Zoological Studies

Sex Ratio and Mating Behavior in the Calanoid Copepod *Pseudodiaptomus annandalei*

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Gaël Dur, Sami Souissi, François G. Schmitt, Shin-Hong Cheng, and Jiang-Shiou Hwang (2012) Sex ratio and mating behavior in the calanoid copepod *Pseudodiaptomus annandalei*. *Zoological Studies* **51**(5): 589-597. Information on mating is one of the primary requirements for successful population maintenance of copepods. Several studies on copepod mating were conducted, but none has ever investigated the effect of the sex ratio. Using optical systems, this study examined the plasticity of encounters, the rejection rate, and the mate guarding duration as a function of the sex ratio in the little known tropical species *Pseudodiaptomus annandalei*, that lives in aquaculture ponds in southern Taiwan. Our study results exhibited strong variability that may have obscured the effect of the sex ratio. Nevertheless some patterns did emerge. The number of encounters, very low with a highly male-biased sex ratio, increased as the sex ratio became more balanced. After reaching a maximum with an even sex ratio, it decreased again as the sex ratio became more female-biased. The male rejection rate exhibited a similar trend, higher for an even sex ratio and decreasing with a more-unbalanced sex ratio, except for a strongly female-biased sex ratio. The rejection rate was associated with the number of encounters in four of the 5 tested conditions. Females exhibited stronger choosiness when encounters were higher and relaxation when encounters were low. However, under female-biased sex ratio conditions, despite a lower encounter rate, females were very selective. This result is in agreement with theoretical models that predict a possible slackening of mate selection when encounters are mate limited. Although the sex ratio is supposed to induce a modification in mate guarding, no differences were found here. This pioneer study should lead to interesting debates and new insights on the effects of the sex ratio on copepod behavior.
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Key words: Pre-copulatory behavior, Mate selection, Calanoid copepod, *Pseudodiaptomus annandalei*.

The sex ratio in diploid populations plays a key role in population dynamics by determining gene mixing levels (Milchtainch 1992) and reproductive strategies (Kokko and Jennions 2008). With the potential reproductive rate, the sex ratio influences the ratio of males to females that are sexually competing and ready to mate in a population at a given time, what is known as the operational sex ratio (OSR) (Clutton-Brock and Vincent 1991, Kvamemo and Ahnesjo 1996, Clutton-Brock 2007). The latter, when biased, determines in part the relative strength of sexual

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selection (competition and choice) that operates on each sex (Emlen and Oring 1977, Jirotkul 1999). Therefore, inter-population variations in the adult sex ratio cause a shift in the OSR and consequently induce variations in the intensity of sexual selection (Kodric-Brown 1988, Carroll and Salamon 1995, Pröhl 2001). For instance, in the typical case of asymmetrical parental investment (males being the sex investing fewer resources and females the sex investing more), male-biased OSRs result in females becoming more selective when they have a greater opportunity to choose mates (Souroukis and Murray 1995, Balshine-Earn 1996) and males tending to compete more intensively for females due to the presence of more potential competitors (Jormalainen et al. 1994, Dick and Elwood 1996). In the opposite situation, female-biased OSRs, a relaxation in female selectivity and male competition may be observed (Jirotkul 1999). Indeed, in the case of a low male density, it is difficult for a female to find an alternative mate, and so she will mate indiscriminately.

