REPRODUCTIVE BIOLOGY OF TWO SPECIES OF SQUAT LOBSTERS – FEMALE RECEP TIVITY AND INTERBROOD INTERVALS

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A B S T R A C T

The reproductive biology of many species of anomuran crabs is only poorly known. Herein we studied the reproductive biology of two species of squat lobsters, Cervimunida johni Porter, 1903 and Pleuroncodes monodon (H. Milne Edwards, 1837), which are target of a trawl fishery operating on the continental margin along the Chilean coast. During the reproductive period (May-November) we maintained squat lobsters in the laboratory to examine whether mating is related to the reproductive molt of the female and to determine the interbrood interval between successive broods. In both species females mated during the intermolt period. Females became receptive shortly after having released larvae from a previous brood, when they formed pairs with males. The interbrood interval (from larval release until having a subsequent brood) lasted <72 hour in the majority of female C. johni, but was longer in P. monodon, where most females took 72-144 hours before producing a new brood. Despite longer interbrood intervals, copulatory mate-guarding was substantially shorter in P. monodon than in C. johni. These differences in reproductive behavior might be due to differences in the general biology of the two species, including mobility and intraspecific aggression. Mating during the intermolt period may have several advantages, namely reducing the risk of cannibalism and energy costs of molting during the reproductive season.

KEY WORDS: female receptivity, mating, reproduction, squat lobsters, trawl fishery

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INTRODUCTION

Decapod crustaceans of commercial interest are found from shallow coastal waters to the deeper parts of the continental margin (Caddy, 1989). Good knowledge about their biology is essential for a sustainable management of crustacean fisheries (Orensanz et al., 1998). Basic information about the reproductive biology of a species such as fecundity, size at sexual maturity, population sex ratio, or proportion of reproductive females are relatively easily obtained from data collected during commercial fishery activities (Skáladóttir, 1998; Roa and Tapia, 2000; Aragón-Noriega and Alcántara-Razo, 2005; Aragón-Noriega and García-Juárez, 2007). In contrast, other parameters such as the mating potential of males and females, duration of embryo incubation, length of planktonic development, and the number of broods produced during a given reproductive season are difficult to obtain. Identification of these parameters requires the observation of individuals over time and usually involves laboratory surveys or time-consuming field observations. For example, laboratory observations have shown that mating and ovulation in many crustacean species is closely linked to the female’s reproductive (parturial) molt (Correa et al., 2003; Thompson and McLay, 2005; Bauer, 2011). However, there are also numerous species, including many anomurans, in which mating and ovulation occur during the intermolt period (Molenock, 1975; Hartnoll, 2000; Hines et al., 2003; Brockerhoff and McLay, 2005a, b; Wada et al., 2007). Furthermore, in some species, e.g., lobsters, female mating is highly plastic and females can mate either shortly after the reproductive molt or during the subsequent intermolt period (Cowan and Atema, 1990; Atema and Voigt, 1995; MacDiarmid and Sainte-Marie, 2006).

While many studies have been conducted during the past decade to elucidate the reproductive biology and mating behavior of fished crustaceans, biological knowledge about squat lobsters (Decapoda: Anomura) is very limited, even though some species are intensively fished or have been proposed as new fisheries resources (Zeldis, 1985; Tapella et al., 2002; Hernández-Llamas et al., 2006; Claverie and Smith, 2007; Wehrtmann and Acuña, 2011).

Present knowledge about the mating behavior of anomurans is mostly limited to king crabs and hermit crabs. In most king crabs, mating occurs after the female’s reproductive molt (Somerton and MacIntosh, 1985; Paul, 1992; Lovrich, 1997; Wada et al., 2000; Paul and Paul, 2001). In hermit crabs, females of some species mate after their reproductive molt but those of other species mate during the intermolt period (Wada et al., 2007). Similar observations of post-molt mating in some species and intermolt mating in other species have been reported for porcelainid crabs (Molenock, 1975).

