Pacific Science (1998), vol. 52, no. 2: 161–169

Functional, Simultaneous Hermaphroditism in Female-Phase *Lysmata amboinensis* (Decapoda: Caridea: Hippolytidae)[1]

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ABSTRACT: Several species of hippolytid shrimp of the genus *Lysmata* are described as protandrous hermaphrodites, with speculation that some *Lysmata* are simultaneous hermaphrodites and/or store exogenous sperm. The objective of this study was to ascertain the presence of simultaneous hermaphroditism in *L. amboinensis* De Man. For this experiment, four pairs of female-phase *L. amboinensis* were isolated until each shrimp spawned two fertile clutches of eggs. For two of the four pairs, pair-mates were then separated and isolated in an identical fashion. Paired individuals continued to spawn and hatch fertile eggs. Isolated individuals spawned only infertile eggs. Paired shrimp also synchronized their molt cycles in a staggered fashion, such that individuals alternated sexual roles. Histological and morphological examination shows that each female-phase individual possessed an active male and female portion of the gonad with corresponding gonoducts. The results indicate that this species is a functional, simultaneous hermaphrodite. Previously, this pattern has not been adequately described in any decapod crustacean.

Hermaphroditism is known from relatively few (~40) species of decapod crustaceans in 10 families (for reviews, see Carpenter 1978, Policansky 1982, Bauer 1986) (for recent examples, see Sukumaran 1981, Bundy 1983, Nakashima 1987, Gherardi and Calloni 1993). Only protandrous sex change, where individuals change from male to female, has been reported, and it appears to be most common among caridean shrimp (Bauer 1986). Protandrous sex change is known to be common in only one family, the Pandalidae, of which the genera *Pandalus* and *Pandalopsis* are thought to be composed entirely of protandrous species (Bauer 1986). The family Hippolytidae has several species that display protandry in at least two genera, *Thor* and *Lysmata* (Sukumaran 1981, Policansky 1982, Bauer 1986).

Within the genus *Lysmata,* protandry has been reported in *Lysmata seticaudata, L. wurdemanni, L. ensirostris, L. grabhami, L. nilita,* and *L. amboinensis* De Man (Sukumaran 1981, Policansky 1982, Bundy 1983, Debelius 1984). Each individual matures as a male and then upon reaching a certain size or age begins functioning as a female (Charniaux-Cotton 1975). However, some *Lysmata* species are thought to retain male function during the "female phase" of life. Bundy (1983) and Crompton (1992) noted that pairs of female-phase *Lysmata wurdemanni* spawned fertile eggs without the presence of male-phase individuals. Bundy (1983) further showed, histologically, the simultaneous presence of mature oocytes and spermatocytes in *L. wurdemanni.* Kagwade (1981) observed the same gonadal state in *L. ensirostris.* Unfortunately, Kagwade (1981) provided no functional evidence (i.e., ability to fertilize other female-phase individuals) of simultaneous hermaphroditism. Though Bundy (1983) did give some functional evidence, no controlled fertility experiments were conducted. Furthermore, the possibility that individuals exhibited either self-fertilization or exogenous sperm storage was not ruled out. Because demonstration of functionality

[1] Support was provided by the Department of Zoology and the Hawai'i Institute of Marine Biology (HIMB) at the University of Hawai'i at Mānoa. This is HIMB contribution no. 1033. Manuscript accepted 4 August 1997.

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is the ultimate criterion for the determination of hermaphroditism (Sadovy and Shapiro 1987), the definitive proof of simultaneous hermaphroditism in the decapod Crustacea has yet to appear.

Lysmata amboinensis is a small (6 cm total length [TL]) hippolytid shrimp found in shallow waters of the Indo-Pacific, except for the eastern Pacific (Takeda 1982, Wicksten 1990). A similar species, *Lysmata grabhami,* is known from the tropical Atlantic; it varies slightly in color pattern and cannot interbreed with *L. amboinensis* (Debelius 1984). *Lysmata amboinensis* is often found in pairs, but has occasionally been observed in large groups (Debelius 1984). This species and some of its congeners are known as "cleaner shrimps" and have been observed servicing several species of fish, including eels (Randall 1958).

