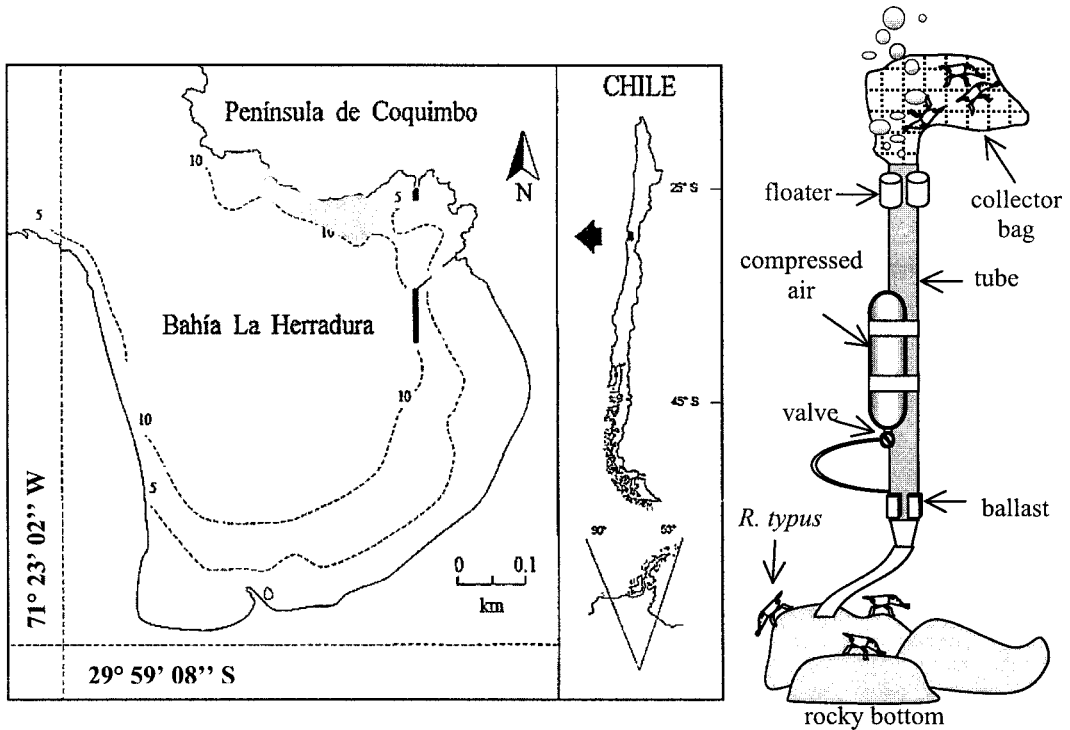


Fig. 1. Sampling area (gray shading) in La Herradura Bay (Coquimbo, Chile) and sketch of the airlift used to collect shrimp; 5 and 10 m isobaths are drawn.

Robustus male (=R): Final molt stage; characterized by extremely developed 1st chela and 3rd maxilliped. Propodus and dactylus of 1st chela feature an extensive patch densely covered with hairs similar in coloration and position to late intermedius; dorsal part of dactylus entirely covered by hairs. Both dactylus and propodus feature only one tooth on distal tip. Last segment of 3rd maxilliped is hairless, slightly curved and with only one spine on distal tip.

The chelae and maxillipeds of the females are similar in morphology to those of the typus males. Based on the morphology of the abdomen, we distinguished three categories of females, namely sexually immatures and two categories of adult (i.e., sexually mature) females, which differed in their reproductive status (see below). Adult females are characterized by enlarged epimeres (pleural plates) and abundant setae on their pleopods, both adaptations to accommodate embryo mass. Hence:

Immature female: The ventral region of the abdomen is not yet sufficiently developed to accommodate the embryo mass.

Ovigerous adult female (OF): Adult carrying embryos beneath the abdomen.

Nonovigerous adult female: Adult without embryos, but having an enlarged abdomen.

Analysis of the Population Structure of Rock Shrimp

Sex Ratio.—We determined whether the relative frequencies of males and females (regardless of sexual maturity) varied seasonally by analyzing a 2×4 contingency table (2 sexes

vs. 4 seasons). To test whether the sex ratios of each season fitted the expected 1:1 relationship, a Chi-square goodness-of-fit test was performed separately for each season.

