2008

Experimental confirmation of protandric simultaneous hermaphroditism in a Caridean shrimp outside of the genus Lysmata

Helio Laubenheimer
Universidade Santa U´ rsula

Andrew L. Rhyne
Roger Williams University, arhyne@rwu.edu

Recommended Citation

Laubenheimera, H. and A.L. Rhyne. 2008. "Experimental Confirmation of Protandric Simultaneous Hermaphroditism Outside of the Genus Lysmata." *Journal of Marine Biological Association of the United Kingdom* 88: 301-305.

Journal of the Marine Biological Association of the United Kingdom, 2008, 88(2), 301–305.
doi:10.1017/S0025315408000702 Printed in the United Kingdom

Experimental confirmation of protandric simultaneous hermaphroditism in a Caridean shrimp outside of the genus *Lysmata*

HELIO LAUBENHEIMER[1] AND ANDREW L. RHYNE[2]

[1]Universidade Santa Úrsula, Instituto de Ciências Biológicas e Ambientais, Rua Jornalista Orlando Dantas 59, Botafogo 22231-010, Rio de Janeiro—RJ, Brazil, [2]University of Florida, Indian River Research and Education Center, 2199 South Rock Road, Fort Pierce, Florida, 34945 USA

Caridean shrimps display a variety of sexual systems including gonochorism and various forms of protandry but rarely simultaneous hermaphroditism. Protandric simultaneous hermaphroditism (PSH) has thus far only been demonstrated in the genus Lysmata. *The first report of simultaneous hermaphroditism in a caridean shrimp was with* Exhippolysmata ensirostris. *However, this was not confirmed, since this species was also considered to be strictly protandric. Therefore, inconclusive results about this species' true sexual system led us to examine* Exhippolysmata oplophoroides. *Mating between female phase individuals resulted in successful spawning, embryonic development and hatching of viable larvae. Furthermore, we have confirmed that this species is not capable of self-fertilization. Juveniles reared in the laboratory matured in a similar manner to that of* Lysmata. *Data were limited due to the loss of all individuals to a* Vibrio *infection. However, the results obtained in this study conclusively affirm functionally that PSH occurs outside the genus* Lysmata, *in* E. oplophoroides. *Theories examining the evolution of PSH within decapods must be re-examined in light of the present data.*

Keywords: hermaphoditism, *Lysmata*, *Exhippolysmata*, sexual system

Submitted 19 June 2007; accepted 27 November 2007

INTRODUCTION

Sexual systems of caridean shrimps are characterized by their high diversity and intraspecific plasticity, including gonochorism and various forms of protandric or simultaneous hermaphroditism (Correa & Thiel, 2003). Different patterns of protandry are frequent among carideans, and sex determination can be plastic either on evolutionary or on ecological time scales (Correa & Thiel, 2003). Protandrous hermaphroditism has been previously described in some species belonging to the family Pandalidae (e.g. Allen, 1959; Butler, 1964, 1980). Individuals first mature as males and with increasing size, change sex to females. Typical caridean sexual male characters are the presence of cincinnuli on the endopodite of the first pair of pleopods and spines on the inner margin of the appendix masculina in the second pair of pleopods (Butler, 1964; Hoffman, 1972). These copulatory organs are present during the male stage and later get atrophied or disappear when changing to the female stage. Simultaneous hermaphroditism had only been suggested in some species of decapods, based solely on their reproductive morphology (Spitschakoff, 1912; Buchanan, 1963; Berreur-Bonnefant & Charniaux-Cotton, 1965; Kagwade, 1982).

Sukumaran (1973, 1982) examined the secondary sexual characters and gonad of *Exhippolysmata ensirostris* (Kemp). He observed that smaller individuals (20–30 mm total length) were mostly males, possessing cincinnuli on the endopodites of the first pair of pleopods. On the second pair, appendices masculinae were armed with 5–6 spines and an appendix interna with cincinnuli. The gonad of males is a true testis containing sperm at different stages of development. Medium sized individuals (31–40 mm) were considered to be in the early stage of transition from male to female. Endopodites of the first pair of pleopods are more slender and in a state of reabsorption. Appendices masculinae are reduced in size without strong spines. The gonad is only different from males by having immature eggs inside the gonad. Larger individuals (>40 mm) are females (majority berried), possessing slender and tapering endopodites of the first pair of pleopods. On the second pair of pleopods the appendices masculinae are greatly reduced and in a state of atrophy; the appendix interna has an increased number of cincinnuli. The gonad of these individuals was an ovotestis, having an anterior ovarian portion and a posterior testicular portion with a pair of vas deferens laterally. Sukumaran (1982) concluded that *E. ensirostris* cannot be functional males through the female stage, as they are devoid of fully developed copulatory organs and the testicular portion showed signs of degeneration and absorption as the size of the shrimp increased.