Male function has been suspected in female-phase *L. amboinensis* and has been the topic of articles in popular aquarium magazines (Debelius 1985, Wilkerson 1994). One aquarist has even suggested that the female phase of this shrimp stores sperm and that lone individuals produce several successive clutches of fertile eggs with no partner (Wilkerson 1994). My observations of captive *L. amboinensis* suggest that paired female-phase individuals spawn fertile clutches of eggs with each molt. Unfortunately, no information exists in the primary literature on the reproductive biology of this species. In this paper, I provide experimental and histological evidence that *L. amboinensis* is a simultaneous hermaphrodite during its female phase and describe sexual role switching between pairs of female-phase individuals in successive spawnings.

MATERIALS AND METHODS

I hypothesized that if female-phase individuals are true simultaneous hermaphrodites, they would spawn fertile eggs when paired and infertile (or no) eggs when isolated singly. Each female-phase individual should also show histological and morphological evidence of simultaneous hermaphroditism. If *single* individuals produce fertile eggs, "selfing" or exogenous sperm storage are possible alternatives. To determine if female-phase individuals have the ability to act as males, the clutch fertility of isolated single and paired individuals was compared over time in a controlled experiment.

Eight female-phase *L. amboinensis* collected from the leeward coast of O'ahu, Hawai'i, were used in this experiment. Individuals were grouped into four pairs and isolated in separate aquaria at the Hawai'i Institute of Marine Biology in Kāne'ohe, Hawai'i. Aquaria were provided constant aeration, running seawater, and a 13:11 hr light cycle for the duration of the experiment. The experimental animals were fed small pieces of either previously frozen shrimp and squid or "fish fudge" (gelatin fish food) ad libitum on a daily basis. Individual *L. amboinensis* were identified using variations in white pigment patterns on the uropods. The shrimp were kept in pairs for the preexperimental phase until each individual of each pair was observed to have spawned at least two successive fertile clutches of eggs to ascertain that all individuals were able to spawn fertile eggs. The preexperimental phase took place from 16 October 1994 to 20 January 1995.

For the experimental phase, two of the four pairs were randomly selected, and individuals of these pairs were separated and isolated in their own aquaria. Thus, two treatment groups were created: an isolated singles group (four individuals that were previously paired) and an isolated pairs group (four individuals that remained paired). These treatment groups were created concurrently to control for any environmental effects, such as a change in temperature, that could have affected the results. Animals were kept in this fashion until each individual had spawned at least four clutches of eggs. The experimental period occurred from 21 January 1995 to 2 June 1995.

During both the preexperimental and experimental phases, all aquaria were censused daily for the presence of molts, which could

be identified to individuals based upon uropod pigmentation. Further, during the intermolt phase, a few eggs from each individual were sampled on several days using a polypropylene transfer pipette and fixed in 10% formalin. Eggs were sampled in this way until their fertility could be ascertained with a microscope. A clutch of eggs was considered fertile if eyes could be seen on embryos or if hatching of larvae was observed. A clutch of eggs was considered infertile if no evidence of cleavage or embryo development was recorded over 4 days in sampled eggs.

At the completion of the experimental phase, all individuals were sacrificed and fixed in Dietrich's fixative (Gray 1954). The external secondary sex characteristics (presence of gonopores and pleopod morphology) of all individuals were observed and photographed with a dissection microscope. The appendages, abdomen, and carapace were later excised from fixed specimens. The remaining cephalothorax was embedded in paraplast media, following decalcification (with Fisher CalEx), dehydration (EtOH), and clearing (xylene). The entire cephalothorax was used to observe the location and morphology of gonoducts. Two specimens were sectioned longitudinally in the lateral plane, and the remaining six were sectioned transversely. In all cases, 10-μm serial sections were made for detailed observation of the morphology and histology of the entire gonad. Sections were later stained with Harris progressive hematoxylin and eosin (Galigher and Kozloff 1971).

RESULTS

During the experimental phase, a total of 26 clutches was produced by paired shrimp and 19 clutches from single shrimp. All clutches from paired individuals were fertile, but none of the clutches from single individuals were fertile. All individuals produced eggs following each molt, but never during the intermolt period. The infertile eggs produced by the single shrimp all disappeared within 4 days, well short of the incubation period for fertile eggs. The mean intermolt period ranged from 20.8 days at the beginning of the experimental phase to 18.3 days at the end. Incubation time for eggs was typically a day (or less) shorter than the intermolt period.

The molt cycles of paired and single shrimp also differed during the experimental phase. Paired individuals molted and reproduced in a synchronized, staggered fashion (Figure 1). Pair-mates typically underwent ecdysis midway through their partner's intermolt. In contrast, single individuals drifted from a regular molting cycle and did not remain synchronized with their former pair-mates.

