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Protandric simultaneous hermaphroditism and sex ratio in *Lysmata nayaritensis* Wicksten, 2000 (Decapoda: Caridea)

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Abstract

Caridean shrimps display a wide variety of sexual systems, including the newly discovered protandric simultaneous hermaphroditism. Protandric simultaneous hermaphroditism is known only from seven species of *Lysmata*, and it is not clear if this condition is fixed within the genus or if *Lysmata* includes species that are simply protandric or gonochoric (with separate sexes). This study uses anatomical data, aquarium experiments, and field observations to demonstrate that *Lysmata nayaritensis* is another protandric simultaneous hermaphrodite. It is shown that, despite occurring in the tropics, this species fits into the “crowd” species category, with high densities in the field and that the field sex ratio is highly male-biased. Information on the sex allocation and sexual system of more species needs to be examined before these observations can be put into a comparative context within the genus.

Keywords: Caridea, Decapoda, *Lysmata*, protandry, sex allocation, sex change, simultaneous hermaphroditism.

Introduction

Sexual systems vary considerably among caridean shrimps. While most species are gonochoric, with individuals reproducing exclusively as male or female during their lifetime (Correa and Thiel 2003), others are reported to be protandric hermaphrodites, where individuals change from male to female (Bauer 2006). Variants of protandry also occur. In the hippolytid *Thor manningi* Chase, 1972, a mixture of primary males, a few primary females, and protandric hermaphrodites has been reported (Bauer 1986). Finally, simultaneous hermaphroditism with an early protandric phase (i.e., protandric simultaneous hermaphroditism), where individuals initially mature as males and later become simultaneous hermaphrodites, has recently been described for various species of *Lysmata* (Wirtz 1997; Bauer and Holt 1998; Fiedler 1998; d’Udekem d’Acoz 2003; Bauer and Newman 2004; Baeza and Anker forthcoming). This variation makes caridean shrimps an

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ideal group in which to examine the evolution of sexual systems; however, the sexual systems of more species need to be documented before ideas of evolution in this group can be refined.

In shrimps, protandric simultaneous hermaphroditism is known only in the genus *Lysmata*, and has been described in detail for seven species (*L. grabhami* (Gordon, 1935)—Wirtz (1997); *L. amboinensis* (De Mann, 1888)—Fiedler (1998); *L. wurdemanni* (Gibbes, 1850)—Bauer and Holt (1998); *L. seticaudata* (Risso, 1816) and *L. nitida* Dohrn and Holthuis, 1950—d'Udekem d'Acoz (2003); *L. californica* (Stimpson, 1866)—Bauer and Newman (2004); *Lysmata* undescribed species, under description by Baeza and Anker (forthcoming). Soon after settlement, juvenile shrimps develop as males with typical caridean external male morphology. The gonads of these males are ovotestes, with well-developed paired testes but undeveloped ovaries, and these animals reproduce as males (Bauer and Holt 1998; Baeza 2007a, 2007b). Eventually, the ovarian portion of the ovotestes matures. Unlike protandric species which lose the male characteristics during ovary development, protandric simultaneous hermaphrodites maintain most male anatomical characteristics (except for the coupling hooks, cincinnuli, and appendices masculinae on the endopods of the first and second pleopods). Therefore, male shrimps from protandric simultaneous hermaphrodites mature as functional simultaneous hermaphrodites capable of reproducing both as male and female. There is no evidence of sex reversal (to males) once shrimps have become simultaneous hermaphrodites. Although a hermaphroditic shrimp can successfully function as both male and female, they are unable to self-fertilize (Bauer and Holt 1998).

The general sociobiology of *Lysmata* species has been divided into two distinct categories: temperate and subtropical “crowd” species and tropical “pair” species (Bauer 2000). Crowd species such as *Lysmata wurdemanni*, *L. seticaudata*, and *L. californica* live in large groups with high population densities in subtropical and warm temperate regions. They are nocturnal generalized foragers, and have a subdued reddish coloration (Limbaugh et al. 1961). Their mating system appears to be a pure searching mating strategy, with roaming males attempting to locate and mate with as many receptive females as possible (Baeza 2007a, 2007b). In contrast, pair species such as *L. grabhami* and *L. amboinensis* have low population densities. Pair species are usually dark red with bright white spots and stripes that seem to be used as colours signalling “cleaning services” to fish (Bauer 2006). Their mating system appears to be prolonged mutual mate guarding because functional hermaphrodites are mostly found in pairs dwelling on sessile invertebrates (Bauer 2000).

