

Absence of a prezygotic behavioural barrier to gene flow between the two sympatric morphs of the squat lobster *Munida gregaria* (Fabricius, 1793) (Decapoda: Anomura: Galatheidae)

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Abstract *Munida gregaria* and *M. subrugosa* have been considered two different species for more than a century; however, after a recent molecular phylogenetic study, they are considered a single polymorphic species. Yet, the use of markers to diagnose species may be misleading when divergence between species is recent, since a speciation event may be obscured by the retention and stochastic sorting of ancestral polymorphisms. The morphs *gregaria* and *subrugosa* of *Munida gregaria* constitute an interesting case for the study of behavioural isolation since they are sympatric, breed at the same time of the year, and might have experienced a recent speciation. Mating behaviour observations and mate choice mating trials were conducted in order to investigate the potential existence of a behavioural prezygotic barrier to gene flow between these two morphs. Since factors involved in mate choice in galatheids are unknown, the four possible combinations of the two different morphs in trios were used to test for the existence of mate choice. Video recordings of all the possible trio combinations revealed that there was cross-attraction between males and females of different morphs. Females

bearing partial broods participated in encounters as well as non-ovigerous females. The frequency and duration of homo- and heterotypic encounters were registered, and a reproductive isolation index was calculated for each variable for each trio. The isolation indexes calculated were not different from zero indicating random mating, and were not affected by the composition of the trio or the partial ovigerous condition of females. These results provided evidence of the absence of behavioural prezygotic barriers to gene flow between the morphs *gregaria* and *subrugosa* of *M. gregaria*.

Keywords Crustacea · Mating behaviour · Reproductive isolation · Speciation

Introduction

The use of molecular markers in the identification of species has revealed that cryptic species are more common among marine organisms than previously thought (Knowlton 1993; Miya and Nishida 1997). Yet, cases in which morphologic differentiation occurs in the absence of genetic divergence have also been reported, suggesting a recent separation or continuing gene flow (Schubart et al. 2001a, b). However, using molecular markers to diagnose species may be misleading when divergence between species is recent, since a speciation event may be obscured by the retention and stochastic sorting of ancestral polymorphisms, i.e. incomplete lineage sorting (Maddison and Knowles 2006).

The completion of speciation depends on the magnitude of the pre- and/or postzygotic isolation developed (Via 2001; Kirkpatrick and Ravigne 2002). Recent studies suggest that prezygotic reproductive isolation, especially behavioural isolation, is more effective than postmating

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isolation in the formation and maintenance of sympatric species (Coyne and Orr 1998; Gavrillets and Boake 1998; Boake et al. 2000). The contribution of mating behaviour to the isolation of species is widespread among invertebrate and vertebrate taxa (Gavrillets and Boake 1998; Boake et al. 2000). Sympatric species that experience no temporal or habitat isolation and rarely or never hybridize are appropriate cases for the study of behavioural isolation (Coyne and Orr 2004).

The sympatric forms “gregaria” and “subrugosa” of the squat lobster *Munida gregaria* (Crustacea: Anomura: Galatheidae) are commonly found off the southern tip of South America, New Zealand and southern Australia (Baba et al. 2008). A recent molecular genetic study revealed that these two morphs could not be consistently separated based on four (three mitochondrial and one nuclear) gene fragments (Pérez-Barros et al. 2008). Authors concluded that these two forms might either represent a case of a very recent speciation not resolved by the molecular markers employed, or a dimorphic species. The fact that these two forms might be undergoing a speciation process makes them an interesting case to explore the mechanisms that could be involved in the establishment of reproductive isolation (Boake et al. 2000).

Conspecific communication signals are expected to control and regulate courtship and reproductive behaviours to prevent interspecific matings (Bushmann 1999). In crustaceans, this communication is based on chemical, acoustic and visual signals, being the first ones of major importance in most aquatic species (Jones and Hartnoll 1997; Díaz and Thiel 2004 and references therein). Waterborne odours may be elicited by either sex to attract mates, as shown for *Homarus americanus*, *Rhynchocinetes typus*, *Callinectes sapidus*, *Chionoecetes opilio* and *Carcinus maenas* (Díaz and Thiel 2004 and references therein; Atema and Steinbach 2007). In decapod crustaceans, chemicals released by the brood may prompt different female behaviours, from grooming to synchronization of egg hatching (Rittschof and Cohen 2004 and references therein). Eggs have also been proposed as a source of chemical cues that may elicit some reaction from males (Bouchard et al. 1996). In the Beagle Channel—the southernmost extreme of the geographical distribution of *Munida gregaria*—the reproductive cycle is annual: ovigerous females occur between May and September and a single larval hatching per female takes place between September and November (Tapella et al. 2002a; Pérez-Barros et al. 2007). Adult females moult between larval release and the next oocyte extrusion (Tapella 2002). At the beginning of the reproductive season, i.e. May or June depending on the year, most of the brooding females carry partial clutches that are found complete 2–4 weeks later in the season (Tapella et al. 2002a). These clutches bear eggs

at the initial phases of their division or, less likely, recently extruded oocytes (Tapella et al. 2002a). So far, causes for these partial clutches are not understood, and their presence at the beginning of the reproductive season of *Munida gregaria* morph subrugosa led Tapella et al. (2002a) to postulate that eggs may attract mates.

In squat lobsters, mating behaviour, size composition of mating couples and mate choice are so far unknown. In arthropods, there is a general preference for large mates (Crespi 1989), and body size is positively correlated with mating success and fecundity (Andersson 1994). Larger males are often stronger competitors for females (Hoefler 2007), can provide more sperm (Sato and Goshima 2007a), can mate with several females in a single mating season (Paul and Paul 1990; Paul and Paul 1997; Sato et al. 2005), or have an advantage in struggles with females to capture or physically control them during the mating and guarding phases (Lee and Seed 1992). In turn, females may resist mating and copulate only with males that overcome female reluctance to mate (Kokko et al. 2003). For example, some lithodid females prefer larger males since they are able to assess whether males can transfer sufficient sperm for successful fertilization (Sato and Goshima 2007b). However, in other lithodids, larger females can mate with males much smaller than themselves, but at the cost of lower fertilization rates (Sato and Yoseda 2010). Hence, mate choice is nonrandom in the majority of animal species (Real 1990), and males and females mutually prefer larger mates (e.g. Aquiloni and Gherardi 2008). Moreover, male–male competition is also unknown in squat lobsters. Male–male competition implies trade-offs between time spent feeding, growing (moulting), interacting agonistically with other males, courting, and mating (Kendall and Wolcott 1999). High male–male competition is expected in cases when females are briefly and infrequently receptive, because they spend most of their time taking care of their progeny (Rondeau and Sainte-Maire 2001).