If brood production occurs during the intermolt period, i.e., independent from a reproductive molt, determining the number of subsequent broods and the duration of the interbrood interval requires maintenance of reproductive females through several brood cycles (González-Gurriarán et al., 1998; Takahashi and Kawaguchi, 2004; Vinuesa and...
knowledge about the reproductive biology of both species can only be resolved by direct observations of their reproductive behavior, the objectives of this study were to: 1) determine whether mating is linked to the female’s molt or whether it occurs during the intermolt period, and to 2) estimate the interbrood interval for both species.

Materials and Methods

Collection and Maintenance of Squat Lobsters

Individuals were obtained from the commercial trawl fishery operating on the continental margin off the coast of Coquimbo, Chile (29°59′S, 71°23′W). Squat lobsters were sampled during the period May to November 2007, immediately placed in large coolers with seawater, and within 12 hours after capture transferred to a communal tank with flowing seawater and ad libitum food supply (dead fish and crushed mollusks). The day after capture, all individuals were carefully sorted, and depending on availability of healthy individuals, each month we selected a maximum of 60 ovigerous females and 60 non-ovigerous females from both species for mating experiments. Ovigerous females used in this study had a carapace length (CL) of 22–42 mm, while non-ovigerous females were slightly smaller (CL 21–37 mm in C. johni and 24–34 mm in P. monodon). The males usually were larger than the females in both species (C. johni: 25–46 mm; P. monodon: 29–43 mm).

For C. johni we obtained ovigerous females (n = 270) between May and October, and non-ovigerous females (n = 146) in May, June, July and September. In P. monodon ovigerous females (n = 256) were obtained between June and November (except in September) and non-ovigerous females (n = 29) only in November. Both species adjusted well to the laboratory environment. Mortality of female C. johni was low throughout the study period (11.3% from May to August, 6.0% from September to November), but was higher in P. monodon (20.6% from June to August; 45.7% from September to November). The high mortality during the time period September to November was due to the fact that individuals were close to molting and reached the laboratory in poor status. Furthermore, cannibalism of newly molted individuals commonly occurred in the laboratory tanks, contributing to the high mortality later in the year.

Some females were maintained for several months in the laboratory, during which time they could produce several subsequent broods (158 females C. johni and 64 females P. monodon). Other females (258 females C. johni and 221 females P. monodon) only remained for a few weeks in the laboratory, namely until they produced a new brood in mating experiments. To analyse whether female receptivity is related to the molt, we utilized pooled data from all females related to the molt, we utilized pooled data from all females maintained in this study (n = 416 females producing 539 broods for C. johni; n = 285 females producing 216 broods for P. monodon), including long-term laboratory inhabitants and females used in short-term experiments (see above).

To determine the female latency (from releasing one brood to pair formation) and the interbrood interval, we only used ovigerous females that had recently been brought to the laboratory (n = 142 for latency & copulatory duration, and n = 175 for interbrood interval in C. johni; n = 148 for interbrood interval in P. monodon). For all broods produced...
in the laboratory we maintained females until they released the brood in order to confirm that the eggs had been fertilized and developed normally.

Female Receptivity

Ovigerous females of both species were held in “incubation tanks” of 300 l volume with flowing seawater and regular food supply. All females were checked every 3 days in order to identify females that had recently released larvae (post-ovigerous), which were then placed in “pairing tanks” of 300 l volume with flowing seawater (Fig. 1). Here they were maintained with a corresponding number of males (CL male > CL female) and regular food supply.