Protandric simultaneous hermaphroditism has been documented in both crowd and pair species (Bauer 2000, 2006), but details of sex allocation such as sex ratio have seldom been reported. Documentation of the sexual system, mating system, and natural history of additional species in the genus is necessary before in-depth, comparative analyses of the evolutionary origins and adaptive value of this unusual sexual system can be attempted. In this study, we used dissections and breeding experiments to test the hypothesis that the shrimp *Lysmata nayaritensis* Wicksten, 2000 is a functional simultaneous hermaphrodite with an early male phase. We also describe the population structure, distribution, and sex ratio of this species in the field, to gain a better understanding of its overall biology and mating system.

Materials and methods

Between December 2006 and February 2007, specimens of *Lysmata nayaritensis* were collected during low tide with aquarium nets from the rocky intertidal of Chumical (8°52'60"N,

79°39'0"W), near the town of Veracruz on the Pacific coast of Panama. The species was identified using the key of Wicksten (2000). Immediately after collection, shrimps were transported to the laboratory where they were maintained in 21-litre aquaria at a water temperature of 26–31°C and 34–36 ppt salinity. Shrimps were fed every other day with commercial fish food (Clorofin Sinking Granules). Some individuals that were selected haphazardly for dissections and for experiments conducted to determine this species' sexual system.

Reproductive anatomy was examined in a total of six specimens, four small individuals expected to be males (5.9, 5.7, 5.6, and 4.7 mm carapace length (CL)) and two potential hermaphrodites that carried embryos beneath their abdomen (CL 7.2 and 7.3 mm). Specimens were defined as males or hermaphrodites following Fiedler (1998) and Bauer and Holt (1998), by the presence (males) or absence (hermaphrodites) of coupling hooks (cincinnuli) and appendices masculinae on the endopods of the first and second pleopods, respectively.

If male gonopores on the coxae of the third pereopods were observed, the sperm mass contained in their ejaculatory ducts was retrieved by electro-ejaculation following the method of Baeza (2007b). Each shrimp was then dissected to extract the gonad, and a stereomicroscope was used to determine the presence of ovarian and/or testicular tissue. Finally, the first and second pleopods were dissected and the presence or absence of appendices internae and masculinae was recorded.

To examine the sexual system, shrimps were placed into one of three experimental treatments: (1) to determine experimentally whether shrimps reproducing as females (brooding embryos) could function as males, five replicated pairs of brooding shrimps were maintained in 21-litre aquaria; (2) to determine whether shrimps could self-fertilize six brooding shrimp were each maintained alone, and (3) to determine whether males mature into hermaphrodites five pairs of males (small non-brooding shrimp with no externally visible female gonad and visible cincinnuli and appendices masculinae) were maintained separately in 21-litre aquaria for at least 50 days. All treatments were examined daily for hatching of the embryos, the presence of exuvia from moulting, development of mature oocytes in the gonad (visible through the carapace), and spawning of a new batch of eggs. The development of any newly spawned embryos was examined in detail after 4 days of development.

If ovigerous shrimps paired together produced normally developing broods, it was inferred that either the other ovigerous shrimp in the aquarium acted as a male to inseminate its partner, or that the shrimp was capable of self-fertilization. Both cases demonstrate functional hermaphroditism. If shrimps in isolation failed successfully to produce and brood normally developing eggs, the possibility that shrimps can self-fertilize was eliminated. If animals that were inferred to be male at the beginning of the experiment developed the ovarian portion of the ovotestis and produce eggs, it was inferred that male shrimps mature as hermaphrodites.

Abundance, size distribution of the sexes, and sex ratios (males: hermaphrodites) of *L. nayaritensis* were collected from the field. The carapace length and number of shrimps of each sexual phase captured on each of three sampling dates were recorded.

Results

Anatomical data

All of the shrimps that were dissected (brooding or non-brooding) had male gonopores located at the coxae of the third pair of walking legs (Figure 1A), stored a spermatophore

containing sperm cells shaped in the form of inverted umbrellas (Figure 1B, C), and had ovotestes containing sperm (Figure 1F). This is strong evidence that all individuals can function as males. Brooding shrimps had an ovotestes with a relatively large anterior female portion full of green vitellogenic oocytes. In contrast, non-brooding shrimps had a poorly developed female portion full of immature oocytes lacking green coloration (Figure 1G). The posterior male gonad, containing sperm (Figure 1D, E), was relatively small in ovigerous shrimp. In both brooding and non-brooding shrimps, vas deferentia and oviducts extended laterally from the male and female gonad, respectively (Figure 1D–F). Shrimps brooding embryos lacked cincinulli on the endopod of the first pleopods and appendices masculinae on the second pleopods (Figure 1H, I). In contrast, numerous cincinulli and appendices masculinae bearing large spines were observed on the endopod of the first and second pleopods of non-brooding shrimps (Figure 1J, K). These anatomical observations provide evidence that the population of *L. nayaritensis* is composed of small shrimps that are functionally males and larger shrimps that are functionally hermaphrodites.

