Protandric Simultaneous Hermaphroditism Is a Conserved Trait in *Lysmata* (Caridea: Lysmatidae): Implications for the Evolution of Hermaphroditism in the Genus

J. Antonio Baeza

ABSTRACT. Shrimps from the genus *Lysmata* are unusual because of their peculiar sexual system. Individuals in a population first reproduce as males, to change later in life to functional simultaneous hermaphrodites. The evolutionary origin of this sexual system, called protandric simultaneous hermaphroditism (PSH), is a longstanding question overdue for consideration. A previously proposed "historical contingency" hypothesis suggested that PSH evolved in the tropics from an ancestral protandric species of *Lysmata* that became socially monogamous and symbiotic with sea anemones. The restricted probability of encountering mating partners by shrimps because of their association with their hosts would have favored PSH. Here, I first provide evidence that PSH is a fixed trait within the genus. Second, I examine whether the historical contingency hypothesis appropriately explains the origin of PSH in the genus. Using anatomical observations and laboratory experiments combined, I demonstrate that two shrimps from the genus *Lysmata*, *L. galapagensis* and *L. boggessi*, feature PSH. Study of museum specimens suggests that nine other species of *Lysmata* are protandric simultaneous hermaphrodites. The foregoing information indicates that PSH represents a fixed trait in the genus *Lysmata*. Ancestral character state reconstruction using Bayesian inference allowed testing whether the ancestral *Lysmata* featured a symbiotic lifestyle and a socially monogamous mating system, as proposed by the historical contingency hypothesis. In agreement with this hypothesis, analysis indicated that the most common recent ancestor of *Lysmata* was most likely socially monogamous. However, the ancestral lifestyle was equally likely to be free-living or symbiotic. Thus, the present study provides partial support for the historical contingency hypothesis. Studies on the sexual system and lifestyle of more species and development of a more robust phylogeny are needed to reveal the evolutionary origin of PSH in the genus *Lysmata*.

INTRODUCTION

In decapod crustaceans, the greatest diversity of sexual systems is found in the infraorder Caridea. Most caridean shrimps are gonochoric, with individuals in a population producing only male or female gametes during their entire life. Well-studied examples include *Rhynchocinetes typus* (Correa et al., 2000), *Hippolyte obliquimanus* (Terossi et al., 2008), *Pontonia margarita* (Baeza, 2008a), and *Hippolyte williamsi* (Espinoza-Fuenzalida et al., 2008). The second most common sexual system is protandry. In at least 31 species of shrimps, individuals in a population reproduce first as males and change to females later in life

---

J. Antonio Baeza, Smithsonian Tropical Research Institute, Panama, and Smithsonian Marine Station at Fort Pierce, 701 Seaway Drive, Fort Pierce, Florida 34949, USA (baezaa@si.edu). *Received 9 June 2008; accepted 20 April 2009.*

(Bauer, 2000). Although several variants of protandry have been reported (e.g., protandry with primary females in *Crangon crangon*; Schatte and Saborowski, 2006), no study has reported protogyny (changing sex from female to male) among shrimps. Most recently, a particular variant of simultaneous hermaphroditism, that is, adolescent protandry sensu Ghiselin (1974), protandric cosexuality sensu Policansky (1982), or protandric simultaneous hermaphroditism (PSH) sensu Bauer (2000), has been described for shrimps from the genera *Lysmata* (Baeza et al., 2008) and *Exhippolysmata* (Kagwade, 1982; Braga et al., 2009). It must be noticed that a recently developed molecular phylogeny for *Lysmata* and other related genera demonstrated that the genus *Exhippolysmata* represents a derived group of shrimps within the genus *Lysmata* (Baeza et al., 2009). Thus, species of *Exhippolysmata* are treated here as members of the genus *Lysmata*.

In protandric simultaneous hermaphroditic shrimps, juveniles consistently mature as functional male individuals (also called male-phase [MP] shrimps; Bauer and Holt, 1998) bearing typical caridean male characters (i.e., coupling hoods and appendix masculina on the first and second pleopods, respectively) (Bauer and Holt, 1998; Baeza, 2008b; Baeza and Anker, 2008; Baeza et al., 2008). These functional males later attain female sexual function and develop into functional simultaneous hermaphrodites (hereafter, hermaphrodites; but also called female-phase [FP] shrimps; Bauer and Holt, 1998). Resembling females of caridean gonochoric species, hermaphrodites mate as females shortly after molting, spawn oocytes to an abdominal chamber where fertilization takes place, and brood their embryos for relatively long periods of time (e.g., 10–15 days in *Lysmata wurdemanni*; Baeza, 2006). These hermaphrodites retain testicular tissue, male ducts, and gonopores and thus have the ability to reproduce as both male and female (Bauer and Holt, 1998). After becoming hermaphrodites, individuals do not revert to males (Baeza, 2007a), and no self-fertilization has been demonstrated (Bauer and Holt, 1998; Baeza, 2008b; Baeza and Anker, 2008; Baeza et al., 2008).

So far, the various studies on the sexual biology of shrimps from the genus *Lysmata* suggest that all species exhibit PSH. Protandric simultaneous hermaphroditism is suspected to be a fixed trait in the genus. Nonetheless, additional information from more species is needed to confirm this notion. In turn, other life history traits differ within these two genera. Shrimps have been reported to inhabit the shallow subtidal and intertidal of subtropical and tropical rocky and coral reefs around the world. Some species of *Lysmata* live in groups, others are solitary, while some species are socially monogamous (pair-living; e.g., *L. grabhami* (Gordon, 1935)) (Wirtz, 1997). Several species with an inconspicuous coloration dwell freely among rocks in temperate zones, while other more colorful species inhabit tropical sponges (*L. pederseni* Rhyne and Lin, 2006) (Rhyne and Lin, 2006). Other strikingly brilliant species clean fishes (*L. amboinensis* (De Man, 1888)) (Limbaugh et al., 1961). Species from this genus represent ideal candidates to explore the role of ecological conditions in explaining evolutionary innovations in the marine environment (see Baeza and Thiel, 2007).