In this study, we investigated the potential existence of prezygotic behavioural barriers to gene flow between the sympatric forms of *M. gregaria*. Since the knowledge about the reproductive behaviour of galatheids is poor (Kronenberger et al. 2004), a first description of the mating behaviour of this species was carried out. We predict that if behavioural reproductive isolation exists between the two forms then: (a) mating encounters between individuals of the same morph (homotypic) will be more frequent than those between different morphs (heterotypic), and that (b) the total time spent in such behaviours will be greater between individuals of the same morph than between individuals of different morphs. Positive responses to both (a) and (b) will indicate a preference for mating with individuals of the same morph, therefore constituting a behavioural barrier to gene flow. Furthermore, we expect

that if partial broods elicit cues involved in morph recognition, ovigerous females will experience more and longer homotypic than heterotypic mating encounters.

Materials and methods

Collection and maintenance of breeding stocks

Munida gregaria specimens were collected in the Beagle Channel, Argentina (55°S 68°W) by epibenthic trawling. Since the reproductive cycle starts in May–June with egg extrusion and fertilization (Tapella et al. 2002a), animals were captured in late April 2004 and 2006. Individuals were separated in the laboratory by morph and sex. They were maintained in two 4,000-l tanks: one for males and one for females, with independent supplies of seawater. Within each tank, individuals of each morph were placed in different cages and kept at $7 \pm 0.5^\circ\text{C}$ and 30 psu salinity, under natural photoperiodic conditions (7 light:17 dark). They were fed with squid three times a week. Sexually mature (i.e. CL > 10 mm, Tapella et al. 2002a) and healthy individuals, i.e., without parasites and with all pereopods, were randomly selected and transported to a refrigerated chamber (water temperature: $7 \pm 0.5^\circ\text{C}$) 2 days before the beginning of the experiments.

Mating experiments

Mating behaviour was described on the basis of both direct observations (Experiment A) and video recordings of mate choice mating trials described below (Experiment B). The potential existence of prezygotic behavioural isolation between the gregaria and subrugosa morphs of *M. gregaria* was investigated by means of mating trials (Experiment B).

Experiment A: direct observations of mating behaviour

Eight couples (2 of each of the 4 possible types of couples: 2 homotypic and 2 heterotypic) were observed directly during 2 days and 2 nights to describe the basic mating interactions of squat lobsters. A male and a female were placed in a glass tank (25 × 20 × 15 cm) filled with seawater ($7 \pm 0.5^\circ\text{C}$), under a natural photoperiod (7 light: 10 h to 17 h—17 dark: 17 h to 10 h). Between 9:00 and 22:30 h, each pair was observed at different hours of the day (range of observation time/aquarium/day = 35–195 min) and of the night (range of observation time/aquarium/night = 35–160 min). During night observations, light was provided by a red bulb. Observations were done using the ad libitum method (Altmann 1974), i.e. non-systematic and informal. Records consisted of annotations of interactions between animals during the observation period. The

minimum continuous observation time was of 35 min, and observation intervals were not necessarily spaced regularly during the 48-h experiment. As a general rule, observations were done once during the morning, afternoon and night.

Experiment B: mate choice mating trials

Mating trios (2 males + 1 female or 1 male + 2 females) were placed in a 27 × 23 × 15.5 cm transparent plastic container filled with seawater (hereafter “aquarium”) for the observation of mating interactions. The following trios were used for mating trials:

Trio type FFMG: two females -one of each morph- and a gregaria male,

Trio type MMFG: two males -one of each morph- and a gregaria female,

Trio type FFMS: two females -one of each morph- and a subrugosa male,

Trio type MMFS: two males -one of each morph- and a subrugosa female.

where F: female, M: male, G: gregaria and S: subrugosa.

The rationale for the election of a trio as experimental unit was to (1) give both sexes the same opportunity to choose its partner, and (2) minimize interactions (i.e. competition for the opposite sex) between individuals of the same sex. To avoid size-assortative mating interference, when there were more than one female or more than one male in the trio, they were selected so that sizes of individuals of the same sex were similar.

Each trio was placed in the aquarium 10 min before recording to allow individuals to get used to the new environment. Each set of 4 trios was recorded only once for a total time of 3 h. Video recordings were made using a Hitachi VM 2500A camcorder connected to a video capture board Pinnacle Systems AV/DV Deluxe. All videos were processed by the same observer using the Pinnacle Studio version 9 software. Since recording was done from above (Fig. 1), animals were marked on the carapace using white nail varnish in order to enable recognition of sex and morph. Marking was performed at least a day before recording to allow animals to recover from this procedure. To visually isolate the different aquaria, we covered the aquarium walls and floor with white paper. After each trio was removed, aquaria were washed. Each aquarium was always used for the same type of trio. When animals were removed from the aquaria they were checked for the presence of spermatophores by unfolding their abdomens and by inspecting them with a 2x magnifier lamp. After this, the carapace length of the three animals in each trio was measured. Due to experimental procedures (2 daily sets of 4 trio-recordings), we could not maintain females to check for egg extrusion and fertilization. However, similar

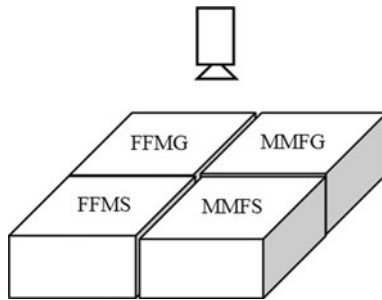


Fig. 1 Schematic view of the arrangement of the aquaria containing the four different types of trios (FFMG: two females -one of each morph- and a gregaria male, MMFG: two males -one of each morph- and a gregaria female, FFMS: two females -one of each morph- and a subrugosa male, MMFS: two males -one of each morph- and a subrugosa female) and recording equipment

numbers of viable homo- and heterotypic larvae were obtained in other controlled cross-breeding experiments (Pérez-Barros 2008).

A first group of 24 replicates of the 4 trio types (see Fig. 1), in which males were on average 10% larger than females, were recorded from June to July 2004 (Treatment 1). Ten of these replicates were composed of trios with all females bearing partial broods, with recently extruded oocytes/eggs (see Tapella et al. 2002a). These latter females were caught in the field with the partial brood already extruded and kept until the experiment in the laboratory in the same conditions as the non-ovigerous females. This treatment was motivated by the hypothesis that partial broods could elicit cues involved in species recognition (Bouchard et al. 1996; Tapella et al. 2002a).

A second group of 14 replicates of the 4 trios, where males were on average 30% CL larger than females, was recorded in June 2006 (Treatment 2). The rationale for this experiment was to maximize the number and duration of encounters since observations made a posteriori of the mating trials suggested that the duration of the mating embrace was dependent on the size difference between male and female. Embraces in pairs formed by large males and small females lasted longer than in pairs formed by males and females of similar size. During 2006 when encounters exceeded our recording time (3 h), videotaping was extended in order to determine maximum encounter duration. However, for the reproductive isolation index calculations, the duration time was considered until the moment when the 3 h were completed.