Experimental data

The experiments demonstrated that brooding shrimps are able to fertilize each other and do not self-fertilize. All six brooding animals retained in isolation produced eggs after moulting but these eggs disappeared after the first 2 days, suggesting that they did not develop normally. These animals were capable of normal female reproduction since their previous broods had hatched normally. In contrast, all 10 brooding shrimps in the paired treatment spawned and retained eggs that developed normally. These results demonstrate that the second individual in the pair probably acts as a male and fertilizes its partner.

At least one male in every replicate of paired males matured as a functional hermaphrodite in less than 50 days. In all replicates, the larger of the two males moulted, developed mature oocytes (visible through the carapace as a green coloration of the gonad), and subsequently spawned and brooded the eggs. Two replicates continued for over 60 days, and eventually the second male in both replicates matured into a functional hermaphrodite.

Field data

Abundance of *L. nayaritensis* at Chumical was high, with 211 individuals collected over 4 h of collecting. The population was male-biased, and 91.5% (193 out of 211) of the collected shrimps were males (Figure 2). Male carapace length [4.0 ± 0.83 (2.4–6.1) mm] was almost always less than female carapace length [7.02 ± 1.05 (5.2–9.0) mm], with only a few individuals (23 shrimps) of the two sexes overlapping in size (range of overlapping size: 5.2–6.1 mm CL). Using binary logit logistic regression, the size at which 50% of the shrimps were predicted to have changed to hermaphrodites (L_{50}) is 6.12 mm CL.

Two shrimps with male external characters and a developing ovary with small white oocytes that were visible through the carapace, giving the impression that they were likely to become hermaphrodites during their next moult, were collected (Figure 2). As expected, these animals were intermediate in size between males and hermaphrodites. *Lysmata nayaritensis* appears to have a patchy distribution at the study site because numerous shrimps were collected from below some rocks but none were found under other similar rocks in the same location.