Recent studies have examined various aspects of the biology of various *Lysmata* and *Exhippolysmata* shrimps (Baeza, 2008b; Baeza and Anker, 2008; Baeza et al., 2008; Lopez-Greco et al., 2009). Furthermore, shrimps from the genera *Lysmata* and *Exhippolysmata* are currently being used as models in evolutionary biology and behavioral ecology because of their peculiar sexual system (Baeza and Bauer, 2004; Baeza, 2006, 2007a, 2007b, 2007c). In spite of the increasing knowledge regarding the behavior and ecology of several species of *Lysmata*, the evolutionary origins of PSH in the genus remain uncertain. Although recent studies have shown that the variety of lifestyles of *Lysmata* is greater than originally recognized (Baeza, 2008b; Baeza and Anker, 2008; Baeza et al., 2008), an emerging dichotomy in social organization and ecology was noted in initial studies. One group of species (named "Crowd" species by Bauer, 2000) was described as inhabiting warm subtropical environments, occurring as dense aggregations in their refuges, and exhibiting no specialized fish-cleaning behavior (i.e., *L. californica*: Bauer and Newman, 2004; *L. wurdemanni*: Baeza, 2006). A second group (named "Pair" species by Bauer, 2000) was described as mostly tropical, occurring at low densities in the subtidal, and dwelling as socially monogamous pairs on sea anemones used as spots for fish-cleaning activities (i.e., *L. grabhami*: Wirtz, 1997; *L. amboinensis*: Fiedler, 1998). Based on this initial dichotomy, Bauer (2000) proposed that PSH evolved in the tropics from an ancestral symbiotic protandric species of *Lysmata* that became a specialized fish cleaner. Restricted mobility of individuals resulting from their association with the host and, hence, reduced probability of encountering mating partners would have favored PSH (also see Bauer, 2006). Under such a scenario, the "Crowd" warm temperate species that do not exhibit specialized cleaning behaviors would have evolved from tropical species with specialized cleaning behaviors and more complex mating systems (Bauer, 2006). A recent phylogeny developed for the genus found no support for Bauer's hypothesis because socially monogamous species presented a more derived position than gregarious species (Baeza et al., 2009). However, no formal testing of Bauer's ideas was conducted. Current advances in ancestral character state reconstruction using Bayesian inference (Pagel et al., 2004) make it possible to test whether the ancestral *Lysmata* featured a symbiotic lifestyle and a socially monogamous mating system, as proposed by Bauer (2000).

Here, I provide evidence that PSH is a fixed trait within the genus *Lysmata* (including *Exhippolysmata*), as suspected by previous studies (see Bauer, 2000; Baeza, 2008b; Baeza and Anker, 2008; Baeza et al., 2008). For this purpose, I examined the sexual system of two shrimps from the genus, *L. galapagensis* Schmitt, 1924 and *L. boggessi* Rhyne and Lin, 2006, using anatomical observations and laboratory experiments. I also examined specimens from another nine species deposited at the National Museum of Natural History (NMNH), Washington, D.C. The information altogether strongly suggests that PSH is a conserved trait within the genus *Lysmata*. My second goal was to examine Bauer's (2000) hypothesis regarding the evolution of PSH in *Lysmata*. I tested whether the ancestral *Lysmata* was socially monogamous (1) and strictly symbiotic with, for example, sea anemones (2), as proposed by this author. To accomplish this second goal, a review of the literature on the socioecology of *Lysmata* was conducted. Next, the lifestyle of shrimps was mapped onto the phylogeny of the genus, and the likelihood of specific traits to occur at particular ancestral nodes in the phylogeny was tested.

METHODS

Collection and Maintenance of Shrimps

Individuals from the two studied species were collected between February and August, 2006, at different localities in Panama and Florida, USA. Individuals from *L. boggessi* were collected at night during low tides from seagrass beds at Madelaine Key (27°38′51.87″N, 82°42′56.50″W), Fort De Soto National Park, Florida. Specimens from *L. galapagensis* were collected from Islas Secas (7°58′37.54″N, 82°02′18.02″W), Gulf of Chiriqui, Panama. Immediately after collection, specimens were transported to the R/V Urraca and then to the Naos Marine Laboratories, Panama (*L. galapaguensis*) or directly to the Smithsonian Marine Research Station at Fort Pierce, Florida (*L. boggessi*). Individuals were maintained in 15–70 L aquaria at a water temperature of 22°–33°C and 34–36 ppt salinity and were fed every other day with shrimp pellets before being selected for dissections or experiments.

Dissections

Observations on reproductive anatomy were conducted as in Baeza (2008b) in a total of six specimens of each species, three presumptive males (3.6–3.8 and 4.0–4.6 mm carapace length [CL] in *Lysmata galapagensis* and *L. boggessi*, respectively) and three presumptive hermaphrodites that were brooding embryos (4.4–5.1 and 6.5–5.6 mm CL in *Lysmata galapagensis* and *L. boggessi*, respectively). First, the presence or absence of male gonopores on the coxae of the fifth pereiopods was recorded for each individual. Individuals with male gonopores (all) had sperm collected from the ejaculatory ducts using short electric shocks that results in the ejection of a spermatophore (as noted in Baeza, 2006, 2007c). Each individual was then dissected to extract the gonad for examination under the stereomicroscope. Finally, the first and second pleopods were dissected and the presence or absence of appendices internae and masculinae, respectively, were recorded. Specimens were defined as males or hermaphrodites by the presence (males) or absence (hermaphrodites) of coupling hooks (cincinnuli) and appendices masculinae on the endopods of the first and second pleopods, respectively (see Baeza, 2007c, 2008b).

Experiments

Three experiments, as described in Baeza et al. (2008) and Baeza (2008b), were conducted to determine the sexual system of the three species under study. In summary, the different experiments determined whether (1) brooding shrimps (reproducing as females) were capable of mating as males, (2) brooding shrimps were capable of self-fertilization, and (3) males were capable of becoming hermaphrodites with time (see Results). In the first experiment ($n = 5$), pairs of brooding shrimps were maintained in 21 L aquaria. In the second experiment, five brooding shrimp were each maintained alone. In the third experiment ($n = 5$), pairs of males (small nonbrooding shrimp with no externally visible female gonads and visible cincinnuli and appendices masculinae) were maintained separately in 21 L aquaria for at least 50 days. Individuals were examined daily for hatching of the embryos, the presence of exuvia from molting, 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 four days of spawning.

Following the rationale developed by Baeza et al. (2008), if in the first experiment ovigerous shrimps that paired together produced normally developing broods, then 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. If in the second experiment shrimps in isolation failed to successfully produce and brood developing eggs, then the possibility of self-fertilization was eliminated. If in the third experiment individuals identified as males at the beginning of the experiment developed the ovarian portion of the ovotestis and produced eggs, then I inferred that male shrimps mature as hermaphrodites (see Baeza et al., 2008).