On the other hand, Kagwade (1982) reported, based only on morphological evidence, that *E. ensirostris* is a simultaneous

Corresponding author:
H. Laubenheimer
Email: heliousu@yahoo.com

hermaphrodite. He observed that individuals ranging from 43–63 mm in total length have cincinnuli on the endopodite of the first pair of pleopods. The appendix masculina (AM) on the second pair of pleopods was observed to become shorter as size of the shrimp increased, even though a small number of specimens have well-developed appendices masculinae. Because of this variation in AM length, this character is not adequate to establish sex reversal. All individuals ranging from 20–100 mm total length in size had an ovotestis. The fact that sperm is noticed in immature as well as ovigerous specimens made Kagwade establish *E. ensirostris* as a hermaphrodite throughout its life. Both presence of sperm (testicular part) and ova (ovarian part) in ovigerous females shows synchronous hermaphroditism, ruling out the case of protandry.

Chacur & Negreiros-Fransozo (1999) collected *Exhippolysmata oplophoroides* (Holthuis, 1948) from the Ubatuba, São Paulo, Brazil coastline and did not find any males in their samples, which led them to believe that this is a protandrous species. Fransozo *et al.* (2005) also studied *E. oplophoroides* population biology in Ubatuba. They were not able to sex the specimens since ovigerous shrimps had the same sexual morphology as non-ovigerous ones.

Fiedler (1998) (*Lysmata amboinensis* De Man, 1888) and Bauer & Holt (1998) (*L. wurdemanni* (Gibbs, 1850)) described for the first time in decapods a sexual system, protandric simultaneous hermaphroditism (PSH), followed by Lin & Zhang (2001) for *Lysmata ankeri* Rhyne & Lin, 2006, using both morphology and mating experiments. Juveniles first go through a typical caridean male phase (MP) and later pass to a female phase (FP), maintaining male characteristics such as male gonopores and an ovotestis terminating in ejaculatory ducts containing sperm, allowing them to copulate successfully both as males and females (Bauer & Holt, 1998; Fiedler, 1998). Bauer (2000) suggests that this sexual system may be widespread throughout the genus. Recent investigations demonstrate that *Lysmata californica* (Stimpson, 1866) (Bauer & Newman, 2004), *L. nilita* Dorn & Holthuis, 1950 and *L. seticaudata* (Risso, 1918) (D'Udekem D'Acoz, 1999), *L. pederseni* Rhyne & Lin, 2006, *L. bahia* Rhyne & Lin, 2006 and *L. boggessi* Rhyne & Lin, 2006 display this same sexual system.

Observations by both Sukumaram (1973, 1982) and Kagwade (1982) make us believe that PSH is not solely confined to *Lysmata*. The genus *Exhippolysmata* is taxonomically closely related to the genus *Lysmata*.

The present study was conducted to experimentally confirm that *Exhippolysmata oplophoroides* is a protandric simultaneous hermaphrodite.

MATERIALS AND METHODS

This study was conducted at the University Santa Úrsula's Aquaculture and Global Information System Laboratory in 2006. Adult *Exhippolysmata oplophoroides* were collected by trawl by local collectors off the coast of Victoria, Espirito Santo, Brazil and brought to Rio de Janeiro. Shrimps were maintained in pairs in 42 l aquaria. Their sex was determined and total length (TL: from post-orbital margin to the tip of the telson) and cephalothorax length (CL: from post-orbital margin to the posterior margin of the carapace) were measured in mm. Salinity was maintained at 35 ± 1 ppt, temperature at 26 ± 0.5°C and photoperiod at 12 h day:12 h night. Shrimps were fed daily with frozen shrimp and squid.