Morphologically, each individual possessed both male and female gonopores at the typical locations expected for gonochoristic decapods. Male gonopores could clearly be seen at the base of each fifth pereiopod, and female gonopores, though more difficult to locate, were found at the base of the third pereiopods. Endopods of the second pleopods did not bear any recognizable appendix masculina, the copulatory appendage of male caridean shrimp (Charniaux-Cotton and Payen 1983). Endopods of the first pleopods were greatly tapered. However, with light microscopy it was not possible to determine the presence of the groove thought to transfer spermatophores during copulation in male gonochoristic shrimp (Charniaux-Cotton and Payen 1983).

Histologically, all individuals showed evidence of active male and female tissues within the gonad. As in protandrous *Lysmata* species (Charniaux-Cotton 1975, Sukumaran 1981), each gonad was composed of a posterior testicular and an anterior ovarian zone (Figure 2*a–h*). Furthermore, separate pairs of sperm and oviducts were observed originating from their respective portions of the gonad (Figure 2*d,g*). All eight individuals had vitellogenic oocytes within the ovary (Figure 2*e,f*) and mature spermatocytes within the sperm ducts and terminal ampulla (Figure 2*d*). One individual (L4A) that had molted just before fixation possessed spent ovaries with only a few vitellogenic oocytes,

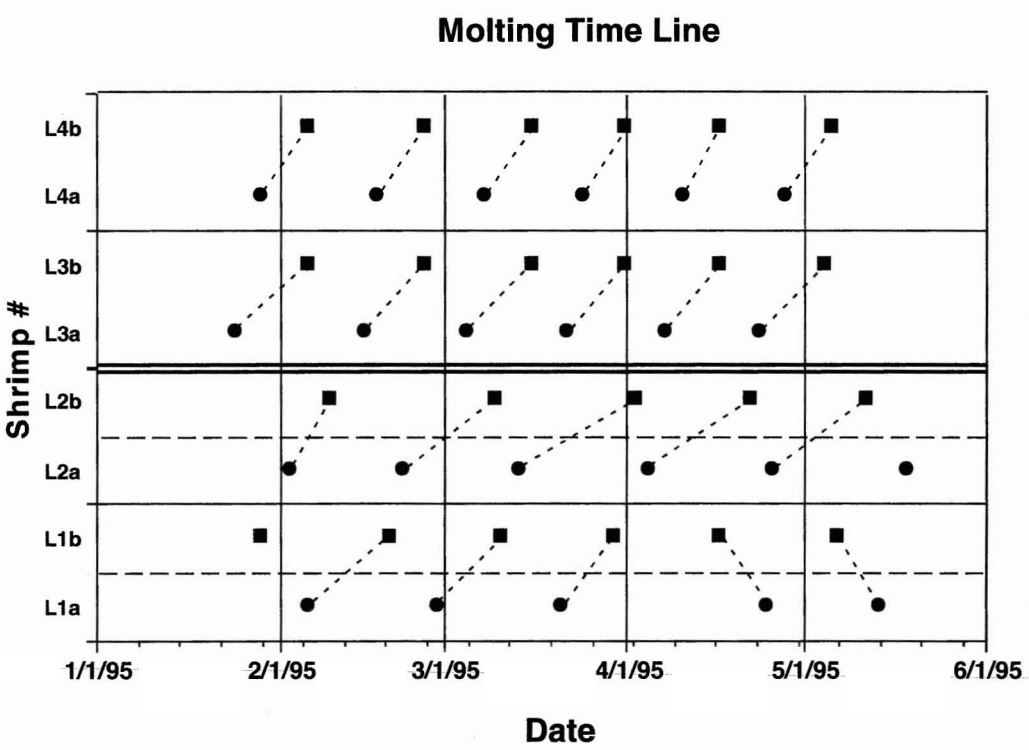

FIGURE 1. Molting time line for all individuals during the experimental phase. Each symbol on the graph represents the day ecdysis was observed for that individual. Paired shrimp are presented on the top half of the graph, and singles on the lower half. Single shrimp are separated from their former pair-mates with a horizontal dashed line. Dotted lines are drawn between molt dates of pair-mates and former pair-mates for illustrative purposes only. Note that paired shrimp synchronize their molt cycles in a staggered fashion. Isolated shrimp do not appear to remain synchronized, and their molt cycles drift.

but many previtellogenic eggs. Another individual (L3A) that spawned three days before fixation had many of both previtellogenic and vitellogenic oocytes.