Fig. 1. Schematic overview of set-up to detect whether female receptivity is linked to a reproductive molt or whether females become receptive during the intermolt. Ovigerous females (indicated by grey patch under their pleon) were maintained in incubation tanks where they were monitored for their reproductive status (ovigerous or non-ovigerous) every 3 days. Once a post-ovigerous female was identified it was transferred together with large adult males to pairing tanks, which were monitored every 12 hours in order to identify precopulatory pairs. Pairs were isolated in a mating tank and monitored every 12 hours. If the pair had separated, the reproductive state of the female was examined, and if it was ovigerous it was placed in a new incubation tank. If the female was not ovigerous it was left for 48 hours in the mating tank and if no new precopula formed during that time it was returned to the pairing tank. All females in the pairing tanks were also checked every 3 days for the appearance of ovigerous females, which were then transferred to the respective incubation tanks. During the regular surveys of the incubation, pairing and mating tanks, special attention was given to the potential appearance of shed exuviae and females with soft carapace.
The pairing tanks of both species were surveyed every 12 hours (at approximately 8:00 and 20:00) to reveal whether precopulatory mate-guarding (male holding the female at one of its chelae) occurred. Pairing tanks were also checked every 3 days for ovigerous females which had mated without being seen in precopula with a male. Precopulatory pairs were removed, placed in mating tanks (see below), and if necessary a new male was added to the pairing tank in order to maintain a sexual proportion of about 1 male per 3 females. This sex ratio was chosen in order to not over-populate tanks and to reduce the risk of agonistic interactions among males; at least in *C. johni* the effective sex ratio was higher because as soon as male-female pairs were removed new males were added to the pairing tanks. Non-ovigerous females were immediately placed in pairing tanks and then surveyed in the same way as mentioned above.

Females that became ovigerous in the laboratory (coming from pairing or mating tanks) were placed again in special incubation tanks where females that became ovigerous in the same week were maintained together to verify that their eggs had been fertilized and developed normally. During the surveys of the tanks particular attention was paid to the eventual appearance of recently shed exuvia or females with soft exoskeletons, thereby testing whether mating is related to the female’s molt or not (Fig. 1).

Females were maintained in pairing tanks for a maximum of 6 weeks, and if they did not pair or mate with a male during that time period, they were considered to not produce another brood during that reproductive period. If during their time in pairing tanks a female molted, it was maintained in this pairing tank for another 6 weeks after the molt; if it did not pair with a male or no new brood appeared during this time period, the female was removed from the pairing tank.

### Female Latency and Interbrood Interval

Precopulatory pairs of *C. johni* with post-ovigerous females that formed in the pairing tanks were carefully transferred to small (12 l) “mating aquaria” with flowing seawater. Pairs were moved with a dip net and they occasionally separated during transfer, but usually re-established quickly in the mating tanks. Pairs were maintained individually in the mating tanks. These pairs were then monitored every 12 hours to reveal whether the pair persisted or had separated. If the male had released the female, the latter was carefully examined for its reproductive status (ovigerous or non-ovigerous). Furthermore, every 3 days we monitored the reproductive status of the females that remained in precopulatory pairs in these mating aquaria. Precopulatory pairs were maintained until the male released the female. If the female was ovigerous, it was immediately transferred to an incubation tank. If the released female was not ovigerous it was left for another 48 hours in the mating aquarium with the corresponding male. If after these 48 hours the female remained non-ovigerous and the male did not take it again in the precopulatory embrace, it was returned to the pairing tank (Table 1).

For *C. johni*, this method allowed us to obtain the approximate time periods from the moment when the female was identified as post-ovigerous female, i.e., having recently released larvae, until the moment it formed a pair with a male (ld = latency duration), and from first formation of a pair until it became ovigerous again (dpo = duration from pair formation until ovigerous). For *P. monodon* we only obtained the total time period (ld + dpo = duration of interbrood interval) from the moment the female was identified as post-ovigerous until it became ovigerous again (Fig. 2), because the duration of the copulatory pair was extremely short in this species (<15 min, M. Thiel et al., unpublished data).

### Table 1. Observation protocol of mating pairs of *Cervimunida johni*, which is based on a dichotomous key, indicating the different treatments depending on the condition and duration of the pair or the reproductive status (ovigerous or non-ovigerous) of the female. All pairing tanks were surveyed every 12 hours at about 08:00 in the morning and 20:00 in the evening.