In a recent review on copepod mating, Titelman et al. (2007) stated that "sexual selection is more important than it has been given credit for in the copepod literature, and that obviously it is an integral part of the life history strategies and behavior of copepods". Using several examples of copepod behavior, the authors showed that both sexes assess and choose among available mates. A previous investigation also concluded that mate choice in copepods occurs in both pre- and post-copulatory stages (Palmer and Edmands 2000). Among the different processes, complicated precopulatory dances, escaping, stroking, pre- and post-copulatory mate guarding, and post-copulatory mate choice were observed (Titelman et al. 2007). Each of these behaviors may be affected by variations in the adult sex ratio. Adult sex ratios of copepods are often female biased (Hirst and Kiørboe 2002, Kiørboe 2006, Gusmão and McKinnon 2009). Nonetheless, in some macrotidal estuaries (Devreker et al. 2008), as in some environments with visual predator pressures (Castonguay and FitzGeralt 1990, Ludovisi et al. 2008) and in some populations at low density (Schmitt et al. 2008), the sex ratio is in favor of males. Sex ratios considerably fluctuate within a given copepod population throughout the year (Irigoien et al. 2000, Beyrend-Dur 2010, Devreker et al. 2010). Such fluctuations in the sex ratio may be associated with differential longevity and mortality (Kiørboe 2006) as well as the effect of the environment on sex determination (Gusmão and Mc Kinnon 2009). To the present, the effect of sex ratio variations on copepod sexual selection has never been investigated.

The calanoid copepod *Pseudodiaptomus annandalei* is a suitable biological model for conducting such an investigation. *P. annandalei* is a widespread copepod species, occurring in brackish waters of the Indo-Pacific Ocean (Walter 1987). In Taiwan, this species is abundant in the heavily polluted Danshuei estuary (Hwang et al. 2010, Beyrend-Dur et al. pers.comm.), and is important as live food for aquaculture (Doi et al. 1997, Moorthy and Altaff 2002). Despite its importance, this species is poorly studied (Bollens et al. 2002), as is its reproductive ecology (Cheng et al. 2008). Nevertheless, a recent project that focused on comparing *P. annandalei* to a temperate analogue (*Eurytemora affinis*) discovered relevant information (Dur 2009). Concerning reproduction, it has to 1st be noted that *P. annandalei* females carry their eggs, and such significant maternal investment is expected to be associated with significant mate choice (Deutsch and Reynolds 1995). Dur et al. (2010) recently investigated the swimming behavior of *P. annandalei* and reported that sex-specific swimming modes can be recognized and associated with mate-finding mechanisms. Additional qualitative observations suggested that females produce chemical signals to advertise their presence and position to potential males (Dur et al. 2011) as suggested earlier by Jacoby et al. (1983) for other *Pseudodiaptomus* species. This behavior can be seen as an adaptation to increase the encounter rate, which in turn, offers greater potential for mate choice (Kokko and Rankin 2006). Investigations of *P. annandalei*'s mating behavior also revealed that after competing for access to a female and grasping her with his geniculate antennules, the male has to overcome specific female escape behaviors which take the form of a 'rejection dance'. Females may thus exhibit choice in the extent to which they struggle when a male attempts to clasp them (Dur et al. 2011). The fact that *P. annandalei* females are able to produce several clutches after a single copulation (Beyrend-Dur et al. 2011) supports the idea of male selection. When a sufficient number of mates are available, selection performed by females assures the acquisition of "good genes" not for only 1 but for 2 clutches. Nevertheless, the cost of choice (in a reduced reproductive rate) may outweigh potential benefits when it is difficult

to find an alternative mate because of a low male density, and it will pay to mate indiscriminately. In *P. annandalei*'s copulation process, the transfer of a spermatophore can be completed in a short time, 10 s. However, the duration of copulatory association in *P. annandalei* is often extends beyond the time required for such a transfer (Dur et al. 2011). Similar observations were made for several species of the same genus (Jacoby and Youngbluth 1983). Such post-copulatory guarding may be associated with sperm competition. While attached to the female, the male may place another spermatophore (Jacoby and Youngbluth 1983), which serves as a block for re-mating and prevents the female from returning to the pool of available mates. This prolonged mating duration is believed to be an adaptive trait that enhances male reproductive success in the absence of visual predators (Jersabek et al. 2007). This study considers this to be similar in cases when females are not numerous. However, in the opposite situation, shortening the copulation duration allows the male to return faster to the pool of competitors.