In order to test the hypothesis that FP shrimps can mate and produce viable offspring, a mating experiment consisting of five gravid FP pairs was conducted. Both shrimps in each pair displayed a full gonad, indicating readiness to spawn. All shrimps had previously spawned at least one fertile clutch. Each tank was checked daily for moults and observations on the egg development were made. In order to follow their mating; one pair's activity was observed visually during the night using an infrared light. After all individuals moulted, mated and spawned, embryonic development was followed daily until a clutch of viable larvae hatched.

To confirm that this species is not capable of self fertilization, five FP shrimps with full gonads were maintained in isolation. All shrimps had previously spawned at least one fertile clutch. Each tank was checked daily for moults and observations on the egg development were made. After each moult, the presence of eggs attached to their pleopods was recorded and embryonic development followed.

In order to follow the sexual morph development, larvae were reared following the protocols described in Calado *et al.* (2003) and adapted by Laubenheimer (2004). Ten newly metamorphosed juveniles were placed individually in 1 l beakers until they reached the FP. These shrimps were fed with newly hatched *Artemia* nauplii *ad libitum* and a 100% water change was conducted daily. Each beaker was checked daily for moults, which were removed with a pipette and observed under a stereoscopic (Zeiss–Stemi SV11) and/or optical microscope (Zeiss–Axioskop). The observed characters were presence/absence of cincinnuli (coupling hooks) on the endopodites of the first pair of pleopods, appendix masculina (AM) and appendix interna (AI) of the second pair of pleopods.

RESULTS

A total of twenty individuals were obtained from field collected specimens for this study and were maintained in the laboratory for approximately 50 d prior to being lost to bacterial infections (*Vibrio* sp.). Specimens ranged in size from TL 28.2 mm (CL 9.0 mm) to TL 39.8 mm (CL 11.5 mm). Only one, the smallest individual was a male, characterized by the presence of appendices masculinae on the second pair of pleopods (Figure 1 A & B). No cincinnuli could be observed on the endopodites of the first pair of pleopods. These fragile structures might have been lost during 'handling', as observed by Kagwade (1982). This shrimp did not display a visible gonad, nor did it show signs of development during the experiment. This specimen died from a bacterial infection after approximately three weeks in captivity. When kept with a FP individual, it was only able to successfully fertilize its mate, never capable of spawning a clutch. All other individuals were euhermaphrodites (mean TL 39.5 mm, CL 11.1 mm), characterized by the absence of both cincinnuli on the endopodites of the first pair of pleopods and appendices masculinae on the second pair of pleopods (Figure 1). All were observed to hold eggs at some point of our study.

A mating experiment (N = 5) to test the hypothesis that FP specimens can copulate successfully both as male and female was conducted. In each of the five replicate pairs, both shrimps moulted, copulated, and incubated embryos. A successful fertilization event was characterized by the presence