<table>
<thead>
<tr>
<th>Treatment of pairs</th>
<th>1. Status of surveyed pair.</th>
<th>2. Continue regular 12 h surveys of pairs for 20 days</th>
<th>3. As long as pair remains together examine the reproductive status of female (ovigerous or non-ovigerous) every 3 days.</th>
<th>4. Measure carapace length of male and replace with new male; continue regular surveys of new pair.</th>
<th>5. Examine reproductive status of female</th>
<th>6. Measure carapace length and transfer female to incubation tank; observation of pair ends!</th>
<th>7. Continue regular 12 h surveys for 48 h</th>
<th>8. Measure carapace length of male and female and return both to the pairing tank; observation of pair ends!</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a. Pair together</td>
<td>1b. Pair is separated</td>
<td>2a. Pair together for &lt;20 days</td>
<td>2b. Pair is together for &gt;20 days</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>6</td>
<td>8</td>
</tr>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
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<td>5</td>
<td>6</td>
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<td>8</td>
<td></td>
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</table>
Fig. 2. Schematic overview of the time intervals determined in this study. The interval from the moment the female was identified as post-ovigerous, i.e., has released her larvae, until she forms a pair with a male in the mating tank was termed the latency period. The interval from first pair formation until the female becomes ovigerous was called copulatory mate-guarding. In most cases the pair separated as soon as the female became ovigerous, but in some cases the male continued to guard the female even when she was ovigerous. The total time period from the moment the female is identified as post-ovigerous until she produced a new clutch is called the interbrood interval.

During the 3-day surveys of the reproductive status of the females in the incubation tanks, we briefly examined the developmental stage of embryos in the egg mass. The eyes were clearly visible in advanced embryos (starting at about day 30 of incubation), indicating that the egg mass had been successfully fertilized and developed normally. Females that lost their brood <30 days after they had first been registered as ovigerous were considered to have aborted an unfertilized brood. These females were then removed from the incubation tanks and replaced in the pairing tanks. When females released their broods at the end of embryonic development, the tanks were usually filled with larvae. Often, some embryos and empty egg cases could still be seen on the pleopods of females that had just released their brood, but these were then cleaned off by the fifth pereiopods. For both species of squat lobsters, females that were identified as post-ovigerous could have released their larvae at any moment during the 3-day intervals between subsequent surveys. Consequently, there is a margin of imprecision of 0-72 hours for all estimates of latency duration (ld) or total interbrood interval (ld + dpo).

RESULTS

In *C. johni* we surveyed a total of 173 precopulatory pairs, of which 158 formed after the female had successfully released larvae from a previous brood (Table 2). Fifteen females formed a precopulatory pair after they had aborted a previous brood. Of the 158 females that had successfully released larvae, 142 produced a new brood and of the 15 females that had aborted 12 females produced a new brood. The remaining 19 females (3 of which died while paired with a male) did not become ovigerous again (Table 2).

Female Receptivity

In none of the 142 females of *C. johni* that mated successfully after having released a brood, did we observe a molting event immediately before the female became ovigerous again. In general, of all females maintained during the 6 months of this study (n = 416 ovigerous + non-ovigerous females of *C. johni*), only 98 molted in the laboratory, which primarily occurred during the last 3 months of the study (September-November 2007), and none of these females became ovigerous within the first 15 d after their molt (Fig. 3). All females that molted had previously successfully released their larvae. Only 4 females produced a new brood within 18-42 d after the molting event (Fig. 3).

In *P. monodon* we obtained 148 ovigerous females during the regular 3-day surveys in the pairing tanks. In none of these cases did we observe a molt in the tank and all females had a hard exoskeleton, i.e. there was no indication of a recent molting event. Similar as in *C. johni*, we only registered a molting event for 50 of all ovigerous and non-ovigerous female *P. monodon* maintained in the laboratory during the 6-month study (n = 285). Ten of these 50 females produced a new brood within 3-18 days after the molt, but always after their new exoskeleton had hardened again (Fig. 3).

In both species, the majority of females that molted in the laboratory released their broods about 20-40 d before the molting event (Fig. 3). Furthermore, males showed no reproductive attraction towards recently molted females – to the contrary, on several occasions we observed that males and other females cannibalized the recently molted female.