Mature spermatocytes were tack-shaped (Figure 2*c*), the typical morphology found in caridean shrimp (Pochon-Masson 1983). Mature spermatocytes were also noted within the testis of six shrimp (Figure 2*b*), but were seen within the proximal sperm ducts of the other two individuals. One of these two (L3A, again) was 3 days past molting (with mixed vitellogenic and previtellogenic oocytes) and had many mature sperm in the duct and terminal ampulla. No androgenic glands were observed near the terminal end of the sperm duct in any individual, as reported in *L. wurdemanni* and *L. sedicaudata* (Charniaux-Cotton 1975, Bundy 1983).

DISCUSSION

The results clearly indicate that *Lysmata amboinensis* is a simultaneous hermaphrodite, morphologically, histologically, and functionally. This is the first definitive demonstration of this phenomenon in the decapod Crustacea. The inability of isolated individuals to spawn fertile eggs indicates that this species is not storing exogenous sperm or "selfing." The apparent synchronization of the molt cycles of pair-mates ensures that individuals will be ready to fertilize their partners. It may further facilitate alternation of sexual roles between pair-mates.

Because all paired *L. amboinensis* spawned fertile eggs, it is reasonable to assume that they were fertilized by their female-phase partners. This conclusion is supported by the

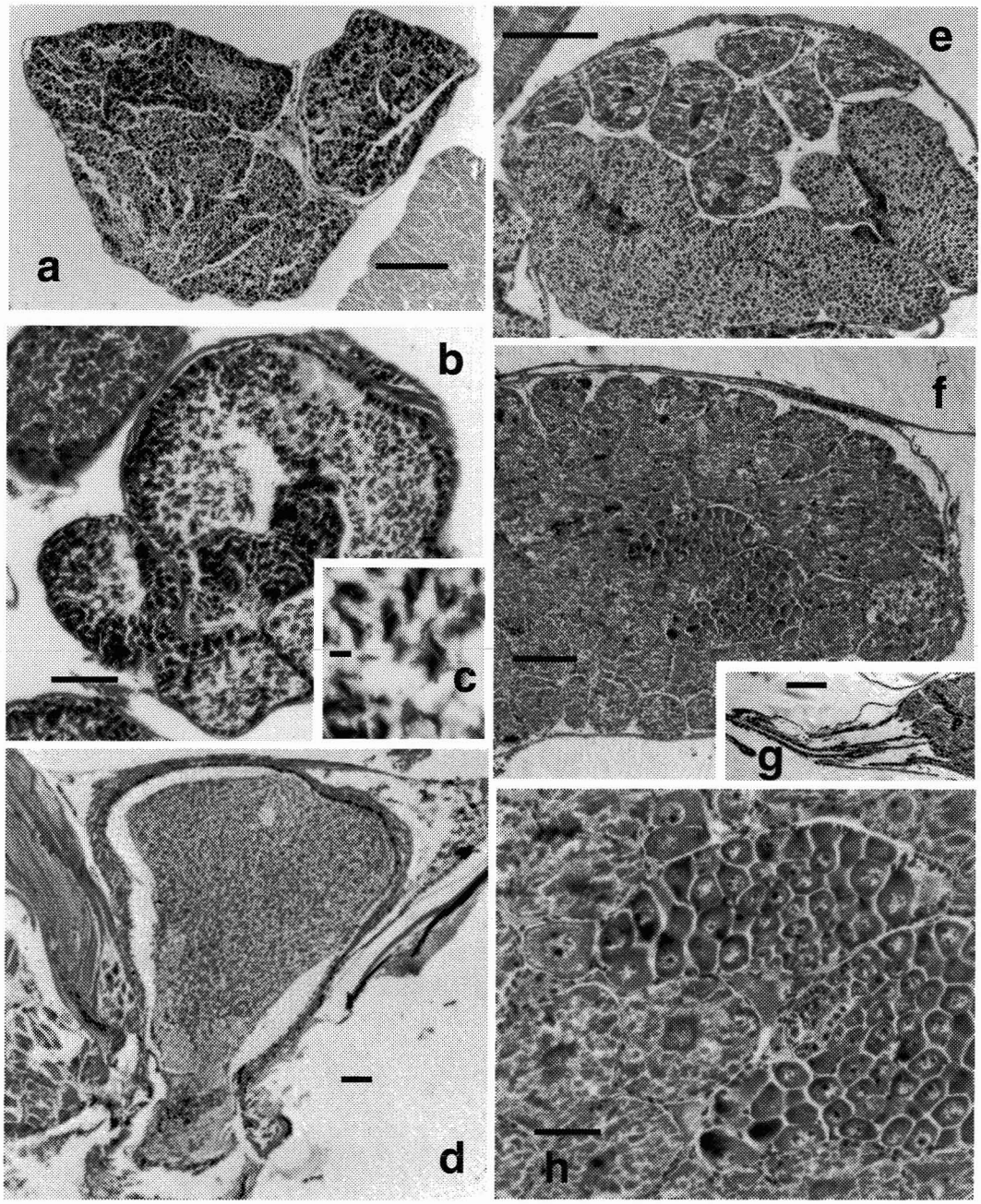

FIGURE 2. Representative micrographs of histological sections of *Lysmata amboinensis* gonads. *a,* testicular (posterior) portion of gonad. *b,* testicular portion with lumen containing sperm. Note the vitellogenic oocyte in upper left corner. *c,* inset of *b* showing mature tack- or parasol-shaped sperm cells. *d,* terminal ampulla of sperm duct. The lower portion is the distal end. *e,* mixed ovarian and testicular portion of gonad. *f,* half of a completely ovarian portion of the gonad (anterior). Note the central core of previtellogenic oocytes, surrounded by vitellogenic oocytes. *g,* proximal portion of oviduct extending from gonad. *h,* portion of *f* magnified, showing zone of proliferation of oocytes. Scale bars: *a, e, f, g,* 200 μm; *b, d, h,* 100 μm; *c,* 10 μm. All photomicrographs were taken with a Nikon FX-35DX camera mounted on a Nikon Labophot 2 compound microscope, using ASA 100 Kodak Tri-Pan X film.