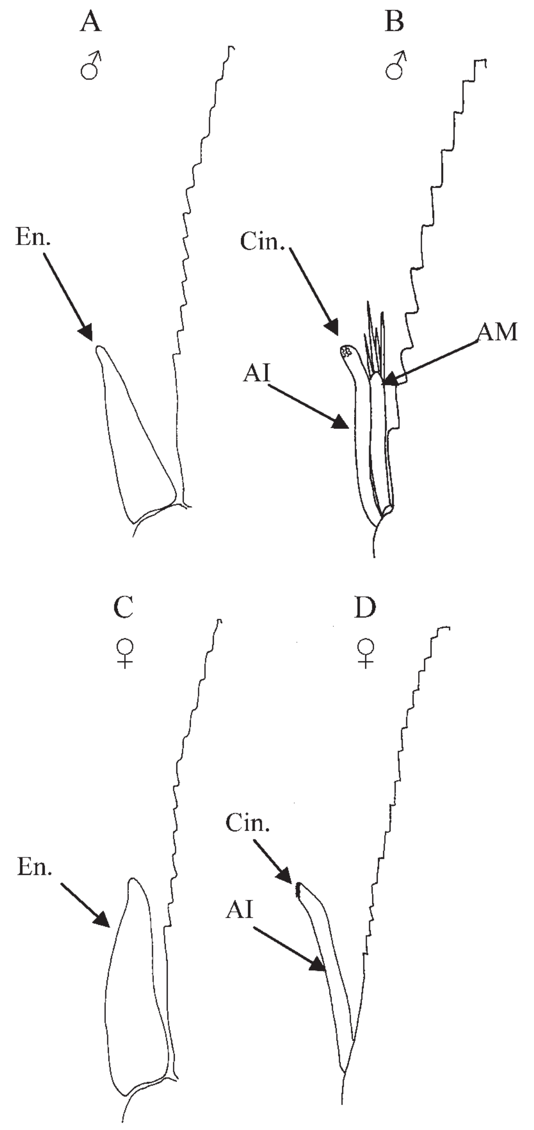

Fig. 1. *Exhippolysmta oplophoroides* sexual morph development. (A) First pair of pleopods in a male phase shrimp; En. (endopodite) thin and long, without cincinnuli (probably lost due to its fragile nature); (B) second pair of pleopods in a male phase shrimp; presence of AM (appendix masculina) with several spines on tip; and AI (appendix interna) with Cin. (cincinnuli) on tip; (C) first pair of pleopods in a euhermaphropdite shrimp, no cincinnuli present; En. larger and longer; and (D) second pair of pleopods in a euhermaphrodite shrimp, no appendix maculina present; AI longer with Cin. on tip (dense setation of endopodites in (C) were not drawn).

of eggs which developed by changing colour from bright green to a dark yellowish-brown over a 9–10 d period, resulting in hatching of viable larvae. Individuals kept separately were not able to self-fertilize, characterized by the extrusion of eggs to the abdomen of the shrimp and a total loss of those eggs within 5 d (normally less than 24 h) (Fiedler, 1998).

After settling to metamorphosis, juvenile *Exhippolysmata oplophoroides* presented endopodites of the first pair of pleopods without coupling hooks. The endopods of the second pair of pleopods were provided with an AI with 2–6 coupling hooks. In the MP (Figure 1 A & B) the endopodites of the first pair of pleopods were more slender and tapering. No coupling hooks could be observed. On the second pair of pleopods, AM presented 4 spines on its tip reaching approximately three-quarters or until the end of the AI, which presented more then 6 coupling hooks. In the FP (Figure 1 D & C), the endopodite of the first pair of pleopods was broader, displaying no coupling hooks. On the second pair of pleopods the appendices masculinae regressed totally and the AI presented two rows of coupling hooks.

DISCUSSION

Exhippolysmata oplophoroides displays a PSH sexual system. Young individuals first develop as males and later, larger (older) individuals are functional hermaphrodites, serving as a reproductive female and male at the same time. This is the first study to confirm empirically PSH outside of the genus *Lysmata*.

Sukumaran (1973) noticed that all individuals of *Exhippolysmata ensirostris* he examined have an AM on the second pair of pleopods. In smaller individuals (males) this structure is well developed bearing strong spines. As shrimps increased in size, this structure started to decrease (transitional phase) until it almost disappeared. At this stage, shrimps were females holding eggs. The endopodites of the first pair of pleopods in male shrimps had cincinnuli on their tip. In females, these structures disappeared and the endopodite was slender and tapering. Sukumaran (1973, 1982) proposed that this species is a protandrous hermaphrodite. On the other hand, Kagwade (1982) did not support the idea that this species had a male phase, suggesting that this species is hermaphroditic throughout its life. All the specimens examined in his study, from the smallest TL (20 mm) to the largest (100 mm) were found to possess ovotestes and an AM on the second pair of pleopods. However, appendices masculinae did decrease in size in larger specimens, supporting the observations made by Sukumaran (1973). Kagwade (1982) states that 'even though appendix masculina is reduced in size in higher lengths, there still are some individuals, in very small percentage, in which it is well developed, rendering it difficult to rely fully on this character to establish sex reversal in this species'. Delayed sex change, which has been observed in populations of *Lysmata ankeri* held in the laboratory (Lin & Zhang, 2001), could explain the sampling bias. Bauer (2002) suggested that the occurrence of large MP individuals could be explained by abiotic factors. Under suboptimal conditions (lower temperatures during autumn/winter) rates of change from the male to female phase were much lower. Shaikmahmud & Tembe (1960) noticed that the fishery of *E. ensirostris* was mainly supported by females throughout the year, and males only during certain months. Specimens collected for Kagwade's (1982) study were collected during November 1971 to December 1974, which could explain the reason for the appearance of larger males in both authors' samples. Even though abiotic factors could be the cause for delayed sex change, recent studies (Lin & Zhang, 2001 Bauer & Baeza, 2004; Zhang & Lin, 2005; Baeza, 2006) indicate that social factors also have an influence over sex change. The social control in *E. oplophoroides* is not known; more studies are needed to investigate in depth the reason for the occurrence of mostly FP individuals.