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**Table 2.** Pairs of *Cervimunida johni* that formed from ovigerous females that had come from the field and became non-ovigerous in the laboratory. Two groups of females were distinguished, those that successfully released larva in the lab and those that had aborted their clutch prematurely. For each of these groups, the number of females that mated successfully and produced a new brood (mated successfully) and the number of females that paired up with a male but did not produce a new brood within 6 weeks (mated unsuccessfully) are given.

<table>
<thead>
<tr>
<th>Females</th>
<th>Successfully released larva</th>
<th>Aborted a previous brood</th>
<th>Total pairs</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Successfully released larva</td>
<td>Aborted a previous brood</td>
<td>Total pairs</td>
</tr>
<tr>
<td>Pairs mated successfully</td>
<td>142</td>
<td>16</td>
<td>173</td>
</tr>
<tr>
<td>Pairs mated unsuccessfully</td>
<td>16</td>
<td>12</td>
<td>3</td>
</tr>
</tbody>
</table>
Fig. 3. Percent of molted females and the time intervals before the molt (left side of the figure) at which they released the larvae of the last brood before the molt, and percent molted females and the time intervals after the molt (right side of the figure) when they became ovigerous again after their last molt. Values based on all females that molted in the laboratory between May and November 2007 ($n = 98$ for *Cervimunida johni*; $n = 50$ for *Pleuroncodes monodon*).

Interbrood Intervals

The latency duration until precopulatory guarding in *C. johni* was relatively short. Most females (94.4%) were taken into the precopulatory embrace by a male within 12 hours after being identified as post-ovigerous and placed in the pairing tanks, and only 5.6% required more than 12 hours before forming a pair with a male (with a maximum of 144 hours) (Fig. 4a). The pairs with those 142 females of *C. johni* that mated successfully after releasing a brood did not last very long (Fig. 4b). The majority (57.7%) of these females became ovigerous within 12 hours after being taken in the precopulatory embrace by the male and placed in the mating tank. About 20% of these females became ovigerous after 12-24 hours, and the remaining 22.5% stayed in precopulatory pairs for $>24$ hours (with a maximum of 612 h) before producing a new brood.

Of the 175 post-ovigerous females of *C. johni* (142 monitored in mating tanks + 33 becoming ovigerous in pairing tanks) that produced a new brood after being brought to the laboratory during the monthly surveys, the majority (87.4%) produced a new brood within 72 hours after the female had been identified as post-ovigerous and only 12.6% had an interbrood interval $>72$ hours (with a maximum of 624 hours) (Fig. 5). In *P. monodon* the interbrood intervals were substantially longer than in *C. johni*. Of the 148 females of *P. monodon* that became ovigerous in the laboratory, only 25.7% did so within 72 hours after being identified as post-ovigerous. In the majority (41%) of the post-ovigerous females *P. monodon*, the interbrood interval lasted 72-144 hours, and in a substantial proportion it even took $>144$ h (with a maximum of 1080 hours, i.e., 45 days for one female) (Fig. 5).

**DISCUSSION**

The results of this study demonstrate that both species of squat lobsters from the continental margin off Chile mate during the intermolt period. However, despite this general similarity, there are also important differences between the two species. In particular the interbrood interval was considerably longer in *P. monodon* than in *C. johni*. Also,
based on our data we infer that the duration of mate-guarding is substantially shorter than 12 hours in *P. monodon*, whereas it may extend beyond 12 hours in *C. johni*. Possibly these differences are linked to the general biology, e.g., mobility, resource finding and monopolization, of each species, as discussed below.