Based on simple mating experiments, this study modified the OSRs of *P. annandalei* while maintaining a constant density to examine how variations affected the encounter rate and the mating system of this copepod. We also examined this idea using simple mating experiments and three-dimensional (3D) observations of freely swimming animals. Our hypotheses were: (1) at a constant density, there would be a higher encounter rate at an even sex ratio; (2) when the encounter rate is low, there would be relaxation in the rejection dance performed by the female; (3) as the OSR becomes increasingly male-biased, females would become more choosy and the duration of mate guarding would be extended, and conversely (4) females would be less choosy and the duration of mate guarding would be shorter when the OSR is more female biased.

MATERIALS AND METHODS

Stock culture

Copepods used in this study were originally collected from a natural coastal pond in Tungkang (southern Taiwan) where the salinity was ~20 psu. The population is maintained by the Biotechnology Center of the Fisheries Research Institute in Tungkang (Drillet and Dur 2007). Copepod cultures were maintained in 20-L round plastic tanks at a salinity of ~15, using *Isochrysis galbana* as food, which has a high content of polyunsaturated fatty acids (PUFAs) (Jeffrey et al. 1994) and is small enough (~3-6 μm) to feed all copepod developmental stages. The culture medium was mildly and continuously aerated for mixing and to keep the algae suspended. The culture water was renewed once a week with a mixture of filtered seawater (0.45-μm Millipore filter) and filtered fresh water. All copepod cultures were maintained at ambient temperature ranging from 20°C (in winter) to 30°C (in summer) under a 12: 12-h light/dark photoperiod.

Filming conditions

This experiment studied the plasticity of *Pseudodiaptomus annandalei* mating behavior in relation to 5 sex ratio conditions (Table 1). We kept the final number of individuals constant (n = 30), to avoid any possible density effects. The experimental conditions of the sex ratio were named according to the ratio between males (M) and females (F): F1:M5, F1:M2, F1:M1, F2:M1, and F5:M1. The experiment began immediately after introducing adults into the experimental vessel, and was conducted with 4 replicates for each of the 5 conditions. Before introduction into the vessel, individuals were checked microscopically for morphological integrity and

Table 1. Experimental conditions used for the study of the effect of sex-ratio on *P. annandalei*'s mating behavior

Experiment label	Sex ratio F:M	Number of individual	
		Males	Females
F1:M5	1:5	25	5
F1:M2	1:2	20	10
F1:M1	1:1	15	15
F2:M1	2:1	10	20
F5:M1	5:1	5	25

health. Females carrying spermatophores were discarded. The adults were subsequently placed in the experimental vessel (5 × 5 × 6 cm) filled with 125 ml of brackish water at a salinity of 15 (composed of 0.45-μm filtered seawater and filtered fresh water). This produced a density of 240 individuals /L, as observed in the culture. The behavior of individuals was recorded for 30 min as described below.

Video techniques

The 3D video setup consisted of 2 ortho-gonally oriented black and white, infrared sensitive, charge-coupled device video cameras (JVC-TK250U-1/30Hz) equipped with a 105-mm Nikon macro lenses. Each camera was connected to a separate camcorder (operated at 30 frames/s, Sony DCR-SR100), which served as the recorder. Experiments were conducted in a dark room at a constant temperature (27°C). Illumination was provided from the top of the aquarium by 6 arrays of 8 infrared light-emitting diodes. Each camera overlooked the aquarium from the side, and various components of the setup were adjusted so that the copepods were adequately resolved and in focus. Two-dimensional projections of the swimming tracks were digitized using Labtrack Software (Bioras, Kvistgård, Denmark). Three-dimensional (3D) swimming patterns of individuals were obtained by combining information from the 2-dimensional (2D) views.