Data analysis

Experiment B: mate choice mating trials

A mating encounter is here defined as the behaviour that starts with a male trying to grasp a female and may end in a

copulatory embrace. Hence, a mating encounter can be constituted by either of the following behaviours: approach, or precopulatory embrace, or precopulatory + copulatory embrace (as defined in Table 1). Note that these behaviours were displayed in the sequence described in Table 1 and not all of them culminated in a copulatory embrace. The display “approach” was here defined to last up to 4 s. Behavioural isolation was defined as “all differences that lead to a lack of cross-attraction between members of different species, preventing them from initiating courtship or copulation” (Coyne and Orr 2004). Hence, for the purposes of this study, i.e. homotypic vs. heterotypic choice, we considered approach, precopulatory embrace and precopulatory + copulatory embrace to be indicative of choice and were used to measure behavioural prezygotic isolation as follows.

Two joint isolation indexes (I) were calculated for each mating trial (Gilbert and Starmer 1985; Dodd 1989): one for the frequency of mating encounters (I_f) and the other for the time mates spent in each type of encounter (I_t) as:

$$I_f = \frac{\text{number of homotypic encounters} - \text{number of heterotypic encounters}}{\text{total number of encounters}}$$

$$I_t = \frac{\text{time spent in homotypic encounters} - \text{time spent in heterotypic encounters}}{\text{total time spent in encounters}}$$

The index I ranges from -1 to 1 ; $I = 0$ indicates random mating; $I > 0$ indicates positive assortative mating and $I < 0$ indicates negative assortative mating. Movements of a squat lobster towards another individual and initial contact can be difficult to time accurately. Therefore, each “approach” was arbitrarily assigned a duration of 4 s for the calculations of I_t .

To test the null hypothesis of no preference for mating between individuals of the same morph, we performed Student’s t tests to analyse whether indexes were significantly larger than 0 (Sokal and Rohlf 1995).

In treatment 1, we analysed the effect of the type of trio and partial egg bearing condition on the frequency of homo- and heterotypic mating behaviours (I_f) and on the total time mates spent in each type of encounter (I_t) by means of two-way ANOVAs. In treatment 2, we only tested the effect of the type of trio, since no ovigerous females were used in this treatment, by means of a one-way ANOVA for both indexes, I_f and I_t .

The existence of competition between males of different morphs for the same female may indicate the existence of cross-attraction between male and female of different morphs, since both males are equally attracted to the same female. To evaluate the existence of male intrasexual competition for females, we defined interference as male–male interactions in which females were involved, i.e., while one male was interacting with the female, the other male approached and intended to grasp and pull the other

Table 1 Common reproductive behaviours of squat lobsters in laboratory conditions at $7 \pm 0.5^\circ\text{C}$ (modified from Jivoff and Hines 1998)

Behaviour	Description
Approach	The male moves towards, and tries to grasp the female. The attempt fails and individuals do not remain together for more than 4 s
Precopulatory embrace	The male grasps the female and holds her for more than 4 s, up to hours. They may be positioned one in front of the other: rostrum-to-rostrum position (Fig. 2a), or the male on top of the female so that his sternum rests on her dorsal carapace both facing the same direction: sternum-to-carapace position (Fig. 2b). Durations: CL ♂ \approx ♀: 57 s \pm 3 min 48 s, range: 4 s to 58 min 13 s ($n = 522$ interactions in $N = 88$ trios). CL ♂ $>$ ♀: 12 min 7 s \pm 34 min 38 s, range: 5 s to 3 h 47 min 51 s ($n = 129$ interactions in $N = 38$ trios)
Copulatory embrace	Once the male has the female in a precopulatory position, he places her so that their sternal surfaces are opposed, both individuals face in the same direction: sternum-to-sternum position (Fig. 2c). Durations: CL ♂ \approx ♀: 25 s \pm 22 s, range: 4 s to 1 min 10 s ($n = 7$ interactions in $N = 6$ trios). CL ♂ $>$ ♀: 19 min 12 s \pm 22 min 13 s, range: 5 s to 1 h 16 min 56 s ($n = 14$ interactions in $N = 6$ trios)
Resistance	The female resists/escapes the male's guarding attempt, usually by tail flipping
Submission	The female does not resist the male's guarding attempt, and remains with pereopods extended forwards against body, and with chelipeds folded in and downwards (Fig. 2b)
Corral	The male remains close to the female, and displays his chelipeds in a V shape which physically encloses the female

CL ♂ \approx ♀: males and females of similar sizes; CL ♂ $>$ ♀: males on average 30% carapace length (CL) larger than females

male or the female. We registered the number of trios with and without interference. In trios with interference, we counted the number of times a male interfered while the other male was having an encounter with the female and calculated the intensity of interference as the following proportion:

$$P_i = \frac{\text{number of encounters interfered}}{\text{total number of encounters in the trio}}$$

To test whether the occurrence of interference was homogeneous between treatments (treatment 1: males and females of similar sizes and treatment 2: males on average 30% CL larger than females), respective Chi-square tests were performed for both non-ovigerous MMFS and MMFG trios. To test whether the intensity (P_i) of interference was similar between years, a Kruskal–Wallis test was performed only using trios in which interference existed.

When required, assumptions of normality and homoscedasticity were previously tested with Kolmogorov–Smirnov and Bartlett's tests, respectively (Sokal and Rolf 1995).

Results

Mating behaviour

Mating occurred in the fully hardened intermolt condition. Males approached females with their chelipeds extended forward and grasped females, in general, at their chelipeds. Females often showed signs of resistance (Table 1). Precopulatory rostrum-to-rostrum position (Fig. 2a) was frequent in couples where the female resisted male attempts to position her in the sternum-to-carapace or the sternum-to-sternum position (Fig. 2b, c, respectively). When females

were brought to the sternum-to-carapace position, they often adopted a submissive position (Fig. 2b). While in this position, males would sometimes rock the females to the sides, and the females would make a fast tail flipping movement. Also while in this position, males embraced females with their pereopods and tried to open the female's abdomen introducing the dactylus of their last two pairs of walking legs between the female's abdomen and sternum. Finally, males made several attempts to position females so that their sternites were opposed, i.e. sternum-to-sternum position (Fig. 2c; Table 1). The copulatory embrace was often dynamic with females sometimes leaning on their sides and males struggling to orient them so that their ventral surfaces were against each other. In this position, males also tried to open the female's abdomen with their pereopods. Sternum-to-sternum position might be attained from the rostrum-to-rostrum or sternum-to-carapace positions. During the sternum-to-carapace and sternum-to-sternum positions, couples could role laterally so that they rested on their sides, or on the male carapace. The precopulatory or copulatory positions often finished when females struggled to release themselves from the male embrace. The durations of both precopulatory and copulatory embraces were related to the size difference between the male and female in the mating couple (Table 1).