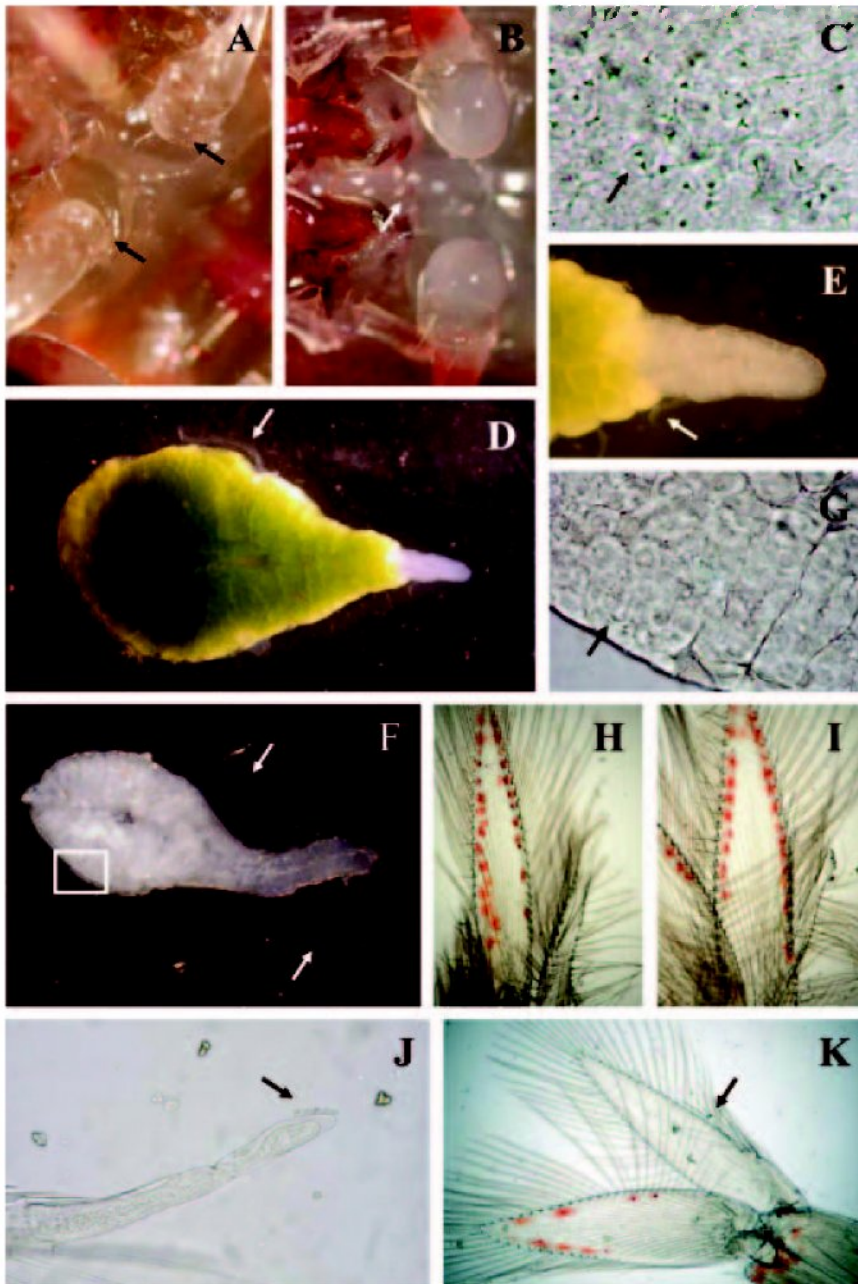


Figure 1. *Lysmata nayaritensis*, anatomical and morphological differences between males and hermaphrodites. (A) Gonopores of male; (B) spermatophores retrieved from gonopores of hermaphrodite; (C) sperm from male; (D) ovotestes from dissected hermaphrodite (anterior female and posterior male portions on the left and right, respectively); (E) close-up of the male gonad portion (arrow points at the left vas deferentia); (F) ovotestes from male (anterior female and male portions on left and right, respectively) (upper and lower arrows point at the right oviduct and left vas deferentia, respectively); (G) close-up of the female gonad portion in male (arrow points at immature oocyte); (H) endopod of first pleopod lacking cincinnuli in hermaphrodite; (I) endopod of second pleopod lacking appendix masculina in hermaphrodite; (J) endopod of first pleopod in male (arrow points at cincinnuli); (K) endopod of second pleopod in male (arrow points at appendix masculina).