Male Population Structure.—We determined whether the relative frequencies of ontogenetic male stages varied seasonally, using a 3×4 contingency table (3 male ontogenetic stages vs. 4 seasons). We then tested separately for each season whether differences existed among the frequencies of different ontogenetic stages using a Chi-square goodness-of-fit test (H_0 : T : I : R = 1:1:1).

Female Population Structure and Breeding Season.—The ratio of ovigerous to total adult females was used to identify the peak of the breeding season. Temporal variation in relative frequencies of adult ovigerous and nonovigerous females was examined using a 2×4 contingency table (2 female reproductive states vs. 4 seasons).

Note About Statistics.—All statistical tests were performed at a 95% confidence level. When a significant difference was found with the contingency tables or Chi-square for goodness-of-fit tests with DF (degrees of freedom) > 1 , the specific differences were identified by subdividing the analysis (Zar, 1999). The χ^2 and P values, however, were presented only for the original test. The statistic χ^2 was calculated with Yates correction for continuity whenever DF = 1 (Zar, 1999).

Temporal Distribution of Receptive Females and "Time In" Factor

To examine the temporal availability of receptive females, molting events of ovigerous females were monitored in the

laboratory. Females were maintained in groups of 20 individuals in five tanks (bottom 30×50 cm, 22.5 L volume) with flowing sea water at ambient conditions and natural photoperiod. All tanks had two large rocks that offered ample space for shrimp to seek shelter underneath or beside the rocks. Females for this study were captured with a hand-held net in the field to avoid sampling-related injuries or loss of embryo masses. Females were captured and placed in tanks in May 1999 (austral autumn). During the following weeks, we recorded the number of females that molted each day. When an exuvium was found in a tank, the recently molted (still soft) female was identified and retrieved from the tank. During daily inspections, the tanks were cleaned and the shrimp were fed *ad libitum* with dead fish, ascidians, and bivalves. Survival of females was high, and only two of the 100 females died during the experiment.

If females molt asynchronously, the average proportion of molted females/day is used in the calculation of the OSR, i.e., the "time in" factor for ovigerous females (TI_{OF}). Female molting can be taken as female "time in" because, after molting, females are receptive to fertilization for approximately 36 h (Correa *et al.*, 2000), but in the field, mating probably occurs shortly after molting (Correa, 2000). We assumed that during each reproductive cycle, females are receptive and available for mating for one day (24 h) after molting.

The product of TI_{OF} multiplied by the number of OF obtained from the field samples is considered as the number of receptive females used to calculate the OSR (see below). At least during the summer months, most ovigerous females that have released their larvae become receptive after molting (Correa *et al.*, 2000). We included only OF in the calculation of the OSR in order to account for seasonal variation in the breeding activity of the population.

"Time In" Factors for Males

We estimated the proportion of time that males are available for mating, i.e., "time in," based on previously obtained results. We distinguished males in different ontogenetic stages (T, I, and R) and, furthermore, the first stage (T) was subdivided into six size classes. Each category has a particular "time in" factor (TI) as inferred from previous studies (Correa *et al.*, 2000; Hinojosa, 2001). In these studies, individual males of the three ontogenetic stages and for *typus* males of different size classes were offered a mating possibility with a receptive female in a non-competitive environment. The TI_i represents the proportion of males from a particular category (i) that was successful in fertilizing a receptive female within a day. Thus, from Correa *et al.* (2000) and Hinojosa (2001), we gathered three sets of "time in" factors from mating experiments conducted with different male categories and at different times of the year. Each set represents one scenario (scenarios A to C). It was necessary to hypothesize the TI_i for those categories for which no empirical data were available. In these cases, we attempted to follow the tendency in a given scenario, typically using conservative estimates.

For each male category, the product of the TI_i multiplied by the number of individuals collected from the corresponding category is equal to the number of males that are available for mating, which was used to calculate the OSR (see below).

Calculation of the OSR

Herein, we follow the original concept of Emlen and Oring (1977) to obtain the OSR of a natural population of *R.*

Table 1. "Time in" factors (TIs) grouped in three scenarios used to calculate the OSR.