Behavioral analysis

Previous observations on another population of *P. annandalei* provided details of the mating process of this species (Dur et al. 2011). First, after successfully chasing its mating partner, the male seizes the female using its geniculate right antennule. Once the rejection dance is over, the male pulls the female by bending its antennule and rotates its body 180°. This enables the male to clasp the female's urosome by the left 5th leg; only then does the male release its antennule grip. The male subsequently places the flask-shaped spermatophore on the female's urosome using its right 5th leg (Fig. 1). The duration that separates the instant when the male clasps the female and when it aligns its spermatophore can last a minimum of 10 s (Dur et al. 2011). Therefore, the present study investigated the effectiveness of the rejection dance and considered encounters successful only when the pairing resulted in

spermatophore transfer. Transfer of a sperma-tophore was considered when the male was observed in the copulation position or when mates were linked to each other for at least 10 s. Copulation duration represented the time during which the mates stayed in tandem and were relatively inactive. Finally, dance and copulation durations were only considered when they were followed on video from beginning to end.

Statistical analysis

Multiple comparisons between sex ratio conditions were conducted using the Kruskal-Wallis (KW) test. To identify homogeneous subsets of means, multiple comparisons were conducted using pair-wise comparisons with the Wilcoxon-Mann-Whitney (WMW) test and the Tukey-Kramer method (TK test) to determine if post-hoc tests were significant. All statistical analyses were performed using MATLAB R2007b® (the Mathworks Company, inc).

RESULTS

While no significant differences were found (KW test, $p > 0.05$) between the different sex ratio conditions, encounters increased as the sex ratio
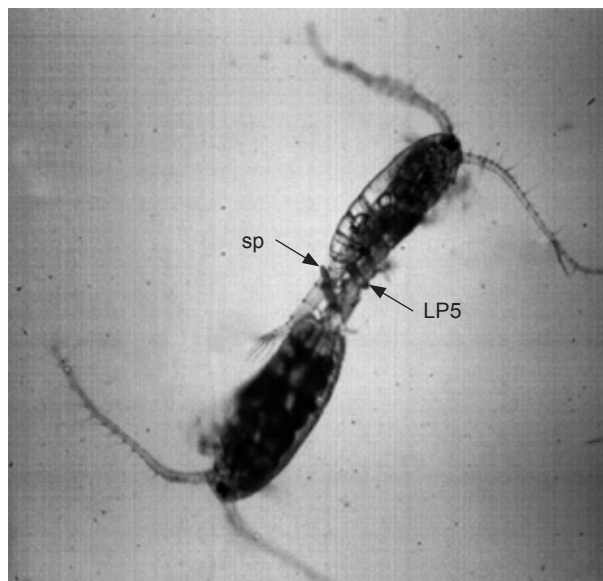

Fig. 1. *Pseudodiaptomus annandalei*'s individuals in the copulation position, in which the male (top) clasps the female (bottom) urosome by its modified left 5th leg (LP5). A spermatophore (sp) is also visible in the picture. Courtesy of D Beyrend-Dur.

was brought into balance (Fig. 2A). The lowest value (3.5 encounters/hr) was observed for a strongly male-biased sex ratio. The rate increased as the proportion of females balanced that of males. A maximum of 40 encounters/hr was obtained with an even sex ratio. By doubling the number of females, the encounter rate decreased to 17 encounters/hr. A proportion of females that was too high resulted in a great decrease in the number of encounters per hour, with a value similar to that of a sex ratio of 1 female for 2 males (about 9 encounters/hr). The number of encounters per hour decreased less considerably when the number of females increases compared to when the sex ratio was increasingly male-biased.

Success of these encounters also did not significantly differ among the sex ratio conditions (KW test, $p > 0.05$). However, we noted a tendency for success to decrease as the sex ratio became less male biased (Fig. 2B). Females were more selective, and had lower encounter success at female-biased sex ratios, with an average of only 14% of encounters leading to copulation. At even sex ratios, the successful encounter rate slightly increased to 24.9%. It continued to increase as the number of males in the vessel population increased. About 31% of encounters led to mating when male density was twice that of females. The encounter success rate reached its maximum value of 50% with a strongly male-biased sex ratio, of 1 female for 5 males (Fig. 2B). With a slightly female-biased sex ratio of 2:1, the percentage of successful encounters, at 36%, was slightly higher than those of an even sex ratio and a slightly male-biased sex ratio.