**Female Receptivity**

In many crustacean species, females mate after the reproductive molt (Correa et al., 2003; Thompson and McLay, 2005). This putative relationship between female molting and mating has been used as justification to close the fishing seasons for both squat lobster species during the period with a high proportion of molted individuals (January-March; SUBPESCA, 1996, 2005). However, our results show that mating in both studied species is unrelated to the female molt and does not occur during the presently established closed seasons. Instead mating occurs during the time when most females are found to be ovigerous in the field (May-November), when there is no or only minor molting activity (Gutiérrez and Zuñiga, 1977; Wolff and Aroca, 1995; Palma and Arana, 1997; Acuña et al., 1998). Both species mate during the intermolt period and females produce successive broods without molting, which is also true for many brachyuran crabs with spermathecae (Jennings et al., 2000; Brockerhoff and McLay, 2005a, b), as well as spiny lobsters (Lipcius et al., 1983), and penaeid shrimp (Yano, 1995; Díaz et al., 2003). In these and other species mating occurs during the intermolt or during the early pre-molt period.

At present, the information about the mating behavior of squat lobsters or closely related species is scarce. In *Munida gregaria* (Fabricius, 1793), females mate during the intermolt period (Pérez-Barros et al., 2011), which had also been suggested for other species (see Thiel and Lovrich, 2011). While in lithodid crabs, mating usually occurs after the female molt (Somerton and MacIntosh, 1985; Paul, 1992; Lovrich, 1997; Wada et al., 2000; Paul and Paul, 2001), in several anomuran species mating occurs during the intermolt period. For example, in the freshwater crab *Aegla platensis* Schmitt, 1942 females mate without any need for molting (Almeraño et al., 2010). Some species of hermit crabs can facultatively mate during the intermolt period, while mating in others is restricted to the intermolt period (Wada et al., 2007). Similarly, in some porcelainid crabs intermolt mating appears to be facultative, while in others it is obligatory (Molenock, 1975). In many majid crabs, which have spermathecae and terminal molt, females can mate immediately after the reproductive (terminal) molt but also at variable periods thereafter (González-Gurriarán et al., 1998). In *C. johni* and *P. monodon* all matings occurred during the intermolt period of the females, and thus it seems to be obligatory.

**Interbrood Interval**

In most cases observed in this study, the interbrood interval was relatively short, usually not lasting much more than a few days. Similarly short interbrood intervals have been reported for many brachyuran crabs (with sperm storage), mysids and shrimps (e.g. González-Gurriarán et al., 1998; Hines et al., 2003; Takahashi and Kawaguchi, 2004; Vinuesa and Ferrari, 2008; Bauer and Thiel, 2011). In some species, the interbrood intervals within the annual reproductive season can be substantially longer. For example, in the intertidal crab *Pilumnus vespertilio* (Fabricius, 1793) 5-10 days pass between successive broods (Kyomo, 2002). In *Cancer anthonyi* Rathbun, 1897, females produce a new brood within 1-2 months after having released a preceding brood (Shields et al., 1991). Species with longer interbrood intervals might require more time to complete gametogenesis than species with short intervals, in which ovary maturation is usually closely synchronized with embryo development (Dellatorre and Barón, 2008).

Interbrood intervals can be divided into two time periods, namely the latency period between hatching of the previous brood and initiation of pair formation, and the mate-guarding period. In *C. johni*, precopulatory pairs formed shortly after a post-ovigerous female was introduced to a pairing tank, suggesting that the latency period in this species is very short. This indicates that: 1) males quickly recognize a female that is ready to produce a new brood, and 2) that these females are receptive to mating shortly after having released their previous brood.

Furthermore, our 12-hour surveys of the pairing tanks allowed us to find >80% of all females that produced a subsequent brood in copulatory pairs. This indicates that mate-guarding in *C. johni* lasts many hours, often >12 hours. In contrast, in *P. monodon*, no copulatory pairs were found during the 12-hour surveys, but many ovigerous females appeared in the pairing tanks during the 3-day checks, which indicates that mate-guarding is very short in this species. The short duration of mate-guarding in *P. monodon* in combination with the comparatively long interbrood interval demonstrates that the latency period in this species is substantially longer than in *C. johni*.