Category	Scenario		
	A	B	C
Females	0.02 ^E	0.02 ^E	0.02 ^E
<i>Typus</i>			
5.0–6.9	0*	0.35 ^B	0*
7.0–8.9	0*	0.20 ^B	0*
9.0–10.9	0*	0.53 ^B	0*
11.0–12.9	0.30*	0.53 ^B	0*
13.0–14.9	0.50*	0.57 ^B	0.20*
≥15.0 mm CL	0.70 ^A	0.72 ^B	0.31 ^C
Intermedius	0.90 ^A	0.60*	0.60*
Robustus	1 ^A	0.65 ^B	1 ^C

^E = This study (experiment; autumn).

^A = Correa *et al.*, 2000 (experiment: fertilization potential of males; summer).

^B = Hinojosa, 2001 (experiment: first sexual maturity; winter).

^C = Hinojosa and Thiel, 2003 (experiment: male performance in consecutive mating, herein was considered only the first mating; spring/summer).

* = hypothesized.

typus. However, for illustrative purposes, we preferred to highlight the relative number of male competitors per fertilizable female instead of the inverse rate as in the original definition. An additional modification is that for each season, we first calculated the operational sex ratio for each ontogenetic male stage. Then the overall OSR was obtained as the sum of the three values from T, I, and R. This is:

$$OSR = OSR(T) + OSR(I) + OSR(R) = \sum_{i=1}^n \left[\frac{fM(i) * TI_i}{fOF * TI_{OF}} \right]$$

Where: $fM(i)$ and fOF are the frequency of males from the category "i" and of ovigerous females respectively. These data were obtained from field samples (see above). TI_i and TI_{OF} are constants, which reflect the readiness to mate of males from the category "i" and of breeding females, respectively ("time in" factors). Herein, we tested three sets of TIs (i.e., three scenarios) to calculate the OSR for each season (see above; Table 1).

The spatial distribution pattern of the two sexes is not considered. Rock shrimp occur at relatively high densities (Caillaux and Stotz, 2003; own observations), and thus time required to find a mating partner is assumed to be negligible (i.e., $\beta = 0$ *sensu* Clutton-Brock and Parker, 1992).

RESULTS

Population Structure of the Rock Shrimp

The relative frequencies of males and females (i.e., sex ratios) varied significantly among seasons ($P < 0.001$). In the spring and autumn, the sex ratio was female- and male-biased, respectively (males : females, 0.85:1 and 1.12:1, respectively). In summer and winter, the relative frequencies of males to females fitted a 1:1 ratio (spring, $P = 0.001$; summer, $P = 0.072$; autumn, $P = 0.006$; winter, $P = 0.466$) (Fig. 2).

There was a significant difference in the relative frequencies of the ratio T : I : R among