After the 3-h experiments finished, and after removing the animals from the aquaria, a visual inspection of specimens participating in the trio revealed the presence of spermatophores outside male gonopores, or on the dactylus of the 5th pair of pereopods and on the first pair of pleopods of males. However, no spermatophores were detected on the female sternum after any of the described behaviours. If sperm transfer occurred, it could not be observed

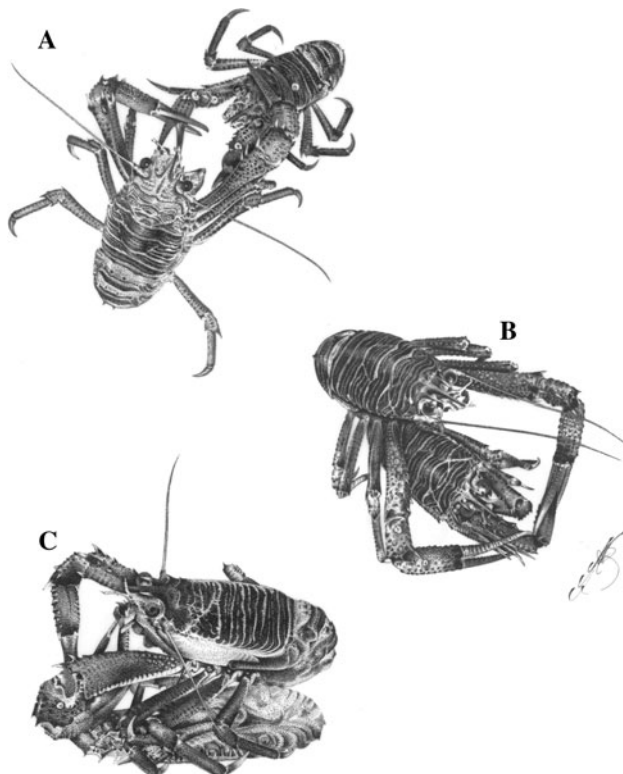


Fig. 2 Mating behaviour of *Munida gregaria*. Precopulatory embrace, **a** rostrum-to-rostrum and **b** sternum-to-carapace (and submission) positions. Copulatory embrace, **c** sternum-to-sternum position

due to the way in which animals were holding each other while performing these behaviours (see also Almerão et al. 2010 for another anomuran crab). Therefore, we cannot assure in which of the described positions sperm transfer occurs. Nevertheless, by comparing the behaviours observed with the copulatory behaviours of other crabs, in particular that of *Munida sarsi*, we defined the copulatory position as sternum-to-sternum as described in Table 1 (see also Hartnoll 1969; Watson 1970; Pothanikat 2005).

Mate choice mating trials

In Experiment B–Treatment 1 (24 replicates of each of the 4 trio types), in which males and females were of similar sizes, a total of 1211 male–female encounters were registered in 288 recorded hours. Of these encounters, 655 were homotypic (350 approaches, and 305 precopulatory and precopulatory + copulatory embraces) and 556 heterotypic (339 approaches, and 217 precopulatory and precopulatory + copulatory embraces). The longest homotypic encounter (a precopulatory embrace) lasted 35 min 2 s and occurred in a trio formed by 2 males (one of each morph) and a subrugosa female bearing a partial clutch. During the 3 h this trio was recorded, only two very short ($\ll 1$ min) heterotypic

encounters took place. The longest heterotypic encounter (a precopulatory embrace) lasted 58 min 13 s, and it was registered for the same type of trio. This embrace was registered after the gregaria male took over the subrugosa female (with a partial clutch) that was engaged in a homotypic precopulatory embrace that had lasted 29 min and 42 s.

In Experiment B–Treatment 2 (14 replicates of each of the 4 trio types), in which males were on average 30% larger than females, 221 male–female encounters were registered in 168 recorded hours. Of these encounters, 114 were homotypic (53 approaches, and 61 precopulatory and precopulatory + copulatory embraces) and 107 were heterotypic (39 approaches, and 68 precopulatory and precopulatory + copulatory embraces). The longest homotypic encounter (a precopulatory embrace) lasted 3 h 47 min 51 s, and took place in a trio formed by two males and a subrugosa female. In this trio, no heterotypic encounters were registered during the 3 h recorded. The longest heterotypic encounter (a precopulatory + copulatory embrace) lasted 4 h 11 min 14 s, and also occurred in a trio formed by two males and a subrugosa female. In this trio, no homotypic encounters were registered.

For both treatments, the values of I_f and I_t were very variable, and average indexes were not significantly different from zero (Student's t tests, $P > 0.05$ for all cases, Table 2), indicating the occurrence of random mating. In our treatments, neither the composition of trios, nor the reproductive condition of females influenced the choice of the morph for mating. In treatment 1, the frequency and the total time spent in homo- and heterotypic encounters were not affected by the type of trio, the egg bearing condition, or the interaction of both factors (ANOVA, $P = 0.26$, $P = 0.36$ and $P = 0.81$; and $P = 0.63$, $P = 0.41$ and $P = 0.96$ for I_f and I_t , respectively; Fig. 3). In treatment 2, the same results were obtained: no effect of the type of trio was observed on the I_f or the I_t (ANOVA $P = 0.13$ and $P = 0.62$ for I_f and I_t , respectively; Fig. 4).

Male intrasexual competition for females was rare since most trios had no interference (i.e. male–male interactions in which females were involved) (Table 3). Furthermore, in the trios that had interference only a small proportion of total encounters were interfered (Table 3). There were no major differences in the form of homo-/heterotypic intervention. In both treatments (males and females of similar sizes and males on average 30% CL larger than females), there were more trios in which no interference was observed than trios with interference (Chi-square, $P = 0.42$ and $P = 0.99$ for trios MMFG and MMFS, respectively). However, when there was interference, it was more intense in trios in which males were on average 30% CL larger than females (Table 3, Kruskal–Wallis, $P = 0.007$).