fact that single shrimp did not produce fertile eggs. Furthermore, copulation was observed in two nonexperimental pairs of *L. amboinensis* (unpubl. data) following ecdysis of one pair-mate. These findings also suggest that exogenous sperm storage and/or "selfing" did not occur. However, the unlikely possibility of self-fertilization induced by pseudocopulation is not ruled out. Parthenogenetic female lizards of the genus *Cnemidophorus* require copulation with females of the same species to produce fertile eggs, although no genetic materials are transferred (Crews and Fitzgerald 1980). This phenomenon has not been reported in the literature for crustaceans.

The decrease in the intermolt period and incubation time during the experimental phase is not surprising and probably follows an increase in the ambient temperature. This relationship with temperature is well known in the Crustacea (Nelson 1991). Staggered synchronization of the molt cycles of pair-mates is, perhaps, a mechanism to ensure that individuals do not molt and reproduce as females at the same time. It also assures that an individual can reproduce as a male when a partner is ready for fertilization. Pair-mates, therefore, alternate sexual roles with their partners during the molt cycle. They act as males in the middle of the intermolt cycle and as females immediately following ecdysis. The staggered molt synchronization may also aid in reciprocation of sexual roles between paired individuals. Intermolt shrimp can more effectively guard their mates from extra-pair fertilization. Individuals who are nearing or have just undergone ecdysis may not be able to monopolize their partners. Role reciprocation is thought to be important in the evolution of social systems in simultaneous hermaphrodites (Leonard 1990).

Gross morphological evidence supports that *L. amboinensis* can act in both sexual roles. Both male and female gonopores were present, but male secondary sex characteristics were unclear. Female-phase *Lysmata seticaudata,* a protandrous species, also possesses female and male gonoducts and gonopores. Those of the opposite sex are thought to be nonfunctional during the respective male and female phases (Charniaux-Cotton 1975). The absence of the appendix masculina, though puzzling, is known from protandrous species of *Lysmata* during the female phase (Charniaux-Cotton 1960, Bundy 1983). Female-phase *L. amboinensis* in the experiment reported here accomplished fertilization without the appendix masculina. This has also been observed in males of *Crangon crangon* (Boddeke et al. 1991), which do not use the appendage though it is present.