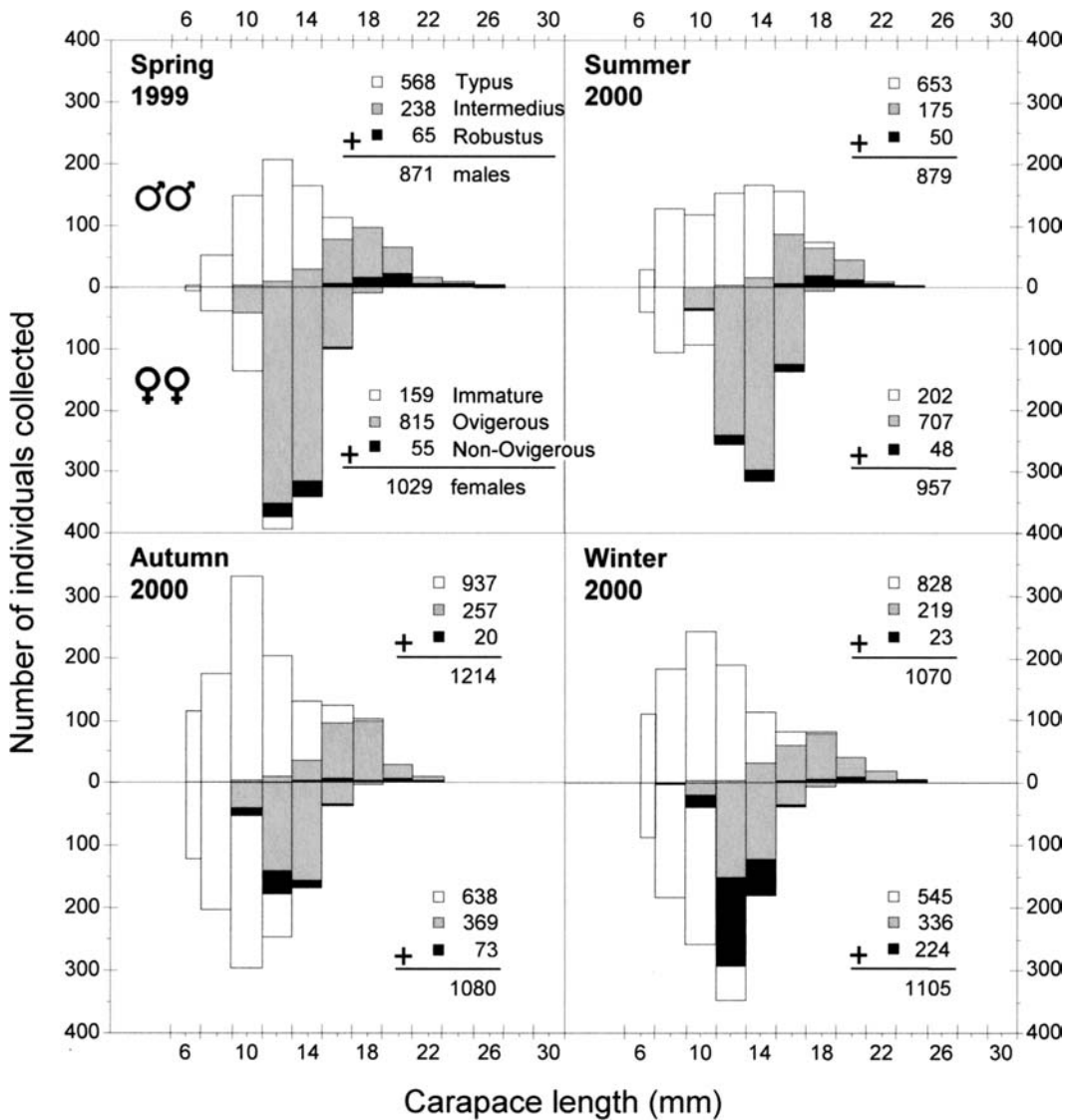


Fig. 2. *Rhynchocinetes typus*. Size-frequency histogram of males of different ontogenetic state and of females of different reproductive status collected during field sampling; size classes include lower limits but not upper limits, e.g., size class 8 mm includes all individuals ≥ 7 mm and < 9 mm. Individuals < 6 mm CL were not sexed and are not presented herein.

seasons ($P < 0.001$) being 9:4:1 in spring, 13:4:1 in summer, whereas autumn and winter did not differ significantly (41:11:1). In all four seasons, the number of early ontogenetic stages was higher than that of later stages (i.e., $T > I > R$) ($P < 0.001$ for the four seasons). Early ontogenetic stages tended to be smaller in size than late stages (i.e., $T < I < R$) but size-frequency distributions partly overlapped (Fig. 2). It should be stressed here that the category T may include males that have not yet acquired full sexual maturity as had been previously

shown in noncompetitive mating experiments (Hinojosa, 2001).

Rock shrimp reproduce year-round in La Herradura Bay as can be concluded from the fact that greater than 50% of the adult females were ovigerous (OF) during the four seasons (Fig. 2). The highest proportions, however, were found during spring and summer (93.7 ~ 93.6%, respectively). In autumn and winter, the relative frequencies of OF declined significantly (83.5% and 60.0%, respectively; $P < 0.0001$).