Table 2 Mean joint isolation indexes (\pm SD: standard deviation), for the frequency of mating encounters (I_f = (number of homotypic encounters – number of heterotypic encounters) \times total number of encounters⁻¹) and time spent in mating encounters (I_t = (time spent in homotypic encounters – time spent in heterotypic encounters) \times total time spent in encounters⁻¹) between individuals of *M. gregaria*

	$I_f \pm SD$	P	$I_t \pm SD$	P
Treatment 1 (CL ♂ \approx ♀)	0.002 \pm 0.667	0.49	0.02 \pm 0.76	0.40
Treatment 2 (CL ♂ $>$ ♀)	0.03 \pm 0.78	0.39	0.02 \pm 0.91	0.44

P : significance level of Student’s t tests used to test the $H_a: I > 0$. Treatment 1: males and females of similar sizes. Treatment 2: males on average 30% carapace length (CL) larger than females

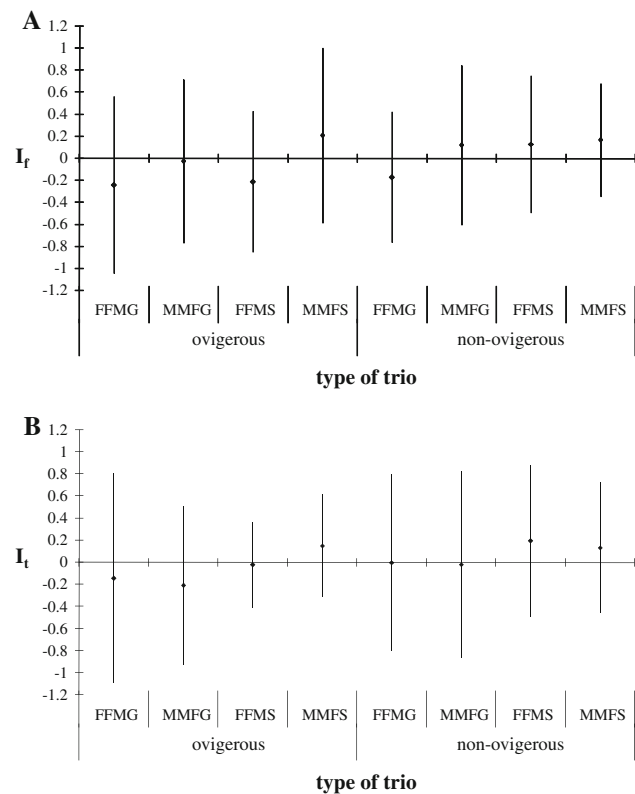


Fig. 3 Mean isolation indexes for **a** the frequency of encounters, $I_f \pm SD$; I_f = (number of homotypic encounters – number of heterotypic encounters) \times total number of encounters⁻¹, and **b** the time spent in encounters, $I_t \pm SD$; I_t = (time spent in homotypic encounters – time spent in heterotypic encounters) \times total time spent in encounters⁻¹ in trios in which males and females were of similar sizes (treatment 1). Codes for trio types are the same as in Fig. 1

Discussion

In this study, we found no morph-specific mating behaviours that could indicate a potential incipient reproductive isolation between the gregaria and subregosa forms of *Munida gregaria*. Individuals responded in the same way to both homo- and heterotypic partners. The frequency and

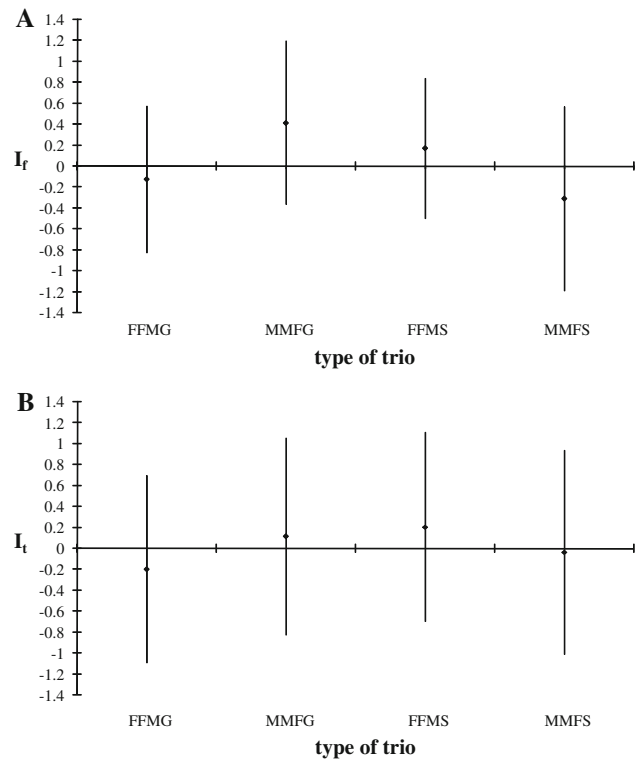


Fig. 4 Mean isolation indexes for **a** the frequency of encounters, $I_f \pm SD$; I_f = (number of homotypic encounters – number of heterotypic encounters) \times total number of encounters⁻¹, and **b** the time spent in encounters, $I_t \pm SD$; I_t = (time spent in homotypic encounters – time spent in heterotypic encounters) \times total time spent in encounters⁻¹ in trios in which males were on average 30% larger than females (treatment 2). Codes for trio types are the same as in Fig. 1

duration of homo- and heterotypic mating behaviours in female and male choice mating trials provided no evidence for a morph-specific mate preference.

Among the Anomura, mating behaviour has been mainly studied for hermit crabs (Hess and Bauer 2002 and references therein) and lithodids (e.g. Goshima et al. 1995; Wada et al. 1997; Sato and Goshima 2007b). Recently, a study has been published on the mating behaviour of *Aegla platensis* (Almerão et al. 2010). However, the knowledge on the mating behaviour of galatheids is still scarce (cf. Pothanikat 2005). Some similarities were found between the results obtained in our study and those reported for *A. platensis*: mating occurred in the fully hardened intermolt condition and no prolonged precopulatory mate guarding behaviour was observed. Almerão et al. (2010) could not observe sperm transfer either, and since aeglids lack copulatory appendages, they suggested the 5th pair of pereopods could be involved in sperm transfer like in other anomurans (e.g. *Paralithodes camtschatica* and galatheids, Pohle 1989). In galatheids, both gonopods and 5th pereopods have a copulatory function since the 5th pereopods assist in spermatophore transfer from male gonopods to the female

Table 3 Average proportion of times (P_i) a male interfered with the male of the other morph while this was having an encounter with the female (SD: standard deviation)

	♀ reproductive condition	Trio	Number of trios with interference	Number of trios without interference	P_i	SD
Treatment 1 (CL ♂ \approx ♀)	Ovigerous	MMFG			0.08	0.09
		MMFS			0.08	0.17
	Non-ovigerous	MMFG	2 (1)	12	0.01	0.04
		MMFS	5 (2)	9	0.04	0.09
Treatment 2 (CL ♂ > ♀)	Non-ovigerous	MMFG	4 (2)	7	0.22	0.40
		MMFS	3 (2)	8	0.20	0.36
Overall			14 (7)	36	0.10	0.23

Treatment 1: males and females of similar sizes. Treatment 2: males on average 30% carapace length (CL) larger than females. MMFG: trio formed by two males -one of each morph- and a gregaria female, MMFS: trio formed by two males -one of each morph- and a subrugosa female. The number of homotypic interferences is indicated in parenthesis

gonopores and pleopods (Pohle 1989). Due to the important development and modification into gonopods of the first and second pleopods of *Galathea intermedia*, Kronenberger et al. (2004) suggested that gonopods, as well 5th pereopods, must play some role in spermatophore transfer or related activities. In *M. gregaria*, the first and second pleopods of males are well developed and modified into gonopods, and spermatophore morphology resembles that of *Galathea intermedia*. Given these similarities and the fact that we observed spermatophores on the first pair of pleopods, as well as on the 5th pereopods of *M. gregaria* we hypothesize that both sets of appendages must be involved in spermatophore transfer/manipulation.