Population Structure, Sex Ratio, and Abundance

Information on the abundance, population structure, and sex ratio (males to hermaphrodites) of each species was collected from the field. The carapace length (CL) and number of shrimps of each sexual phase and each species captured during the different samplings were recorded. The sampling effort (total number of hours spent collecting shrimps) was calculated for each sampling event. Relative abundance of shrimps was estimated by dividing the sample abundance (number of shrimps captured) by the sampling effort.

Museum Specimens

Specimens from nine different species of *Lysmata* deposited at the Collection of Crustaceans, National Museum of Natural History (NMNH; Smithsonian Institution, Washington, D.C.) were examined. Dissection of specimens pertaining to the collection was not possible because only a few individuals were available from several of the examined species and many of the specimens were part of the type series used to describe the species. Therefore, the identification of males and hermaphrodites was mostly based on external morphological characters (see foregoing). When identifying sexual phases, particular attention was given to the presence of male gonopores at the base of the coxae of the fifth pair of pereiopods in brooding shrimps as a likely indicator of simultaneous hermaphroditism (see Results).

Testing the Historical Contingency Hypothesis

To examine whether the historical contingency hypothesis proposed by Bauer (2000) appropriately explains the origins of PSH in shrimps from the genus *Lysmata*, the lifestyle (in terms of the propensity to develop symbiotic partnerships and natural group size) was reconstructed using BayesTraits (Pagel and Meade, 2006; available at www.evolution.rdg.ac.uk).

A pruned set of sequences (from the 16S mitochondrial gene) recently published by Baeza et al. (2009) was used to generate a phylogenetic hypothesis for the group on which to reconstruct the evolution of lifestyles in shrimps. The sequences pertained to 20 species of *Lysmata* and *Exhippolysmata* plus 3 other species (*Merguia rhizophorae*, *Hippolyte williamsi*, and *H. inermis*) used to root the trees during the initial phylogenetic analysis. The set of aligned sequences was first imported to BayesPhylogenies (Pagel et al., 2004) to obtain a Bayesian posterior distribution of phylogenetic trees. Metropolis coupled–Markov chain–Monte Carlo analyses were conducted using a GTR + I (invariant) + G (gamma) model of nucleotide substitution. The analysis was run on two different simultaneous chains. A total of 6,000,000 iterations were conducted, and sampling was performed every 100th tree. The last 1,000 posterior probability trees generated by BayesPhylogenies were then imported to BayesTraits. The submodule MultiState in BayesTraits uses Markov chain Monte Carlo (MCMC) methods to infer values of traits (that adopt a finite number of discrete states) at ancestral nodes of phylogenies. Additionally, this method permits testing for particular ancestral characters at specific nodes taking phylogenetic uncertainty into account (Pagel et al., 2004).

The two traits here analyzed have three states each. For group size, the states were (1) aggregations (including swarms), (2) small groups, and (3) pair-living (social monogamy). The three character states used for describing the symbiotic propensity of different shrimp species were (1) free-living, (2) facultative associate (with different moray eel species, such as *L. californica* and *L. seticaudata*; with sea anemones, such as *L. ankeri*), and (3) strictly symbiotic with either sponges (e.g., *L. pederseni*) or sea anemones (*L. amboinensis, L. grabhami*). Information on the lifestyle of each species was obtained by direct observation of shrimps in nature (personal observations), from the literature (see literature review), or from both sources.

During the analysis, a reversible-jump MCMC search was used with two independent chains that were run for 6,000,000 iterations with a burn-in of 50,000. I choose the prior distribution of the parameters in the model with the option Hyperprior (see Pagel et al., 2004), seeding an exponential distribution from uniform on the interval 0.0 to 30 and a rate deviation of 18. These values were selected considering preliminary runs and were used to keep the acceptance rate at approximately 0.3, as recommended by Pagel et al. (2004). Character states at internal nodes were reconstructed using the most recent common ancestor method. I tested hypotheses about particular character states at specific nodes when comparing the MCMC run-in which the node was "fossilized" (constrained) to one state versus an alternative. The command *Fossil* allows testing whether a particular state is "significantly" more likely at a specific node than an alternative state. For each tested character, the same set of conditions (prior distribution, burn-in) as used in the ancestral character state reconstructions already described were used. However, the MCMC was run 5 times for each trait state tested, and a total of 100,000,000 iterations were conducted. Bayes factors were calculated as the difference between the highest harmonic mean of the marginal likelihood from the five MCMC runs for each state (Pagel et al., 2004). The strength of support for one model over another was measured using the scale from Kass and Raftery (1995).

RESULTS

DISSECTIONS

Dissections demonstrated that all shrimps (brooding or nonbrooding) from the two species had male gonopores at the coxae of the fifth pair of pereiopods (Figure 1A). Female gonopores at the coxae of the third pair of pereiopods were more difficult to reliably observe. From all shrimps (brooding or nonbrooding), sperm cells shaped in the form of an inverted umbrella were retrieved from the male gonopores by electroshocks (Figure 1A,B). Dissections of the gonads from small shrimps not brooding embryos (presumptive males) demonstrated the presence of an ovotestes (Figure 1C) with an undeveloped anterior female portion full of immature oocytes (lacking coloration) (Figure 1D) and a posterior male gonad containing sperm cells with the same morphology as the sperm retrieved from the gonopores (see Figure 1B). Gonads dissected from brooding (presumptive hermaphrodites) shrimps also had ovotestes, but with a large ovarian portion full of mature oocytes and a relatively small posterior testicular portion with sperm (Figure 1E). In both brooding and nonbrooding shrimps, vas deferentia and oviducts extended laterally from the testicular and ovarian portions, respectively (Figure 1C,E).