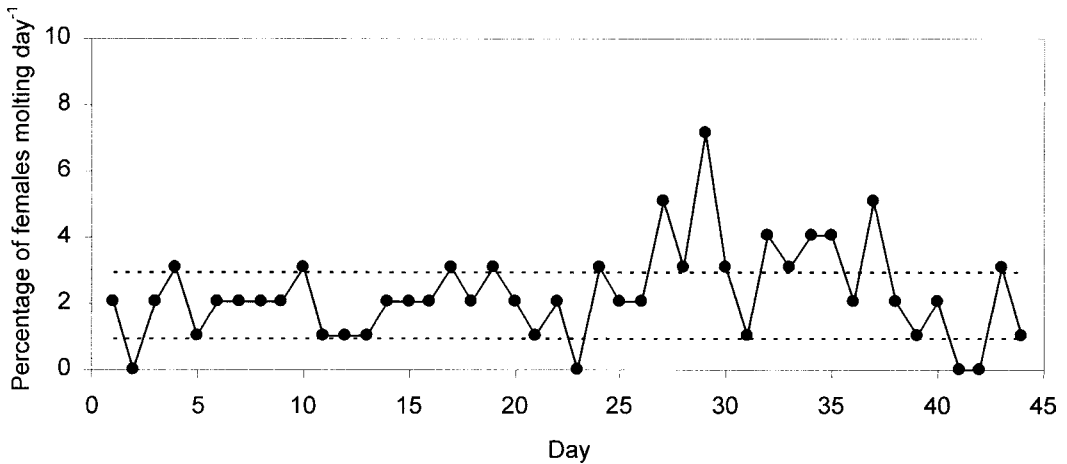


Fig. 3. Temporal distribution of female molt events per day (\sim sexual receptivity, see methods); dashed lines represent 25% and 75% quartiles for overall average; $n = 100$ females.

Temporal Distribution of Receptive Females and Their “Time In” Factor

Female rock shrimp do not molt in synchrony; a few recently molted females were found on almost every day (Fig. 3). Of the 98 surviving females (from the 100 initial females), 0 to 7 individuals molted each day. The daily average proportion of molted females was 2.27%, resulting in a “time in” factor for females $TI_{OF} \sim 0.02$.

“Time In” Factor for Males

In general, males of similar or of larger size than the smallest ovigerous female collected (class 11 mm CL) are “time in” most of the time, i.e., $TI_i > 0.5$. This is in contrast to the low value of female “time in” (Table 1). Early ontogenetic male stages showed lower values of TI (Correa *et al.*, 2000; Hinojosa, 2001). Continuous “time in” has only been reported for the final male stage, robustus, which never failed to fertilize receptive females in those experiments conducted in spring-summer (Correa *et al.*, 2000), producing $TI_R = 1$.

Estimation of the OSR

Under the three sets of TIs providing three scenarios, the OSR of *R. typus* from La Herradura Bay was highly male-biased ($OSR \gg 1$) (Fig. 4). The OSR ranged between 15 and 81 males per receptive female. A large portion of this bias was produced by the relatively high proportion of males from early ontogenetic stages despite their limited readiness to mate (see frequencies in Fig. 2 and TIs in Table 1):

depending on the respective scenario and season, there are 2–58 T, 7–31 I, and 2–4 R competing to mate with each receptive female (Fig. 4).

DISCUSSION

In *Rhynchocinetes typus*, the relative frequencies of potential mates present in the field and their corresponding probability to utilize a mating opportunity (i.e., their “time in” factor), yielded a strongly male-biased OSR under each scenario and during each season (Fig. 4). Even the most conservative estimates resulted in a strongly male-biased OSR (scenario C), demonstrating that competition for receptive females is extremely high. Previous studies (Correa *et al.*, 2003), and our approach to assess the OSR separately for different categories of males, allow us to hypothesize about the dynamics of mate competition. A recently molted female rock shrimp, which becomes receptive in the field, is most likely to be initially found by the relatively abundant and mobile typus males. Given the male dominance hierarchy in *R. typus* ($R > I > T$), a receptive female can be expected to experience successive changes of mating partners, with subsequent males typically being morphologically more developed than previous ones. The few but dominant robustus males are expected to finally gain possession of most receptive females (Hinojosa, 2001; Correa *et al.*, 2003), and the lack of reproductive synchrony in the female population offers robustus males a high chance