In our study, FP *E. oplophoroides* did not have appendices masculinae, unlike what Sukumaran (1973) and Kagwade (1982) observed in *E. ensirostris*. It is believed that the appendix masculina serves as a copulatory projection (Descouturelle, 1971; Bauer, 1986), but its role in sperm transfer has been discounted in *Lysmata wurdemanni* (Zhang & Lin, 2004a). In another caridean shrimp *Palaemonetes pugio* Holthuis, 1949, the appendix masculina is necessary for sperm transfer (Berg & Sandifer, 1984). When the appendices masculinae or endopodites of the first pair of pleopods were removed, *Heptacarpus sitchensis* (Brandt, 1851) (Wicksten *et al.*, 1996) and *H. pictus* Stimpson, 1871 (Bauer, 1976) did not transfer the spermatophore as successfully as when these structures were intact. Even though all secondary sexual male characters are lost in *Lysmata*, FP individuals are still capable of functioning as males and fertilizing successfully other FP individuals. Therefore, it is not surprising that these characters (structures) are not necessary for sperm transfer. Fiedler (2000) states that, in *Lysmata amboinensis*, only the first pair of pleopods are necessary to successfully transfer the spermatophore. In *L. wurdemanni*, only when both first and second pairs of pleopods were removed, fertilization was not successful (Zhang & Lin, 2004a,b). The retention of these structures might be a phylogenetic restriction and/or not be a selective disadvantage (Fiedler, 2000).

ECOLOGY, SOCIAL ORGANIZATION AND IMPLICATIONS FOR THE EVOLUTION OF PSH

Shrimps belonging to the genus *Lysmata* are commonly found on hard bottoms such as rocky ledges, tide pools and coral reefs, often associated with algae, sea grass and various other sessile invertebrates (Bauer, 2004). Even though PSH is widespread in the genus *Lysmata*, their social organization and ecology differ greatly (Bauer, 2000). *Exhippolysmata oplophoroides* is found living on sandy bottoms (Pires, 1992) and in high aggregations (Chakur & Negreiros-Franzoso, 1999; Fransozo *et al.*, 2005). Female individuals with a CL larger than 4.1 mm were the only specimens sampled (Chakur & Negreiros-Franzoso, 1999; Franzoso *et al.*, 2005), indicating that juveniles and/or males might not share the same habitat, or recruit and change sex quickly. Another possibility for this absence of males in the samples from these studies is an inability to catch smaller shrimps in trawls. More sampling must be conducted to further investigate these findings.

Our study demonstrates that PSH is not confined to the genus *Lysmata*, indicating that this sexual system might evolve from a common ancestor. *Exhippolysmata oplophoroides* lives in high aggregations similar to 'crowd living' *Lysmata* spp. If *Exhippolysmata* is an ancestor of *Lysmata* the implications for current theories on how PSH evolved would be profound. Furthermore, studies investigating the cost of maleness or sexual allocation within *Lysmata* should be expanded to *Exhippolysmata* and other closely related genera.

ACKNOWLEDGEMENTS

The authors thank Dong Zhang, Cortney Ohs and two anonymous referees who greatly improved the manuscript; the Universidade Santa Úrsula and the Aquaculture and Global Information System Laboratory for giving us the opportunity to conduct this study; Alexander Talarico for his sponsorship; and Raul Fernandes Marinheiro Neto for his help in the laboratory.