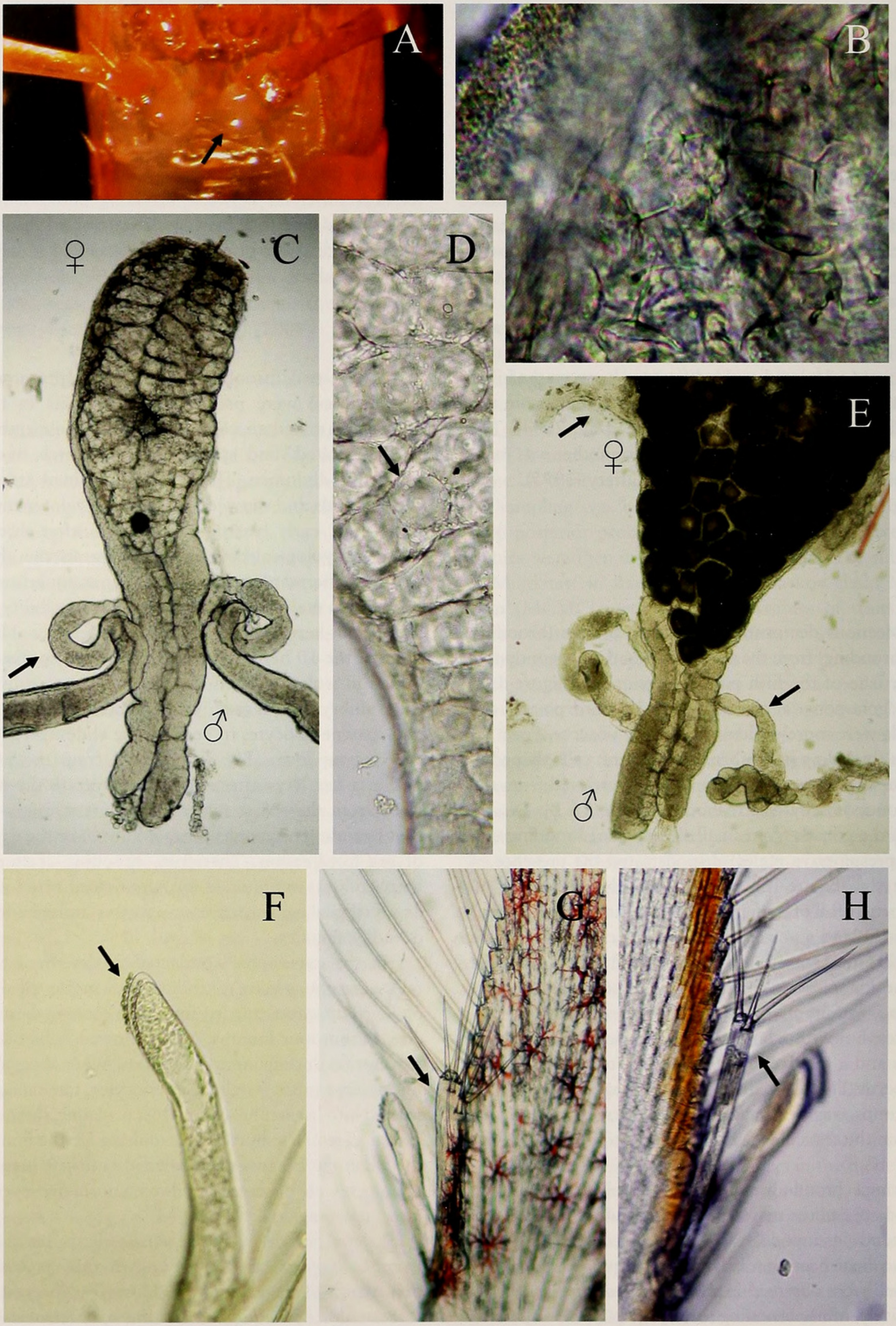
Shrimps brooding embryos invariably lacked cincinnuli and appendices masculinae in the endopod of the first and second pereiopods, respectively. In contrast, appendices masculinae bearing relatively long spines and numerous cincinnuli were observed in the second and first pleopods, respectively, of nonbrooding shrimps (Figure 1F–H). Some minor differences between the two species were noticed regarding the relative length and number of spines borne by the appendix masculinae; in *L. boggessi*, the spines were more numerous and longer than those of *L. galapagensis* (Figure 1G,H). Overall, all the anatomical differences observed between brooding and nonbrooding shrimps indicate that the populations of all the *Lysmata* species studied herein are indeed composed of males and hermaphrodites.

EXPERIMENTS

When two brooding individuals (presumed hermaphrodites) were paired, all individuals in the two species examined successfully hatched their embryos as larvae, molted, and spawned a new batch of oocytes below the abdomen. The oocytes remained attached to the pleopods and showed embryonic development as embryos (i.e., early blastulae formation) after three days. This embryological development suggests the ability of the other hermaphrodites in the same aquarium to reproduce as males or, alternatively, the possibility of selfing by the hermaphrodites acting as females. However, none of the 10 hermaphrodites (5 of each species) maintained in isolation from conspecifics successfully reared their embryos to larvae. These solitary shrimps molted and spawned oocytes to beneath the abdomen. However, the oocytes invariably disappeared from the pleopods within a few days after spawning. Overall, the observations from these first two experiments strongly suggest that brooding hermaphrodites do not have the capability of self-fertilization. Therefore, brooding shrimps (hermaphrodites) maintained in pairs indeed acted as males and fertilized eggs when their partners molted and reproduced as females.

In the experiment conducted to determine whether males mature as hermaphrodites later in life, all six males of *L. galapagensis* turned into simultaneous hermaphrodites within four months. Males showed signs of ovarian maturation during intermolt periods. When the gonad was full of large green (vitellogenic) oocytes, the male shrimps molted into hermaphrodites. Most probably, these shrimps mated as females shortly after molting for the first time in their lifetime because the spawned embryos beneath the abdomen were observed developing normally several days after spawning.

In contrast to *L. galapagensis*, all six male shrimps from *L. boggessi* died of unknown reasons within the first month of the experiment. However, observations on three males of *L. boggessi* in the maintenance aquaria


A
B
♀
C
D
E
♀
♂
♂
F
G
H

indicated that they turn into hermaphrodites before four months. This change of sexual phase was accomplished after a single month, as observed in *L galapagensis*. Thus, it may be concluded that *L. galapagensis* and *L. boggessi* are protandric simultaneous hermaphrodites, incapable of self-fertilization.

POPULATION STRUCTURE, SEX RATIO, AND ABUNDANCE

Abundances of *L. galapagensis* and *L. boggessi* at the different sampling locations were high and low, with a mean of 2.79 and 0.317 individuals collected per minute per sampling period, respectively. In the two species, population was biased toward males. The ratio of males to total shrimps collected during the sampling period was 0.024 and 0.16 for *L. galapagensis* and *L. boggessi*, respectively. The range of body size registered for males varied from 1.9 to 3.8 and from 3.13 to 5.75 mm CL in *L. galapagensis* and *L. boggessi*, respectively. Hermaphrodites ranged in size between 4.1 and 5.1 and 5.63 and 6.5 mm CL in *L. galapagensis* and *L. boggessi*, respectively (Figure 2).