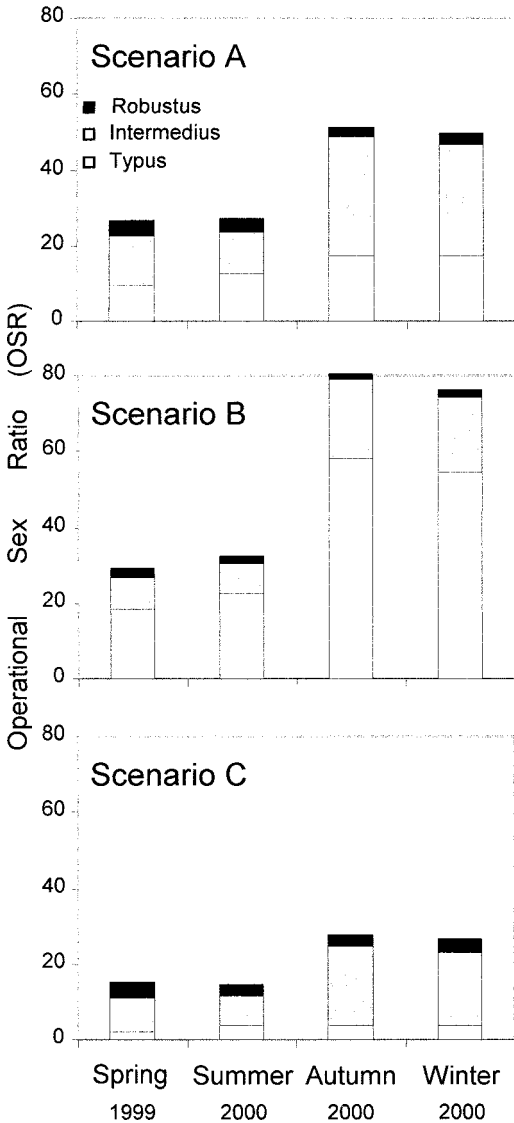


Fig. 4. Seasonal variation of operational sex ratio (OSR) estimated under three scenarios (see also Table 2); OSR = number of males from different ontogenetic stage ready to mate per receptive female.

to accumulate successive matings (see also Emlen and Oring, 1977; Grant, 1993; Blanckenhorn *et al.*, 1998). In the following discussion, we argue that the extremely male-biased OSR of *R. typus* has caused strong sexual selection in males leading to (a) sexual dimorphism with relatively powerful males, and (b) the evolution of alternative mating tactics among subordinate males. Before exploring these evolutionary questions, we briefly discuss our approach to estimate the OSR in *R. typus* and provide

suggestions for estimations of OSR in other decapod crustaceans.

Parameters Used to Estimate the OSR of *Rhynchocinetes typus*

The estimation of OSR in *R. typus* is based on simple and robust parameters that can be obtained with relatively little effort. This and previous studies clearly demonstrated that both sexes and, in males, the ontogenetic stages differ in their capacity to reproduce, making it necessary to determine "time in" independently for these categories. Two parameters determine the relative number of individuals from each category that are ready to mate: their "time in" factor (TI) and their relative abundance.

i) *Time In Factors (TIs)*. Among crustaceans, it is commonly possible to distinguish different categories of potential mating partners even within a sex (e.g., Ra'anán and Sagi, 1985; Shuster and Wade, 1991; Clark, 1997; Sainte-Marie *et al.*, 1997). The TIs reflect the probability that an individual from a particular category will utilize a mating opportunity.

The TI of females stands for the probability that she has molted within the last 24 h, i.e., that she is receptive. Even though receptive females held in isolation in the laboratory can remain receptive for more than 24 hours (Correa *et al.*, 2000), it is considered unlikely that a receptive female in the field remains unmated for more than a few hours (Correa, 2000). Here, we assumed that a female remains receptive for 24 h, a value that probably represents an over-estimation rendering our estimate of the OSR conservative. In *R. typus*, female receptivity is not synchronized, but in many crustaceans and in marine invertebrates in general, reproduction is synchronized with environmental rhythms (e.g., circadian, tidal, lunar, seasonal) (Salmon and Hyatt, 1983; Anderson *et al.*, 1985; Forward, 1987; Morgan and Christy, 1995). Although temporal synchronization of receptive individuals often is not pronounced and probably has little effect on the OSR, in species with highly synchronized reproduction, it may lead to an approximation between OSR and the adult sex ratio.