Experiments were conducted at the end of the ovarian maturation and the beginning of the annual reproductive season in the Beagle Channel (May or June Tapella et al. 2002a). Behaviours here observed led to precopulatory embraces, and eventually to copulatory positions, and therefore were clearly reproductive. Moreover, these behaviours are similar to those described for other decapod species (e.g. Hartnoll 1969; Watson 1970; Jivoff and Hines 1998; Pothanikat 2005; Almerão et al. 2010). Furthermore, the presence of spermatophores in the proximity of male gonopores suggests that sperm transfer must have been imminent, although not observed in any of the trials conducted. In addition, no impediment seems to exist for cross-fertilization between both morphs, given that other cross-breeding experiments complementary to the present study yielded similar numbers of homo- and heterotypic larvae (Pérez-Barros 2008). Since most of the observed copulatory embraces were short, we believe that the copulatory embraces leading to successful spermatophore transfer will show similar characteristics. We furthermore postulate that the copulatory embrace probably occurs several times during a period longer than 3 h. If video recording had continued, we probably would have been

able to register sperm transfer. However, these hypotheses need to be carefully tested in future experiments.

We found no evidence to suggest morph-specific recognition mediated by signals associated with recently extruded oocytes/eggs, since partial egg bearing condition of females neither influenced the frequency of homo- and heterotypic encounters nor the total time males spent with each type of female. However, in other crustaceans, mechanisms for species recognition occur through chemosensory cues released by females during mating (Bushmann 1999; Atema and Steinbach 2007). For example, among species of freshwater shrimps of the genus *Macrobrachium*, females of one species are not able to induce spermatophore release in males of another species (Graziani et al. 2003). In the brachyuran crab *Chionoecetes opilio*, eggs may release chemicals involved in female-male attraction (Bouchard et al. 1996). Tapella et al. (2002a) hypothesized that in *M. gregaria* morph subrugosa, the partial or incomplete broods which appear at the beginning of the reproductive season could constitute a signal to attract males for mating. We had further hypothesized that eggs could be involved in morph-specific female-male recognition, but the present results do not support such hypothesis.

We hypothesize that partial broods observed at the beginning of the mating season by Tapella et al. (2002a) may be indicative of the existence of polyandry for several reasons. First, females mate in intermolt condition that extends throughout the winter (Tapella 2002). Hence, females become receptive as soon as the ovaries are mature during a relatively long period, i.e. from April to July, when compared with other anomurans, like lithodids, in which females are receptive for only a few days while in postmolt condition (see Sainte-Marie 2007 for a review). Second, we observed no prolonged precopulatory mate guarding. However, the existence of some interference of

the second male with the couple, and longer encounters when males were larger than females may be indicative of a temporarily short mate monopolization (see Jormalainen 2007 for a review). Moreover, in the Beagle Channel, sex ratio is generally biased towards females (Tapella 2002), indicating that they are not a limiting resource if they have a prolonged receptivity. Third, *Munida* spp., as all anomuran crabs, lack internal sperm storage organs, and therefore sperm cannot be used in more than one oviposition (Sainte-Marie 2007). For these reasons, we propose that a single egg batch could result from multiple matings as in other anomuran crabs, e.g. *Petrolisthes cinctipes* (Toonen 2004). These multiple matings probably result from several short encounters, in which the female struggles to flee. Once she abandons the couple, another male could grab her and try to mate with her. This is quite plausible, given the high abundance of squat lobsters (maximum of 30 individuals \times m⁻²; Gutt et al. 1999). At the end of embryogenesis, eggs will have the same developmental stage and larvae will hatch all together during one/two nights (Perez-Barros et al. 2007 and personal observations). Hence, it is unlikely that egg extrusion will be gradual, extending over weeks, as suggested by Tapella et al. (2002a). Based on the above considerations, we hypothesize that the mating system in *M. gregaria* is pure search, in which “male mating success depends primarily on their ability to find (and mate with) as many receptive females as possible” (sensu Correa and Thiel 2003), but this needs to be examined in future studies.

In this study, we reject the existence of a prezygotic behavioural barrier to gene flow as the mechanism involved in the maintenance of these two phenotypes. Both morphs of *Munida gregaria* inhabit the same places, breed at the same time of the year (Tapella 2002; personal observations), and show similar levels of intra- and inter-specific genetic divergence (Pérez-Barros et al. 2008). Moreover, similar numbers of viable homo- and heterotypic larvae were obtained in controlled cross-breeding experiments (Pérez-Barros 2008). Thus, there is more evidence in favour of the existence of gene flow between both morphs than arguments for their separation in two different species.

However, the sympatric existence of these two morphotypes in the Beagle Channel leads to the question for the mechanisms involved in their co-occurrence in nature. One possible explanation is the existence of some kind of temporal or habitat isolation not considered in our experimental layout. Secondly, a case of polymorphism maintained by disruptive natural selection, either because different environmental conditions favour different genotypes (multiple niche polymorphism), or because of the existence of inverse frequency-dependent selection (Futuyma 1998). Third, this could be a case of phenotypic

plasticity, i.e., the capacity of a genotype to express different phenotypes when exposed to different environments (West-Eberhard 1989). Within this framework, we can include most of the explanations given so far about the mechanisms that could be involved in the maintenance of these two phenotypes in nature. Pelagic shoals of the post-metamorphic phase of *Munida gregaria* were frequently reported to occur off New Zealand during the summer (Zeldis 1985). However, such swarms seem to be less frequent off southern South America. Only during 2006–2010, they have been reported as frequent and abundant mainly in the Golfo San Jorge (Varisco and Vinuesa 2010) and in the Beagle Channel (personal observations). Williams (1973) proposed that the ontogenetic habitat change (from the pelagos to the benthos) of post-metamorphic *M. gregaria* could alter the morphological characters that are commonly used in the diagnosis of both morphotypes. This means that after settling to the bottom and over several moults, individuals >10 mm CL of pelagic gregaria may acquire the morphology of the benthic subrugosa (Williams 1973, 1980). However, around southern South America the coexistence of adults of both morphs as benthic forms (Tapella et al. 2002b), along with the benthic occurrence of first juvenile stages of subrugosa (Tapella 2002, and personal observations), do not support Williams’ “transformation” hypothesis (see Pérez-Barros et al. 2008 for further discussion). Nevertheless, other hypotheses related to the existence of phenotypic plasticity in *M. gregaria* have been proposed. The production of different phenotypes, gregaria with the ability to remain pelagic after metamorphosis vs. subrugosa settling directly to the bottom as a megalopa or first crab stage, could be triggered by environmental signals perceived during the larval period, e.g., the absence of suitable sea-bottom at a moderate depth (Chilton 1909) or water temperature associated with depth (Bacardit 1986). Our results indicate there is no behavioural isolation between the two morphs, which showed clear signs of cross-attraction in the laboratory and most likely also in the natural environment.