REFERENCES

Allen J.A. (1959) On the biology of *Pandalus borealis* Kroyer, with reference to a population of the Northumberland coast. *Journal of the Marine Biological Association of the United Kingdom* 38, 189–220.

Baeza J.A. (2006) Testing three models on the adaptive significance of protandric simultaneous hermaphroditism in a marine shrimp. *Evolution* 60, 1840–1850.

Bauer R.T. (1976) Mating behaviour and spermatophore transfer in the shrimp *Heptacarpus pictus* (Stimpson) (Decapoda: Caridea: Hippolytidae). *Journal of Natural History* 10, 415–440.

Bauer R.T. (1986) Sex change and life history pattern in the shrimp *Thor manningi* (Decapoda: Caridea): a novel case of partial protandric hermaphroditism. *Biological Bulletin. Marine Biological Laboratory,Woods Hole* 170, 11–31.

Bauer R.T. (2000) Simultaneous hermaphroditism in caridean shrimps: a unique and puzzling sexual system in the Decapoda. *Journal of Crustacean Biology* 20, 116–128.

Bauer R.T. (2002) Test of hypotheses on the adaptive value of an extended male phase in the hermaphroditic shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae). *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 203, 347–357.

Bauer R.T. (2004). *Remarkable shrimps: natural history and adaptations of the Carideans*. Norman: University of Okalahoma Press.

Bauer R.T. and Holt G.J. (1998) Simultaneous hermaphroditism in the marine shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae): an undescribed sexual system in the decapod Crustacea. *Marine Biology* 132, 223–235.

Bauer R.T. and Baeza J.A. (2004) Experimental test of socially mediated sex change in a protandric simultaneous hermaphrodite, the marine shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae). *Marine Biology* 55, 544–550.

Bauer R.T. and Newman W.A. (2004). Protandric simultaneous hermaphroditism in the marine shrimp *Lysmata californica* (Caridea: Hippolytidae). *Journal of Crustacean Biology* 24, 131–139.

Berreur-Bonnefante J. and Charnoioux-Cotton H. (1965) Hermaphrodisme protérandrique et fonctionnnement de la zone germinative chez la crevette *Pandalus borealis* Kröyer. *Bulletin de la Société Zoologique de France* 90, 240–259.

Berg A.B. and Sandifer P. (1984) Mating behavior of the grass shrimp *Palaemonetes pugio* Holthuis (Decapoda: Caridea). *Journal of Crustacean Biology* 4, 417–424.

Buchanan J.B. (1963) The biology of *Colocaris macandreae* (Crustacea: Thalassanidae). *Journal of the Marine Biological Association of the United Kingdom* 43, 729–747.

Butler T.H. (1964) Growth, reproduction, and distribution of pandalid shrimps in British Columbia. *Journal of the Fisheries Research Board of Canada* 21, 1402–1452.

Butler T.H. (1980) Shrimps of the Pacific coast of Canada. *Canadian Bulletin of Fisheries and Aquatic Science* 202, 1–280.

Calado R., Narciso L., Morais S., Rhyne A.L. and Lin J. (2003) A rearing system for the culture of ornamental decapod crustacean larvae. *Aquaculture* 218, 329–339.

Chacur M.M. and Negreiros-Fransozo M.L. (1999) Aspectos biológicos do camarão-espinho *Exhippolysmata oplophoroides* (Holthuis, 1948)

(Crustacea, Caridea, Hippolytidae). *Revista Brasileira de Biologia* 59, 173–181.

Correa C. and Thiel M. (2003) Mating systems in caridean shrimp (Decapoda: Caridea) and their evolutionary consequences for sexual dimorphism and reproductive biology. *Revista Chilena de Historia Natural* 76, 187–203.

D'Udekem D'Acoz C. (2003) *Lysmata seticaudata* (Risso, 1816) and *L. nilita* Dohrn & Holthuis, 1950 are protandrous hermaphrodites (Decapoda, Caridea, Hippolytidae). *Crustaceana* 79, 1149–1152.

Descouturelle G. (1971) Rôles des appendices sexuels mâles d'un la copulation et d'un réceptacle séminal femelle dans la ponte chez *Atyaephyra desmaresti* Millet (Crustacea-Decapoda-Caridea). *Bulletin de l'Académie et de la Société Lorraines des Sciences* 10, 10–14.