MUSEUM SPECIMENS

A variable number of specimens from *L. anchisteus*, *L. argentopunctata*, *L. chica*, *L. kuekenthali*, *L. moorei*, *L. philippinensis*, *L. rathbunae*, *L. trisetacea*, and *L. vittata* were available at the NMNH. Small shrimps in each species appear to be males as they have cincinnuli and appendices masculinae in the second and first pleopod, respectively. In turn, shrimps brooding embryos (the great majority of them above average size) invariably lacked cincinnuli and appendices masculinae in the endopod of the first and second pereiopods, respectively. This last observation suggests they were hermaphrodites. It was not possible to detect transitional individuals in these species because no dissections were possible and gonad condition was not easily observed. The carapace of formaldehyde- and alcohol-fixed specimens is not translucent as it is in living or recently preserved specimens. Also, shrimps less than 3.0 mm CL were not sexed because of the risk of inflicting damage. For all species examined except *L. anchisteus*, *L. argentopunctata*, and *L. philippinensis*, a relatively large sample of specimens was available. The size–frequency distribution of the different species strongly resembled that of the two species studied above, with small shrimps resembling males and large shrimps resembling hermaphrodites (Figure 3). Observations of the coxae of the fifth pair of pereiopods of the largest brooding shrimps in each species demonstrated the presence of male gonopores. Overall, the distribution of the sexes across size classes and the limited observations on the external male and female anatomy suggest that all these other *Lysmata* shrimps are protandric simultaneous hermaphrodites.

FIGURE 1. (*facing page*) *Lysmata galapagensis* and *Lysmata boggessi*: anatomical and morphological differences between males and hermaphrodites. A, spermatophore (arrow) retrieved from gonopores of hermaphrodite (*L. boggessi*); B, sperm from male (*L. galapagensis*); C, ovotestes from male (anterior female and male portions on top and bottom, respectively; arrow points at left vas deferentia) (*L. galapagensis*); D, close-up of female gonad portion in male (arrow points at immature oocyte) (*L. boggessi*); E, ovotestes from dissected hermaphrodite (anterior female and male portions on the top and bottom, respectively; top and bottom arrows point at right oviduct and left vas deferentia, respectively) (*L. galapagensis*); F, endopod of first pleopod in male (arrow points at cincinulli) (*L. galapagensis*); G, endopod of second pleopod in male (arrow points at appendix masculina) (*L. galapagensis*); H, endopod of second pleopod in male (arrow points at appendix masculina) (*L. boggessi*).

LITERATURE REVIEW

The literature review of the 41 species of *Lysmata* (including *Exhippolysmata*) described to date revealed that the geographic and bathymetric distribution, coloration, and habitat of these species are relatively well known. Shrimps from the genus *Lysmata* occur in tropical, subtropical, and temperate waters around the world and can be found among rocks or fossilized coral, live coral, seagrass blades, on muddy and shell bottoms, or associated with sponges or sea anemones in the intertidal or subtidal to 360 m depth. Most species have an inconspicuous coloration (red striped, translucent reddish with reddish flagella on both pairs of antenna). Only 4 species are reported as featuring a striking color pattern (contrasting body colors, bright white flagella on both antenna). This dichotomy in coloration was previously noticed by Bauer (2000). *Lysmata splendida*, one of the 4 species with a brilliant coloration, most probably is a cleaner shrimp. However, nothing is known about its reaction to fish and its propensity to clean them. Similarly, information regarding the degree of specialization of the cleaning behavior is unknown for most of the species (Table 1).

Information on the socioecology and sexual system is, in general, poorly known. Information on lifestyle

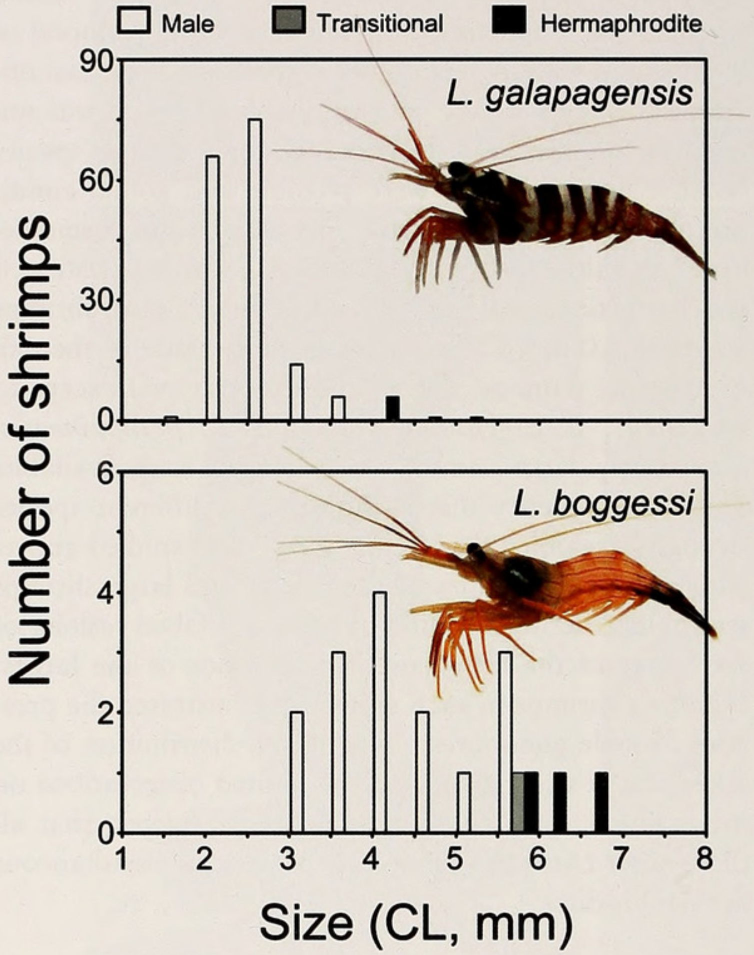


FIGURE 2. *Lysmata galapagensis* and *L. boggessi* population structure ($n = 178$ and 22 shrimps, respectively, from *L. galapagensis* and *L. boggessi*; CL = carapace length).