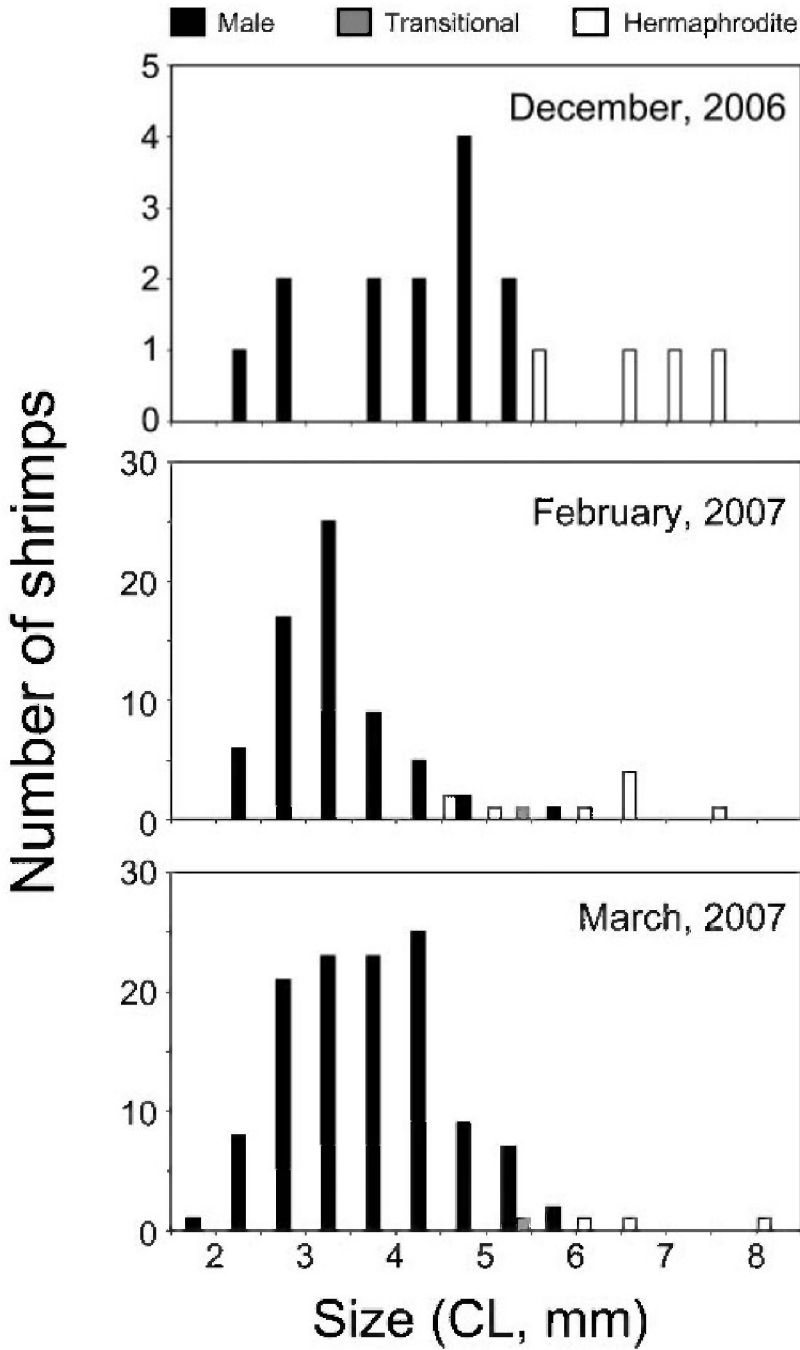


Figure 2. Population structure of *Lysmata nayaritensis* at Chumical, Pacific coast of Panama, between December 2006 and March 2007.

Discussion

In *Lysmata nayaritensis*, both large brooding and small non-brooding shrimps have ovotestes and male gonopores. However, the female portion of the ovotestes is underdeveloped in small non-brooding shrimps. These small non-brooding shrimps have cincinulli and appendices masculinae in the first and second pleopod, respectively. Behavioural experiments demonstrated that these non-brooding shrimps with external male diagnostic characters have the ability to reproduce as males. Furthermore, large shrimps that brood embryos and lacked these male diagnostic characters have the ability to inseminate other shrimps in addition to producing and brooding eggs. These anatomical observations and behavioural experiments together demonstrate that *L. nayaritensis* is a simultaneous hermaphrodite with an early male phase.

The sexual system of *Lysmata nayaritensis* is the same as has been reported for every other species of *Lysmata* that has been examined (Wirtz 1997; Bauer and Holt 1998; Fiedler 1998; d'Udekem d'Acoz 2003; Bauer and Newman 2004; Baeza and Anker forthcoming). This suggests that the overall sexual system does not vary within the genus, and that clues to the origin of this unusual system should be looked for in the sister group of the genus. However, the variation in the social system within *Lysmata* suggests that the details of sex allocation such as sex ratio and the size at which males become hermaphrodites should vary among species.

Although *L. nayaritensis* has the same sexual system as the other species in the genus, it does not fit comfortably into the "temperate crowd"–"tropical pair" dichotomy. Despite living in the tropics, *Lysmata nayaritensis* appears to fit into the crowd category, with high population densities, intertidal habitat, and a dull reddish colour (Wicksten 2000). The habitat on the Pacific coast of mainland Panama, where these shrimps were collected, may be more similar to the temperate habitats in which other *Lysmata* species have been collected than to the tropical habitats, like Hawaii where *L. amboinensis* was collected (Fiedler 1998). The Bay of Panama has unusually high productivity for a tropical site, with seasonal upwelling that can reduce the temperature to 15°C. In addition, there is little coral and the sites where we have collected *Lysmata nayaritensis* are dominated by mud and rock rubble. This suggests that the difference between pair and crowd species may depend more on the specific type of habitat in which they live than on whether they are tropical or temperate.

The sex ratio of *L. nayaritensis* in the field was highly biased towards males. A male-biased sex ratio was also reported for the warm temperate "crowd" species *L. wurdemannii* (Baeza 2007b) and *L. californica* (Bauer and Newman 2004). A male-biased sex ratio would be consistent with the theoretical prediction for sequential hermaphrodites whose sex ratio should be biased towards the first sex (in this case males; Charnov and Bull 1989), however, this theory has yet to be formally extended to protandric simultaneous hermaphrodites. Despite the theoretical predictions, high levels of variation in sex ratio within genera or families of sequential hermaphrodites appear to be the norm (Allsop and West 2004; Collin 2006). Information on more species of protandric simultaneous hermaphrodites needs to be collected before a general picture of variation in sex allocation in this sexual system can be drawn.

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