The causes for the differences between the two species in the latency duration and the interbrood intervals are unknown at present. Several studies had shown that the latency period may vary depending on the operational sex ratio (OSR) and the presence of preferred mates (Wada et al., 2000; Thiel and Hinojo, 2003; Brockerhoff and McLay, 2005a, b). Similarly, variations in the OSR cause differences in the duration of precopulatory mate-guarding (Iribarne et al., 1995; Wada et al., 2000; Rondeau and Sainte-Marie, 2001).

One of the components of the OSR that is most difficult to estimate is the possibility of individuals to find each other in the natural environment. Possibly, the mate-finding ability of *P. monodon* is higher than of *C. johni*, and therefore in *P. monodon* both sexes can afford to delay pair formation until the moment immediately before female ovulation. Pelagic phases have been reported from the genus *Pleuroncodes*, underlining their high mobility (Boyd, 1967; Robinson and Gomez-Aguirre, 2004). Furthermore, sexual size dimorphism (males > females) is more pronounced in *C. johni* (Wolff and Aroca, 1995; Acuña et al., 2008) than in *P. monodon* (Roa and Tapia, 2000), suggesting that male *C. johni* aggressively compete for access to females while male *P. monodon* might use the search strategy to find receptive females. Avoidance of direct body contact might also be advantageous in *P. monodon*, in which members of both sexes were much more active and aggressive in the labora-
tory tanks than male and female C. johni, evidenced herein by the higher mortality of P. monodon due to cannibalism. Female P. monodon might hide their reproductive status and only reveal their receptivity shortly before ovulation.

The capacity to release larvae and produce a new brood within very short time periods had also been suggested for M. gregaria (Dellatorre and Barón, 2008) and Maja squinado (González-Gurríarán et al., 1998). These short interbrood intervals make recognition of subsequent broods via field samples, e.g., the proportion of ovigerous females, difficult, because throughout the reproductive season a high proportion of females is ovigerous. This could easily lead to misinterpretation of reproductive peaks and brood numbers, which can only be avoided by careful and simultaneous analysis of ovary and embryo maturation stages (for an excellent example see Dellatorre and Barón, 2008).

Advantages and Disadvantages of Intermolt Mating

Mating during the intermolt period can be advantageous for crustacean females. Females that mate without the need for molting are less exposed to the risk of predation and cannibalism (Somerton and MacIntosh, 1985; Hartnoll, 2000; Brockerhoff and McClay, 2005a, b). Squat lobsters are usually considered deposit-feeders (Aurioles-Gamboa and Pérez-Flores, 1997; Romero et al., 2004), but they also feed on carrion (Vinuesa and Varisco, 2007) and injured conspecifics (Karas et al., 2007), which is confirmed by our laboratory observations. We also observed multiple incidents of cannibalism, suggesting that recently molted squat lobsters might be very susceptible to aggressive approaches by conspecifics or even the respective other species. In addition to lower predation risk, females that mate during the intermolt are less susceptible to potential damage caused by male harassment or fights among males (Hartnoll, 2006).

Molting also requires energy and if females can reproduce without the need to molt, they can invest all available surplus energy into reproduction. Another benefit is the reduction of the interbrood interval, because a female could produce a subsequent brood shortly after releasing the preceding brood (Wada et al., 2008).

Mating during the intermolt period can, however, also have important disadvantages. At molting, females recover the morphological integrity of their pleopods. Since pleopods most likely suffer wear during incubation, females that incubate successive broods without molting might lose part of their potential to sustain developing embryos on their pleopods (see Wada et al., 2007). Molting can also be advantageous to eliminate parasites and fouling organisms that attach to the exoskeleton (Becker and Wahl, 1996); these parasites might accumulate and be transmitted during intermolt matings. Finally, growth depends on molting, and females that continue to reproduce for extended time periods at small body sizes might forego important increases of their reproductive potential (Hartnoll, 2006).

Intermolt mating appears to be relatively common in anomurans (Molenock, 1975; Wada et al., 2007), and the results of our study confirm this for two species of squat lobsters. Together with the short interbrood interval, this behavior enables these species to produce subsequent broods within relatively short time periods. This could be advantageous under conditions where the reproductive season is limited by environmental conditions.

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REFERENCES


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