(socioecological attributes) is available only for 18 of the 41 described species. Of these, 7 species live in crowds (aggregations), 7 species live in small groups, 3 species live in pairs (i.e., they are socially monogamous), and 1 species is reported as living in extremely large aggregations (in swarms; *Exhippolysmata oplophoroides*). Demonstration of PSH using a combination of experimental, morphological, and anatomical findings and population structure is available for 12 species. A strong indication of PSH exists for another 10 species. Although the information is incomplete (PSH has been reported for a total of 22 species, or 54% of the described species), this review clearly demonstrates that the lifestyle and socioecology of shrimps from this genus are more complex than originally thought and further confirms the idea that PSH is a fixed trait in the genus *Lysmata* (including *Exhippolysmata*).

TESTING THE HISTORICAL CONTINGENCY HYPOTHESIS

The 50% majority-rule consensus tree obtained during the initial phylogenetic analysis confirms the existence of the three natural clades (tropical-American, cosmopolitan, and cleaner) noticed previously by Baeza et al. (2009). However, one important difference between the present consensus tree and that previously published is that *L. olavoi* is not supported as the most basal species within the genus. This difference between trees might (1) be an effect of the different set of species used for the phylogenetic analysis or (2) perhaps have occurred because the different software programs used for phylogenetic inference function with different algorithms. On the other hand, the monophyly of *Lysmata* is well supported in this new tree, with a 100% posterior probability (Figure 4; Baeza et al., 2009: fig. 1).

The lifestyle of shrimps mapped onto the consensus tree indicated that the most recent common ancestor of the species pertaining to the neotropical and cosmopolitan clades was gregarious. In contrast, the ancestor of the species comprising the cleaner clade most probably was socially monogamous (see Figure 4). On average, the node of the most common recent ancestor of all *Lysmata* species is reconstructed to be in state 2 (social monogamy) with 80% of certainty. The degree of certainty varied from tree to tree but was generally high, as indicated by the low standard deviation of this value (SD = 0.03, calculated from 2,000,000 iterations using 1 of 1,000 randomly sampled posterior probability distribution trees at each iteration). The largest harmonic log-likelihood obtained from five independent runs when the node was fossilized to state 0 and 2 was –22.309507 and –20.865237, respectively. The almost three log-unit improvement in likelihood (Bayes factor = 2.89) of the model when the node was fossilized to state 2 represents evidence that the ancestral lifestyle of Lysmata was social monogamy.

With regard to the propensity for developing symbiotic interrelationships, the reconstructions suggest that the ancestor of the neotropical and cosmopolitan clades most probably had a free-living lifestyle and did not develop any symbiotic partnership with other macroinvertebrates. It should be noticed that the degree of certainty of these two inferences is relatively low, as indicated by the large standard deviations of the distribution of the character (see Figure 4). Also, the reconstructions indicate that, with a probability of 0.46 ± 0.20 or 0.41 ± 0.18, either facultative partnerships or strict symbiosis,

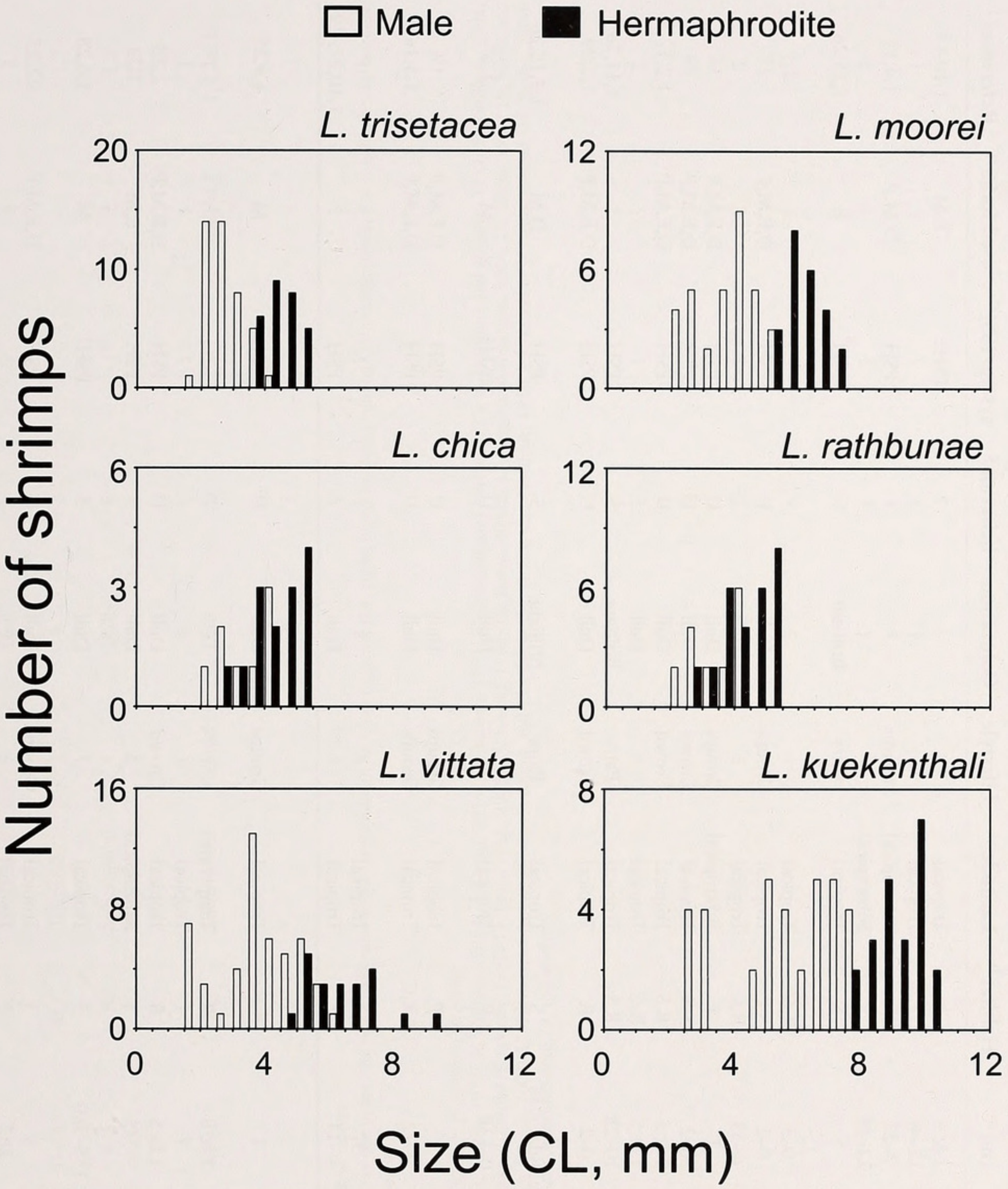


FIGURE 3. *Lysmata* spp. Population structure of selected species from the National Museum of Natural History (n = 71, 56, 22, 31, 70, and 57 shrimps from *L. trisetacea*, *L. moorei*, *L. chica*, *L. rathbunae*, *L. vittata*, and *L. kuekenthali*, respectively).