Table 2 presents the result of the sex ratio influence on the selective dance, copulation, and total mating durations. Durations of successful and unsuccessful dances did not differ between the different sex ratio conditions (KW, $p > 0.05$).
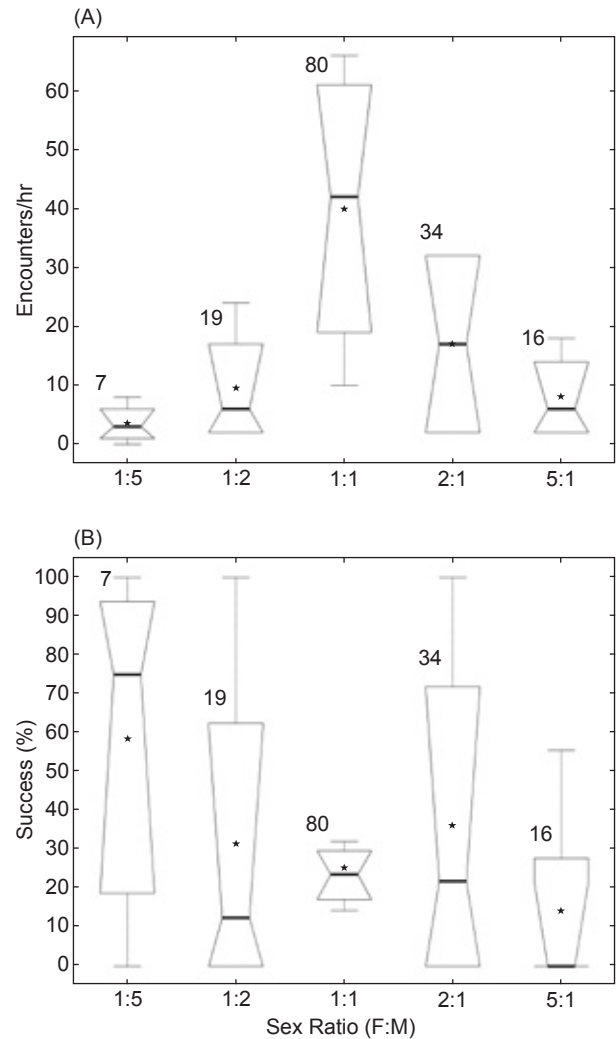
Fig. 2. Boxplot of the number of encounters per hour (A) and encounter success (B) observed for different sex ratios. A boxplot with whiskers provides from bottom to top: the minimum value, the 1st quartile, the median, the 3rd quartile, and the maximum value. Mean values of the encounter rate and encounter success are also provided (black stars). Numbers above the bar indicate the total numbers of encounters observed.

Table 2. Mean duration (± S.D.) of the different processes involved in mating of the copepod *P. annandalei* at 5 different sex ratios. The number of data points from which the values were computed is also presented (Nb)

Sex ratio F:M	Failed dance		Successful dance		Copulation position		Total mating	
	Duration (s)	Nb	Duration (s)	Nb	Duration (s)	Nb	Duration (s)	Nb
1:5	0.36 (± 0.2)	3	11.00 (± 0.0)	1	37.3 (± 0)	1	48.3 (± 0.0)	1
1:2	3.83 (± 5.5)	15	12.22 (± 4.6)	4	581.6 (± 0.0)	1	597.5 (± 0.0)	1
1:1	2.60 (± 2.6)	56	61.70 (± 84.4)	16	233.0 (± 137.1)	16	294.7 (± 132.0)	16
2:1	3.86 (± 6.3)	25	10.04 (± 6.0)	8	233.0 (± 137.1)	7	411.9 (± 193.4)	7
5:1	4.61 (± 6.0)	11	9.30 (± 3.5)	3	402.5 (± 199.1)	3	629.3 (± 291.2)	3