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References

- Almerão M, Bond-Buckup G, Mendonça MS Jr (2010) Mating behavior of *Aegla platensis* (Crustacea, Anomura, Aeglidae) under laboratory conditions. *J Ethol* 28:87–94
- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Andersson M (1994) Sexual selection. Princeton University Press, Princeton
- Aquiloni L, Gherardi F (2008) Mutual mate choice in crayfish: large body size is selected by both sexes, virginity by males only. *J Zool (Lond)* 274:171–179
- Atema J, Steinbach MA (2007) Chemical communication in the social behavior of the lobster, *Homarus americanus*, and other Decapod Crustacea. In: Duffy JE, Thiel M (eds) Ecology and evolution of social behavior: crustaceans as model systems. Oxford University Press, New York, pp 115–144
- Baba K, Macpherson E, Poore GCB, Ahyong ST, Bermúdez A, Cabezas P, Lin CH-W, Nizinski M, Rodrigues C, Schnabel KE (2008) Catalogue of squat lobsters of the world (Crustacea: Decapoda: Anomura—families Chirostylidae, Galatheididae and Kiwaidae). *Zootaxa* 1905:1–220
- Bacardit R (1986) Larvas de Crustacea Decapoda del mar patagónico argentino, incluyendo el talud continental, adyacencias a la Tierra del Fuego e Islas Malvinas. Aspectos morfológicos, ecológicos y filogenéticos. Dissertation, Universidad de Buenos Aires
- Boake CRB, Andreadis DK, Witzel A (2000) Behavioural isolation between two closely related Hawaiian *Drosophila* species: the role of courtship. *Anim Behav* 60:495–501
- Bouchard S, Sainte-Marie B, McNeil JN (1996) Indirect evidence indicates female semiochemicals release male precopulatory behaviour in the snow crab, *Chionoecetes opilio* (Brachyura: Majidae). *Chemoecology* 7:39–44
- Bushmann P (1999) Concurrent signals and behavioural plasticity in blue crab (*Callinectes sapidus* Rathbun) courtship. *Biol Bull* 197:63–71
- Chilton C (1909) Crustacea of the subantarctic islands of New Zealand. In: Chilton C (ed) The subantarctic islands of New Zealand, vol 2. Philosophical Institute of Canterbury, New Zealand, pp 612–613
- Correa C, Thiel M (2003) Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. *Rev Chil Hist Nat* 76:187–203
- Coyne JA, Orr HA (1998) The evolutionary genetics of speciation. *Phil Trans Roy Soc Lon B* 353:287–305
- Coyne JA, Orr HA (2004) Speciation. Sinauer, Sunderland
- Crespi BJ (1989) Causes of assortative mating in arthropods. *Anim Behav* 38:980–1000
- Díaz ER, Thiel M (2004) Chemical and visual communication during mate searching in rock shrimp. *Biol Bull* 206:134–143
- Dodd DMB (1989) Reproductive isolation as a consequence of adaptive divergence in *Drosophila pseudoobscura*. *Evolution* 43:1308–1311
- Futuyma DJ (1998) Evolutionary biology. Sinauer Associates, Sunderland
- Gavrilets S, Boake CRB (1998) On the evolution of premating isolation after a founder event. *Am Nat* 152:706–716
- Gilbert DG, Starmer WT (1985) Statistics of sexual isolation. *Evolution* 39:1380–1383
- Goshima S, Ito K, Wada S, Shimizu M, Nakao S (1995) Reproductive biology of the stone crab *Hapalogaster dentata* (Anomura: Lithodidae). *Crustac Res* 24:8–18
- Graziani C, Moreno C, Villarroel E, Orta T, Lodeiros C, De Donato M (2003) Hybridization between freshwater prawns *Macrobrachium rosenbergii* (De Man) and *M. carcinus* (L.). *Aquaculture* 217:81–91
- Gutt J, Helsen E, Arntz WE, Buschmann A (1999) Biodiversity and community structure of the mega-epibenthos in the Magellan region (South America). *Sci Mar* 63(Suppl 1):155–170
- Hartnoll RG (1969) Mating in the Brachyura. *Crustaceana* 16:161–181
- Hess GS, Bauer RT (2002) Spermatophore transfer in the hermit crab *Clibanarius vittatus* (Crustacea, Anomura, Diogenidae). *J Morphol* 253:166–175
- Hoefler CD (2007) Male mate choice and size-assortative pairing in a jumping spider, *Phidippus clarus*. *Anim Behav* 73:943–954
- Jivoff P, Hines AH (1998) Female behaviour, sexual competition and mate guarding in the blue crab, *Callinectes sapidus*. *Anim Behav* 55:589–603
- Jones DR, Hartnoll RG (1997) Mate selection and mating behaviour in spider crabs. *Estuar Coast Shelf Sci* 44:185–193
- Jormalainen V (2007) Mating strategies in isopods: from mate monopolization to conflicts. In: Duffy JE, Thiel M (eds) Evolutionary ecology of social and sexual systems: crustaceans as model organisms. Oxford University Press Inc., New York, pp 167–190
- Kendall MS, Wolcott TG (1999) The influence of male mating history on male-male competition and female choice in mating associations in the blue crab, *Callinectes sapidus* (Rathbun). *J Exp Mar Biol Ecol* 239:23–32
- Kirkpatrick M, Ravigne V (2002) Speciation by natural and sexual selection: models and experiments. *Am Nat* 159:22–35
- Knowlton N (1993) Sibling species in the sea. *Annu Rev Ecol Syst* 24:189–216
- Kokko H, Brooks R, Jennions MD, Morley J (2003) The evolution of mate choice and mating biases. *Proc Roy Soc Lon B* 270:653–664
- Kronenberger K, Brandis D, Turkay M, Storch V (2004) Functional Morphology of the Reproductive System of *Galathea intermedia* (Decapoda: Anomura). *J Morphol* 262:500–516
- Lee S, Seed R (1992) Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. *Mar Ecol Prog Ser* 84:151–160
- Maddison WP, Knowles LL (2006) Inferring phylogeny despite incomplete lineage sorting. *Syst Biol* 55:21–30
- Miya M, Nishida M (1997) Speciation in the open ocean. *Nature* 389:803–804
- Paul JM, Paul AJ (1990) Reproductive success of sublegal size male Red King Crab. In: Proceedings of international symposium King and Tanner crabs, Anchorage, AK, Alaska Sea Grant College Program, University of Alaska, AK-SG 90-04:37–50
- Paul AJ, Paul JM (1997) Breeding success of large male red king crab *Paralithodes camtschaticus* with multiparous mates. *J Shell Res* 16:379–381
- Pérez-Barros P (2008) Evaluación del estatus taxonómico de las langostillas *Munida gregaria* y *M. subrugosa* (Crustacea: Decapoda: Galatheididae) de la plataforma argentina, mediante el estudio de características genéticas, reproductivas y ecológicas. Dissertation, Universidad de Buenos Aires
- Pérez-Barros P, Thatje S, Calcagno JA, Lovrich GA (2007) Larval development of the subantarctic squat lobster *Munida subrugosa* (White, 1847) (Anomura: Galatheididae), reared in the laboratory. *J Exp Mar Biol Ecol* 352:35–41 and Erratum *J Exp Mar Biol Ecol* 364:124
- Pérez-Barros P, D'Amato ME, Guzmán NV, Lovrich GA (2008) Taxonomic status of two South American sympatric squat lobsters, *Munida gregaria* and *M. subrugosa* (Crustacea: Decapoda: Galatheididae), challenged by DNA sequence information. *Biol J Linn Soc* 94:421–434