respectively, was the ancestral state of the genus *Lysmata*. The improvement in the likelihood of the model (Bayes factor = 1.51) when the node was fossilized to state 2 (strict symbiosis) was low compared to when the node was fossilized to state 0 (free-living). Therefore, there is no evidence indicating that symbiosis is significantly more likely than a free-living lifestyle in the ancestral *Lysmata*.

Overall, the present ancestral character state reconstruction provides partial support for Bauer's (2000) hypothesis about the evolution of PSH in shrimps from the genus *Lysmata*.

TABLE 1. Diversity of lifestyles and sociobiology in shrimps from the genera *Exhippolysmata* and *Lysmata*. A question mark (?) indicates data not available.

Species	Geographic distribution	Bathymetric distribution (m) [a]	Habitat [b]	Latitude	Lifestyle	Coloration	Cleaning behavior [c]	Sexual system (SS) [d]	Evidence used forSS [e]	References [f]
E. ensirostris	Indo-Pacific	I & S	?	Tropical	?	?	?	PSH?	E,M	1,10,13
E. hastatoides	W. Africa	12–48	?	Tropical	?	?	?	?	?	1
E. oplophoroides	W. Atlantic	7–27	R	Subtropical	Swarms	?	?	PSH	D,M,P	1,4,14
E. tugelae	South Africa	22–48	?	Subtropical	?	?	?	?	?	1
L. amboinensis	Red Sea, Indo-Pacific	S	S	Tropical	Pairs	Brilliant	S	PSH	E	1,15,26
L. anchisteus	Caribbean	0–3	R,M	Tropical	?	?	?	?	?	1,3
L. ankeri	Caribbean	0–2	S,C	Tropical	Groups	Dull	U	PSH	D,E,M,P	27
L. argentopunctata	E. Pacific	0–35	R,C	Tropical	?	Dull	?	?	?	2
L. bahia	W. Atlantic	I	F	Subtropical	Groups	Dull	U	PSH	D,E,M,P	16
L. boggessi	Caribbean	0–2	S,R	Tropical	Crowd	Dull	U	PSH	D,E,M,P	29
L. californica	E. Pacific	I & S	R,S	Tropical	Crowd	Dull	U	PSH	D,E,M,P	1,2,17
L. chica	Galapagos	I & S	R,C	Tropical	?	Dull	?	?	?	2
L. debelius	Indo-Pacific	10–28	R,S	Tropical	Pairs	Brilliant	S	PSH	?	1,11,26
L. galapagensis	E. Tropical Pacific	0–2	R	Tropical	Crowd	Dull	U	PSH	D,E,M,P	1,2,29
L. grabhami	Caribbean, Atlantic	Subtidal <55	S	Tropical	Pairs	Brilliant	S	PSH	D,M	1,3,18,26
L. gracilirostris	E. Tropical Pacific	0–138	R	Tropical	?	Dull	U	PSH?	M	2,27
L. hochi	Caribbean	I	F	Tropical	Groups	Dull	U	PSH	D,E,M,P	19
L. intermedia	Caribbean, Atlantic	0–22	A,R,C	Tropical	Groups	Dull	U	PSH	D,E,M,P	1,3,16
L. kempi	Burma	37	?	Tropical	?	?	?	?	?	1
L. kuekenthali	Red Sea, Indo-Pacific, South Africa	0–11	?	Tropical	?	Dull	?	PSH	?	1,10,27, 29
L. moorei	Caribbean, W. Atlantic	I	R,F	Tropical	Groups	Dull	U	PSH?	M	1,9,27
L. morelandi	New Zealand	I & S	R	Temperate	?	?	?	?	?	1
L. multiscissa	Djibouti, Africa	?	?	Tropical	?	?	?	?	?	1
L. nayaritensis	E. Pacific	I & S	R	Tropical	Crowd	Dull	U	PSH	D,E,M,P	2,20
L. nilita	Mediterranean, E. Atlantic	?	?	Subtropical	?	Dull	?	PSH	E,M	1,21
L. olavoi	Azores and Savage Is.	135–360	?	Tropical	?	Dull	?	PSH?	M	1,6,28
L. pederseni	Caribbean	S	S	Tropical	Groups	Dull	U	PSH	D,E,M,P	22,27
L. philippinensis	Philippines	267	?	Tropical	?	?	?	?	?	1
L. porteri	Juan Fernandez, E. Pacific	0–12	R	Subtropical, temperate	?	?	?	?	?	1
L. rafa	Caribbean	I & S	R	Tropical	Groups	Dull	U	PSH	D,E,M	22,27
L. rathbunae	Caribbean	13–119	?	Tropical	?	Dull	?	PSH?	M,P	1,3,23

continued

L. seticaudata	Mediterranean, E. Atlantic, Black Sea	I,S	R,S	Subtropical	Crowd	Dull	U	PSH	D,E,M,P	1,21,24
L. stenolepsis	Cape Verde	150–275	?	Tropical	?	?	?	?	?	1,7
L. striata	Caribbean	I	R,M	Tropical	Crowd	Dull	U	PSH	D,E,M,P	1,25,27
L. splendida	Indo-Pacific	6–35	W,C	Tropical	?	Brilliant	?	?	?	12
L. ternatensis	Djibouti, Indonesia	<62	Sa	Tropical	?	Dull	?	?	?	1
L. trisetacea	Red Sea, New Zealand	0–150	R,C	Tropical	?	?	?	?	?	1,2
L. uncicornis	NW Africa	4–5	R	Subtropical	?	Dull	?	?	?	1,8
L. vittata	Indo-Pacific, Australia, E. Africa	0–54	A	Tropical	?	?	?	?	?	1,5
L. wurdemanni	Caribbean, E. Atlantic, Gulf of Mexico	0–30	R,J	Subtropical	Crowd	Dull	U	PSH	D,E,M,P	1,3,26,27
L. zacae	Indo-Pacific	?	?	?	?	?	?	?	?	1

[a] I = intertidal; S = subtidal; numbers refer to depth in meters.