This result should be carefully considered relative to the small number of measurements recorded for successful dance durations. The shortest unsuccessful dances were observed in environments with strongly male-biased sex ratios. This value aside, the balanced sex ratio condition exhibited the shortest unsuccessful dance duration and the longest successful dance duration. We noted strong variability in dance durations at an even sex ratio despite a high number of observations. Additionally, successful dances were significantly longer than unsuccessful dances for each tested sex ratio (WMW, *p* < 0.05). The value of the condition 1F:2M aside, copulation duration and total mating duration increased with the number of females in the population or with a decrease in males in the studied population. The longest duration during which mates stayed in tandem, at about 15 min, was observed for the sex ratio condition of 5 females to 1 male. The shortest copulation duration of 37.3 s was observed for the 1F:5M sex ratio condition.

DISCUSSION

Like any animal, copepods are likely to exercise mate choice (Titelman et al. 2007). This species might be expected to exhibit variations in mate-choice mechanisms according to the OSR. To test this, the experiment placed copepods in different sex ratio conditions and examined whether these particular conditions influenced the mate encounter rate, mate choice, and male-male competition. To our knowledge, these results are the 1st in the field of copepod sexual selection.

A biased sex ratio was associated with a decrease in the encounter rate (hypothesis 1). The mate encounter rate (E, 1/d) depends on the volume of ambient water in which a male can search for females per unit time (β, L/d), and on the concentration of males (C_m, ind./L) and females (C_f, ind./L), and can be expressed as follows: $E = \beta\, C_m\, C_f$ (Kiørboe and Bagøien 2005). Considering the encounter rate as the number of events per unit of time, and assuming a fixed global density and a constant search volume rate (β), the previous equation gives a higher encounter rate for an even sex ratio condition (Fig. 3). For the same conditions, the encounter rate decreases as the sex ratio becomes increasingly unbalanced with a sharper decrease in male-biased sex ratios. Our results support the idea that the encounter rate reaches a maximum

value for balanced proportions of males and females, and decreases as the sex ratio becomes unbalanced (Fig. 3). A logical answer for the great skew toward a strong male-biased sex ratio is that when males are too numerous, they begin to interfere with each other. Considering again the equation of Kiørboe and Bagøien (2005) and our encounter data, we obtained variable values of β representing 8%, 16%, 56 %, 40%, and 16% of the experimental vessel per day for the 1F:5M, 1F:2M, 1F:1M, 2F:1M, and 5F:1M conditions. The slighter decrease in the search volume rate with female-biased conditions might be associated with the fact that females are less motile than males (Dur et al. 2010) thus creating less interference, but also a slackening in the effort to find a mate. The observed trend thus supports the idea of interference between individuals and highlights the need to consider density dependence in the equation of Kiørboe and Bagøien (2005).

In a natural environment, densities are always fluctuating. Any external pressure may affect the sex ratio and the density and consequently affect female mate choice or resistance and intra-sexual competition (Kokko and Rankin 2006). Considering this density dependence, we chose to maintain a constant total density to separate possible confounding effects of the sex ratio and density. The effect of density on the copepod mating system; thus far, has never been
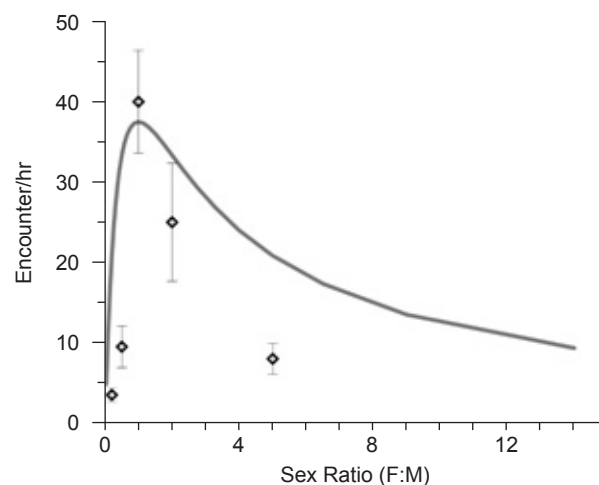
Fig. 3. Encounter rate value as a function of the sex ratio (F: M) according to equation (1) of Kiørboe and Bagøien (2005) for a constant total density of 240 individuals/L, and an arbitrary volume search rate of 4 L/d (gray). Mean values of the encounter rate observed for the tested sex ratio conditions are also presented (black diamond). Vertical bars represent the standard error (*n* = 4).