Fiedler G.C. (1998) Functional, simultaneous hermaphroditism in female-phase *Lysmata amboinensis* (Decapoda: Caridea: Hippolytidae). *Pacific Science* 52, 959–962.

Fiedler G.C. (2000) *Sex determination and reproductive biology of two caridean shrimp genera*: Hymenocera and Lysmata. PhD thesis, University of Hawaii, USA.

Fransozo V., Rogério C.C., Bertini G. and Cobo V.J. (2005) Population biology of spine shrimp *Exhippolysmata oplophoroides* (Holthuis) (Caridea: Hippolytidae) in a subtropical region, São Paulo, Brazil. *Revista Brasileira de Zoologia* 22, 1078–1084.

Hoffman D.L. (1972) The development of the ovotestis and copulatory organs in a population of protandric shrimp, *Pandalus platyceros* Brandit from Lopez Sound, Washington. *Biological Bulletin. Marine Biological Laboratory, Woods Hole* 142, 251–270.

Kagwade P.V. (1982) The hermaphrodite prawn *Hippolysmata ensirostris* Kemp. *Indian Journal of Fisheries* 28, 189–194.

Laubenheimer H. (2004) *Reprodução do camarão ornamental marinho* Lysmata *sp. (Decapoda: Caridea: Hippolytidae)*. Monografia de Bacharel, Universidade Santa Úrsula, RJ, Brasil.

Lin J. and Zhang D. (2001) Reproduction in a simultaneous hermaphroditic shrimp, *Lysmata wurdemanni*: any two will do? *Marine Biology* 139, 919–922

Pires A.M.S. (1992) Structure and dynamics of benthic megafauna on the continental shelf offshore of Ubatuba, southeastern Brazil. *Marine Ecology Progress Series* 86, 63–76.

Rhyne A.L. and Lin J. (2006) A western Atlantic peppermint shrimp complex: redescription of *Lysmata wurdemanni* (Gibbes), description of four new species and remarks on *L. rathbunae* Chace (Crustacea: Decapoda: Hippolytidae). *Bulletin of Marine Science* 79, 165–204.

Spitschakoff T. (1912) *Lysmata seticaudata* Risso, als Beispiel eines echten Hermaphroditismus bei den Decapoden. *Zeitschrift für Wissenschaftliche Zoologie* 100, 190–209.

Shaikmahmud T.S. and Tembe V.B. (1960) Study of Bombay prawns. *Indian Journal of Fisheries* 7, 69–81.

Sukumaran K.K. (1973) On the gonad of the protandric prawn *Hippolysmata ensirostris* Kemp. *Indian Journal of Fisheries* 28, 195–198.

Sukumaran K.K. (1982) Observation on the secondary sexual characters of *Hippolysmata ensirostris* Kemp. *Indian Journal of Fisheries* 20, 626–629.

Wicksten M.K., Flynn R. and Fagarason M. (1996) *Heptacarpus pictus* (Stimpson) synonymized with *Heptacarpus sitchensis* (Brandt) (Decapoda: Hippolytidae). *Crustaceana* 69, 71–75.

Zhang D. and Lin J. (2004a) Fertilization success without anterior pleopods in *Lysmata wurdemanni* (Decapoda: Caridea), a protandric simultaneous hermaphrodite. *Journal of Crustacean Biology* 24, 470–473.

Zhang D. and Lin J. (2004b) Mating without anterior pleopods in a simultaneous hermaphroditic shrimp, *Lysmata wurdemanni* (Decapoda: Caridea). *Crustaceana* 77, 1203–1212.

and

Zhang D. and Lin J. (2005) Comparative mating success of smaller male-phase and larger male-role euhermaphrodite-phase shrimp, *Lysmata wurdemanni* (Caridea: Hippolytidae). *Marine Biology* 147, 1387–1392.

Correspondence should be addressed to:
Helio Laubenheimer
Universidade Santa Úrsula, Instituto de Ciências
Biológicas e Ambientais
Rua Jornalista Orlando Dantas 59
Botafogo 22231-010
Rio de Janeiro—RJ
Brazil
email: heliousu@yahoo.com