For males, the TIs represent the probability that a given individual, in the absence of competition, will mate with a receptive female. The TIs may differ among male categories for several reasons. For example, categories based on the size/age or ontogenetic stage, as in male *R. typus*, may differ in their readiness to mate

due to size- or stage-related tradeoffs of reproduction vs. growth or maintenance (see also Elner and Beninger, 1995; Hinojosa and Thiel, 2003). The specific TIs for each male category provide a relatively simple method to account for these differences. Size- or stage-dependent differences in mating probability may also be expected in males of other crustacean species, as for example in the different male morphotypes or developmental stages of the fresh water prawn *Macrobrachium rosenbergii* (see Ra'anan and Sagi, 1985); the amphipod *Jassa marmorata* (see Clark, 1997); the snow crab *Chionoecetes opilio* (see Sainte-Marie *et al.*, 1997); the isopod *Paracerceis sculpta* (see Shuster and Wade, 1991); and the different sexual types of males and females of hermaphroditic carideans such as *Athanas* spp. (Nakashima, 1987; Gherardi and Calloni, 1993) or *Thor manningi* (see Bauer and VanHoy, 1996).

ii) *Population Structure*. The relative frequencies of individuals from the different categories are important because after being multiplied with the corresponding TI, one obtains the relative frequencies of individuals ready to mate. An appropriate sampling method to obtain reliable estimates of the population structure is thus pivotal in the assessment of the OSR. A suitable method must provide representative (i.e., randomized) subsamples of a population. For crustaceans, baited traps, transect surveys, grab samples, dredge samples, or suction samples have been used. Baited traps are likely to bias the collection of individuals according to their energetic demands, mobility, sensorial capabilities, social rank, etc. For example, females of some sphaeromatid isopods cease to feed after the reproductive molt (Shuster, 1991), rendering baited traps inappropriate. In *R. typus*, the terminal male molt stage (robustus) does not require energy for growth but only for reproduction and maintenance, whereas preceding male stages (typus and intermedius) still need energy for growth. Sampling methods that are unselective, such as the airlift used herein, minimize the risk of sampling biases.

Assessment of the OSR often includes the adult sex ratio as a parameter (e.g., Clutton-Brock and Parker, 1992; Andersson, 1994; Jennings *at al.*, 2000). Here, we avoided this parameter because accurate recognition of adult males in *R. typus*, as well as in many other crustaceans, is a difficult and ambiguous task (see discussion in Conlan, 1989; Elner and Beninger, 1995; Koga, 1995). Typically, a min-

imum size is used to define an adult male (or female), often without knowing exactly whether the respective individuals indeed are sexually active. We therefore propose to examine sexual activity for several size classes of males (and females) in behavioral experiments whenever possible, because an individual's readiness to mate may depend upon conditions other than size or sex (Thornhill, 1981; Correa *et al.*, 2000; Rondeau and Sainte-Marie, 2001).

Our data suggest that the population sex ratio in *R. typus* is balanced, albeit some deviations from the ratio 1:1 were found in two of the four seasons (spring and autumn). Previous data based on baited traps reported pronounced and temporally consistent male-biased sex ratios in the rock shrimp (Vásquez and Castilla, 1982; Arana and Henríquez, 1983; Gaete and Arana, 1986), but because baited traps may be selective, we believe that natural populations of *R. typus* generally are close to an even sex ratio, similar to most other gonochoristic carideans (Correa and Thiel, in press).

Considerations for the Assessment of OSR in Other Crustaceans

In our estimation of the OSR, we excluded for simplicity a few factors that we considered of minor importance, at least in dealing with *R. typus*. Among the most important of these factors, two are related to the spatial distribution of the sexes whereas the third corresponds to seasonal variations in reproductive rates.

i) *Encounter Probabilities Between Mates*. When locating a potential mate is difficult (e.g., high time expenditure in searching), direct intrasexual competition tends to decrease (Dominey, 1984; Benton, 1992; Clutton-Brock and Parker, 1992; Andersson, 1994). In *R. typus*, it is relatively safe to assume that receptive females are quickly located by males allowing us to neglect this factor in the calculation of the OSR (i.e., $\beta \rightarrow 0$ *sensu* Clutton-Brock and Parker, 1992). Many other crustaceans, however, are likely to experience much lower encounter rates among potential mates, and consequently, the assessment of β becomes crucial in estimating the OSR. Characteristics such as population demography, habitat, and sensorial capabilities should be considered when estimating β .