investigated. Such a study represents a continuity of the present work.

Not all encounters led to mating, and emphasis should be laid on fruitful encounters per female. Since *P. annandalei* females can carry several spermatophores and produce up to 2 clutches with only 1 sperm bag (Beyrend-Dur et al. 2011), they may not require repeated mating to remain fertile. Therefore, male selection by females is expected to be stronger when the pool of available mates is large (hypothesis 3). In our experiments, the strength of selection seemed to inversely decrease as the number of available mates increased. Higher values of success (i.e., copulation) were observed with a strong pro-male sex ratio. The reason for such low selection might instead be related to the encounter rate and our 2nd hypothesis, that females would be selective when the encounter rate is higher. The intensity of selection increased with an increasing encounter rate. However, no clear relationship between encounters and rejection plasticity was revealed (r^2 = 0.026) mainly due to the high variability. Additionally, we noted a relaxation in the duration of the rejection dance at uneven sex ratios, when encounters were lower. Our results support the concept that greater encounters may indeed increase female choosiness (Kokko and Rankin 2006). Nevertheless, considering the low number of observations, we view this analysis as tentative. Relaxation in selection observed for the F5:M1 condition can be associated with our hypothesis 3, that females in a mate-restricted environment would be less discriminating in their interactions with males.

When reproductive success is limited by access to gametes of the opposite sex, selection generally favors strategies that improve this access (Kokko and Rankin 2006). Therefore, longer mate guarding would be expected when there are few females (hypothesis 4). The opposite pattern was observed for *P. annandalei*, except in the condition where males were twice as numerous as females. Considering the relatively low number of observations and the high variability of copulation durations observed, further investigations are required before any conclusions can be drawn.

The sex ratio of copepods with a limited capacity to store sperm is close to 1:1 (Kiørboe 2006). However, in *Eurytemora affinis* from the Seine estuary (France), it is in favor of males and slightly varies 0.5-1 (F:M) during the year (Devreker et al. 2010). Similar results were obtained for *P. annandalei* in the Danshuei estuary, Taiwan

(Beyrend-Dur et al. pers. comm.). While these conditions may result in a lower encounter rate, the associated decrease in mate selection allows the maintenance of a basic mating rate sufficient to avoid critical densities. When the sex ratio increases and approaches equilibrium, mate selection is more important, without affecting population growth.

Further studies with a greater number of observations are needed to confirm the observed patterns and provide a typical response of encounter rate and mate selection related to the sex ratio. Additionally, environmental factors such as temperature have an influence on calanoid copepod sex ratios (Lee et al. 2003, Devreker et al. 2010) and are therefore involved in mating pattern plasticity. Climatic differences can account for the use of different mating strategies between temperate and tropical species. For a comparison between species from contrasting environments, OSR-dependent mating strategies must be carefully investigated. Copepods also face anthropogenic problems. In a polluted environment, the presence of contaminants could drive the sex ratio in favor of females (Forget-Leray et al. 2005). Moreover, low food quality (and probably other contaminant-like effects) could alter the sex ratio of estuarine copepods leading to the appearance of inter-sexual individuals (Souissi et al. 2010). The consequences of toxins or low food conditions on sex ratios and repercussions on copepod mating behavior would be an interesting subject for future studies.

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