The histological evidence is similar to that found in the two other so-called simultaneous hermaphrodite *Lysmata* species (Kagwade 1981, Bundy 1983). What is not known is exactly how the activation of male and female portions of the gonad is controlled or maintained. The work of Charniaux-Cotton and her collaborators (for reviews see Charniaux-Cotton 1970, Charniaux-Cotton 1973, Charniaux-Cotton 1975, Charniaux-Cotton and Payen 1983), in part on *Lysmata seticaudata,* demonstrated clearly the glandular and hormonal control of the expression of primary and secondary sex characteristics through surgical implantation and removal of the androgenic gland. The presence of the androgenic gland (or the androgenic hormone it produces) completely inhibits secondary folliculogenesis and vitellogenesis (Charniaux-Cotton and Payen 1983). The androgenic gland is also thought to be solely responsible for male differentiation in all crustaceans (Charniaux-Cotton and Payen 1983). The effect of androgenic gland removal upon the maintenance of male gametogenesis is unclear. However, spermatogenesis is known to continue in the protandrous *L. seticaudata* after the degeneration of the androgenic gland (Charniaux-Cotton and Payen 1983). Though no androgenic gland was detected histologically in the experimental animals, it is still possible that it was present, but not distinguishable. Bundy (1983) and Kagwade (1981) both noted its presence, but claimed that it degenerated in female-phase individuals of *L. wurdemanni* and *L. ensirostris.* Gonads were not dissected from surrounding tissues in the study reported here, so direct observation of the androgenic gland on the distal coiled portion of the sperm duct was not possible.

If the androgenic gland and/or androgenic hormone are indeed present, perhaps their activity decreases or halts, temporarily, after ecdysis. This would allow vitellogenesis to begin again, and the sperm stored in the terminal ampulla ensures that the shrimp could reproduce as a male if necessary. This idea is supported by the shrimp (L3A) with many mixed vitellogenic and previtellogenic oocytes and no mature sperm in the testis. However, more replicates of this stage of the intermolt are needed to confirm this relationship.

The question remains whether we can consider *L. amboinensis* a true simultaneous hermaphrodite. Histologically, *L. amboinensis* can be considered as such because it possesses mature sperm and ova at the same time, like its congeners *L. wurdemanni* and *L. ensirostris.* Functionally, this species cannot reproduce as both sexes at the exact same time. This limitation is due to the restriction of spawning eggs at the time of ecdysis. Because there are sperm in the terminal ampulla at different stages of the molt cycle, it is likely that *L. amboinensis* can reproduce as male at most any time except when eggs are spawned. This is in contrast to barnacles that have morphologically separate gonads (Anderson 1994) and can reproduce as both sexes at the same time (Barnes and Crisp 1956).

Charnov (1982) defined simultaneous hermaphroditism as when "an individual produces both kinds of gametes in each breeding season (more or less at the same time)." Sadovy and Shapiro (1987) defined it as when "individuals function at the same time of life both as male and female." The latter definition is more conservative and conclusive, if we use a literal interpretation of "function." If we apply these criteria to *L. amboinensis,* taking into account the restrictions on their reproduction as females, we can consider this species as a simultaneous hermaphrodite. The molt cycle is essentially a single reproductive cycle or reproductive bout. Female-phase *L. amboinensis* function as both sexes within one reproductive cycle.

Note that this application of the criteria is more conservative than some recent descriptions of simultaneous hermaphroditism, such as St. Mary (1993, 1996). There, two gobies in the genus *Lythrypnus* possess various degrees of male and female gonadal allocation, but have never been observed to function as both sexes at the same time or even within a reproductive cycle. These species can, apparently, change functional sex within a reproductive season. This is clearly an instance of reversible sequential hermaphroditism, as demonstrated in the gobies *Paragobiodon echinocephalus* (Kuwamura et al. 1994) and *Trimma okinawae* (Sunobe and Nakazono 1993). Perhaps clearer criteria are needed to differentiate transitional states from true hermaphroditism.

This study is the first definitive, controlled demonstration of simultaneous hermaphroditism in the decapod Crustacea. It is likely that closer examination of other members of the genus *Lysmata* and other hippolytids will show further examples of this interesting phenomenon. Furthermore, the implications of simultaneous hermaphroditism in the decapod Crustacea are important to the understanding of crustacean reproductive physiology and the evolution of social systems.

ACKNOWLEDGMENTS

I thank Tomoko Yoshikawa and Kazue Asoh for their suggestions on both the manuscript and histological preparations. Gratitude is also given to Yasuhiro Nakashima, Ilan Karplus, Chris Brown, and Ernst Reese for their encouragement. Finally, I thank the two reviewers for their helpful comments and time.

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