ii) *Mating Grounds on Which Individuals Aggregate for Reproductive Purposes*. Many crustaceans are known to migrate variable distances to reach specific areas to mate (e.g.,

the shore crab *Carcinus maenas*—Van Der Meeren, 1994; slender crab *Cancer gracilis*—Orensanz *et al.*, 1995; spider crab *Maja squinado*—González-Gurriarán and Freire, 1994; sand shrimp *Crangon crangon*—Boddeke *et al.*, 1991; isopod *Paracerceis sculpta*—Shuster, 1991). Vásquez and Castilla (1982) suggested that rock shrimp migrate to shallow waters to reproduce, but at present, knowledge is too limited to infer the existence of migrations or preferred microhabitats to mate (e.g., certain cavities). The examined population lived year-round in the studied habitat, suggesting that reproductive migrations are of minor importance in *R. typus*. In species that migrate to reproduce, sex differences in arrival or departure time to/from “mating grounds” may bias the OSR, at least temporarily (Emlen and Oring, 1977; Kvarnemo and Ahnesjö, 1996).

iii) *Seasonal Variations of the Reproductive Rates of Both Sexes*. We assumed these to be negligible (i.e., temporally constant TIs), although seasonal fluctuations in the percentage of breeding females were found. In crustaceans, both the intermolt period and the duration of embryonic development are known to decrease with increasing temperatures (Dupré *et al.*, 1992; González-Gurriarán *et al.*, 1993). Thus, short reproductive cycles during warm months may result in females becoming receptive more frequently, simultaneously increasing the value of TI_{OF} . In the case of males, seasonal variations in growth rate should also alter their reproductive rate because molting events prevent them from mating. Other physiological mechanisms, however, such as changes in the rate of sperm production, are likely to occur. There exists little information about reproductive seasonality in male crustaceans, but Bauer (1976) observed that male *Heptacarpus pictus* stop sperm production during the annual reproductive diapause. Mating experiments with *R. typus* revealed that in winter 35% of the females paired with robust males failed to produce viable clutches, but no such effect occurred during the summer months (see Table 1; Correa *et al.*, 2000; Hinojosa, 2001). Whether these differences are due to male or female mating failure is not clear, because the experimental design did not allow answering this question.

OSR and the Opportunity for Sexual Selection in Crustaceans

The major factor directly leading to sexual selection is a biased OSR (Emlen and Oring,

1977). In many crustaceans such as in *R. typus*, the main factors causing a considerably male-biased OSR are relatively low reproductive rates of females, the absence of synchronization in their reproductive cycles, and a high encounter probability among adult individuals. Given that intensity and direction of these factors may vary across taxonomic groups or ecological environments, different mechanisms may determine the OSR and its effect in different taxa or habitats (see e.g., Orensanz *et al.*, 1995).

Under a male-biased OSR, there exists a high potential for receptive females to be monopolized by few males. This generates a high variance in the reproductive success of males and hence intense sexual selection (Emlen and Oring, 1977; Arnold and Duval, 1994). In some cases such as in *R. typus*, sexual dimorphism is extreme. Males experience sexual size dimorphism and conspicuous morphological changes after acquiring sexual maturity. The extremely developed 3rd maxillipeds and 1st chelae of terminal male stages, combined with aggressive behavior, confer relatively high resource holding power (Correa *et al.*, 2003). In *R. typus*, male mating behavior also reflects the high potential for sexual selection. Males either employ a sophisticated and female-monopolizing mating behavior or a simple and opportunistic tactic, depending on their own ontogenetic stage and on the social environment (Correa *et al.*, 2003). The evolution of such complex morphological (morphotypic differentiation) and behavioral patterns (conditional strategy) suggests that intense male-male competition may lead to a sequence of evolutionary changes. For many crustaceans, similar patterns have been reported (e.g., shrimp *Macrobrachium rosenbergii*—Ra'anan and Sagi, 1985; amphipod *Jassa marmorata*—Clark, 1997).

The empirical study of the OSR in natural populations of crustaceans has received little attention in the past despite laboratory experiments and field samples that have revealed its importance for the understanding of many questions related to mating behavior (Orensanz *et al.*, 1995; Jivoff and Hines, 1998; Debuse *et al.*, 1999; Rondeau and Sainte-Marie, 2001) and sexual selection (Koga, 1995; Jennings *et al.*, 2000; Moreau and Rigaud, 2000). The results of our study demonstrate (a) the importance of estimating the OSR using different categories of potential mating partners even within a sex, and (b) that some essential parameters to estimate

the OSR of a decapod crustacean can be obtained relatively easily.

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