- Pohle G (1989) Gill and embryo grooming in lithodid crabs: comparative functional morphology based on *Lithodes maja*. In: Felgenhauer BE, Watling L, Thistle AB (eds) Crustacean issues, functional morphology of feeding and grooming in Crustacea. AA Balkema, Rotterdam, pp 75–94
- Pothanikat RME (2005) The Behaviour and Ecology of *Munida rugosa* and *Munida sarsi*. Dissertation, Queen's University of Belfast
- Real LA (1990) Search theory and mate choice. I. Models of single-sex discrimination. *Am Nat* 136:376–405
- Rittschof D, Cohen JH (2004) Crustacean peptide and peptide-like pheromones and kairomones. *Peptides* 25:1503–1516
- Rondeau A, Sainte-Marie B (2001) Variable mate-guarding time and sperm allocation by male snow crabs (*Chionoecetes opilio*) in response to sexual competition, and their impact on the mating success of females. *Biol Bull* 201:204–217
- Sainte-Marie B (2007) Sperm demand and allocation in decapod crustaceans. In: Duffy JE, Thiel M (eds) Evolutionary ecology of social and sexual systems: crustaceans as model organisms. Oxford University Press Inc., New York, pp 191–210
- Sato T, Goshima S (2007a) Effects of risk of sperm competition, female size, and male size on number of ejaculated sperm in the stone crab *Hapalogaster dentata*. *J Crust Biol* 27:570–575
- Sato T, Goshima S (2007b) Female choice in response to risk of sperm limitation by the stone crab, *Hapalogaster dentata*. *Anim Behav* 73:331–338
- Sato T, Yoseda K (2010) Influence of size- and sex-biased harvesting on reproduction of the coconut crab *Birgus latro*. *Mar Ecol Prog Ser* 402:171–178
- Sato T, Ashidate M, Wada S, Goshima S (2005) Effects of male mating frequency and male size on ejaculate size and reproductive success of female spiny king crabs *Paralithodes brevipes*. *Mar Ecol Prog Ser* 296:251–262
- Schubart CD, Conde JE, Carmona-Suárez C, Robles R, Felder DL (2001a) Lack of divergence between 16S mtDNA sequences of the swimming crabs *Callinectes bocourti* and *C. maracaiboensis* (Brachyura: Portunidae) from Venezuela. *Fish Bull US* 99:475–481
- Schubart CD, Cuesta JA, Rodríguez A (2001b) Molecular phylogeny of the crab genus *Brachynotus* (Brachyura: Varunidae) based on the 16S rRNA gene. *Hydrobiologia* 449:41–46
- Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research. WH Freeman and Company, New York
- Tapella F (2002) Reproducción, crecimiento, distribución y abundancia de la langostilla *Munida subrugosa* (Anomura: Galatheiidae) del Canal Beagle, Tierra del Fuego, Argentina. Dissertation, Universidad Nacional de Córdoba
- Tapella F, Lovrich GA, Romero MC, Thatje S (2002a) Reproductive biology of the crab *Munida subrugosa* (Decapoda: Anomura: Galatheiidae) in the Beagle Channel, Argentina. *J Mar Biol Assoc UK* 82:589–595
- Tapella F, Romero MC, Lovrich GA, Chizzini A (2002b) Life history of the galatheid crab *Munida subrugosa* in sub Antarctic waters of the Beagle Channel, Argentina. In: Paul AJ, Dawe EG, Elner R, Jamieson GS, Kruse GH, Otto RS, Sainte-Marie B, Shirley TC, Woodby D (eds) Crabs in cold water regions: biology, management, and economics. University of Alaska Sea Grant College Program AK-SG-02-01, Fairbanks, pp 115–134
- Toonen RJ (2004) Genetic evidence of multiple paternity of broods in the intertidal crab *Petrolisthes cinctipes*. *Mar Ecol Prog Ser* 270:259–263
- Varisco M, Vinuesa JH (2010) Occurrence of pelagic juveniles of *Munida gregaria* (Fabricius, 1793) in San Jorge Gulf, Argentina. *Crustaceana* 83:1147–1151
- Via S (2001) Sympatric speciation in animals: the ugly duckling grows up. *Trends Ecol Evol* 16:381–390
- Wada S, Ashidate M, Goshima S (1997) Observations on the reproductive behavior of the spiny king crab *Paralithodes brevipes* (Anomura: Litodidae). *Crustac Res* 26:56–61
- Watson J (1970) Maturity, mating, and egg laying in the spider crab, *Chionoecetes opilio*. *J Fish Res Bd Canada* 27:1607–1616
- West-Eberhard MJ (1989) Phenotypic plasticity and the origins of diversity. *Annu Rev Ecol Syst* 20:249–278
- Williams BG (1973) The effect of the environment on the morphology of *Munida gregaria* (Fabricius) (Decapoda, Anomura). *Crustaceana* 24:197–210
- Williams BG (1980) The pelagic and benthic phases of post-metamorphic *Munida gregaria* (Fabricius) (Decapoda, Anomura). *J Exp Mar Biol Ecol* 42:125–141
- Zeldis JR (1985) Ecology of *Munida gregaria* (Decapoda, Anomura): distribution and abundance, population dynamics and fisheries. *Mar Ecol Prog Ser* 22:77–79