[b] A = associated with algae; S = symbiont (with moray eels in the case of *L. californica* and *L. seticaudata*); Sa = coarse sand; R = rocky bottoms and/or rubble; C = among corals; F = fossilized coral terraces; J = jetties; M = mud; W = caverns, on reef roof walls.

[c] S = specialized; U = unspecialized.

[d] PSH = protandric simultaneous hermaphroditism.

[e] D = dissections; E = experiments; M = morphology; P = population structure.

[f] References: 1, Chace, 1997; 2, Wicksten, 2000; 3, Chace, 1972; 4, Williams, 1984; 5, Kemp, 1914; 6, Fransen, 1991; 7, Crosnier and Forest, 1973; 8, Holthuis and Maurin, 1952; 9, Rathbun, 1906; 10, Holthuis, 1948; 11, Bruce, 1983; 12, Burukovsky, 2000; 13, Kagwade, 1982; 14, Braga et al., 2009; 15, Fiedler, 1998; 16, Baeza, 2008b; 17, Bauer and Newman, 2004; 18, Wirtz, 1997; 19, Baeza and Anker, 2008; 20, Baeza et al., 2008; 21, d'Udekem d'Acoz, 2002; 22, Rhyne and Anker, 2007; 23, Rhyne and Lin, 2006; 24, Dohrn and Holthuis, 1950; 25, Anker et al., unpublished; 26, Bauer, 2000; 27, unpublished observations; 28, Fransen, personal communication; 29, this study.

DISCUSSION

The present study suggests that the sexual system in shrimps from the genus *Lysmata* (including *Exhippolysmata*) represents a fixed trait. Anatomical observations, behavioral experiments, and field samples demonstrated that the 2 species studied here are protandric simultaneous hermaphrodites, as reported for all other *Lysmata* species (Table 1). Size–frequency distributions and additional but limited anatomical observations of museum specimens further suggest that at least 9 other species are protandric simultaneous hermaphrodites. Including the information generated in the present study, PSH has been reported for a total of 22 species, or 54% of the 41 species described worldwide.

The well-conserved sexual system in *Lysmata* contrasts with that reported for other genera from the closely related family Hippolytidae. For instance, two different genera of Hippolytidae shrimps, *Thor* and *Hippolyte*, are known to contain both gonochoric and strict sequentially hermaphroditic species (Espinosa-Fuenzalida et al., 2008, and references therein). The reasons for PSH to be fixed in *Lysmata* are not clear, especially when considering the diversity of environments inhabited by these species (see Table 1). Different habitats with varying degrees of structural complexity, seasonality, and predation regimes should favor different sexual systems. For instance, the rather heterogeneous environment (i.e., seagrass beds, seaweed meadows) in which the gregarious *L. boggessi* and *L. wurdemanni* occur is expected to favor sequential hermaphroditism over PSH. In these complex environments, male mating success most likely decreases with increasing body size because small body size is expected to increase searching ability and, ultimately, male mating success when encounter rate among conspecifics is high (Baeza and Thiel, 2007). This small-male advantage together with the well-reported exponential relationship between fecundity and body size in female shrimps is expected to favor strict protandry over simultaneous hermaphroditism in these species (Charnov, 1982).

On the other hand, hermaphroditic shrimps are known to experience brooding constraints (e.g., *L. wurdemanni*; Baeza, 2007c), a condition that theoretically favors simultaneous hermaphroditism (see Charnov, 1982, and references therein). Similarly, in socially monogamous *Lysmata* (e.g., *L. grabhami*; Wirtz, 1997), infrequent encounter rates among conspecifics should be favoring strict simultaneous hermaphroditism over PSH. It should pay (in term of fitness) for each individual in a pair to reproduce both as male and female as soon as possible during their lifetime because this strategy increases reproductive success through both sperm donation to the partner and female reproduction. Thus, an early male phase in these socially monogamous species should not be adaptive. On the other hand, differing costs between the sex functions might explain the existence of an early male phase before the simultaneously hermaphroditic phase in these monogamous species. The relatively large energetic and temporal costs of producing ova might delay maturation of the female function, resulting in a functional adolescent male phase previous to the simultaneously hermaphroditic phase (see Baeza, 2006). Additional studies in gregarious and socially monogamous cleaner shrimp species should improve our understanding about the conditions favoring PSH under a social monogamous mating system in *Lysmata*.

The literature review conducted herein indicates that the diversity of lifestyles in the genus is greater than previously recognized. Initial studies reported a distribution for the genus restricted to tropical-subtropical waters. The present review suggests that shrimps also inhabit cold temperate environments. *Lysmata porteri* is reported from southern Chile, and *L. morelandi* inhabits New Zealand (see Table 1). Because *Exhippolysmata* spp. represents a derived group of *Lysmata*, the deep water environment represents another environment colonized by the species in this group (see Baeza et al., 2009). Also, the dichotomy in social organization ("Crowd" versus "Pair" species) noted in initial studies (Bauer, 2000) is not supported. In addition to tropical pair-living and temperate gregarious species, the present review indicates other species forming swarms (extremely large aggregations) in temperate deep water soft-bottom environments (i.e., *E. oplophoroides*) or living in small groups in the tropical or subtropical intertidal that might or not associate with sea anemones (*L. ankeri*; Table 1). The possibility of an adaptive radiation in this group of shrimps is currently being explored. The rather unusual sex allocation pattern of this shrimps might represent the key innovation allowing species in these two genera to colonize and persist in environments where species with conventional sexual systems might fail.

The ancestral character state reconstruction analysis conducted in this study provides partial support for Bauer's (2000) hypothesis about the evolution of PSH in *Lysmata*. The analysis suggested that the ancestral *Lysmata* shrimp lived as socially monogamous pairs either facultatively associated to other macroinvertebrates or featuring a strictly symbiotic lifestyle (with sea anemones, for example). The free-living condition of several species pertaining to the cosmopolitan and neotropical clades is likely to be derived according to the present analysis. PSH might have

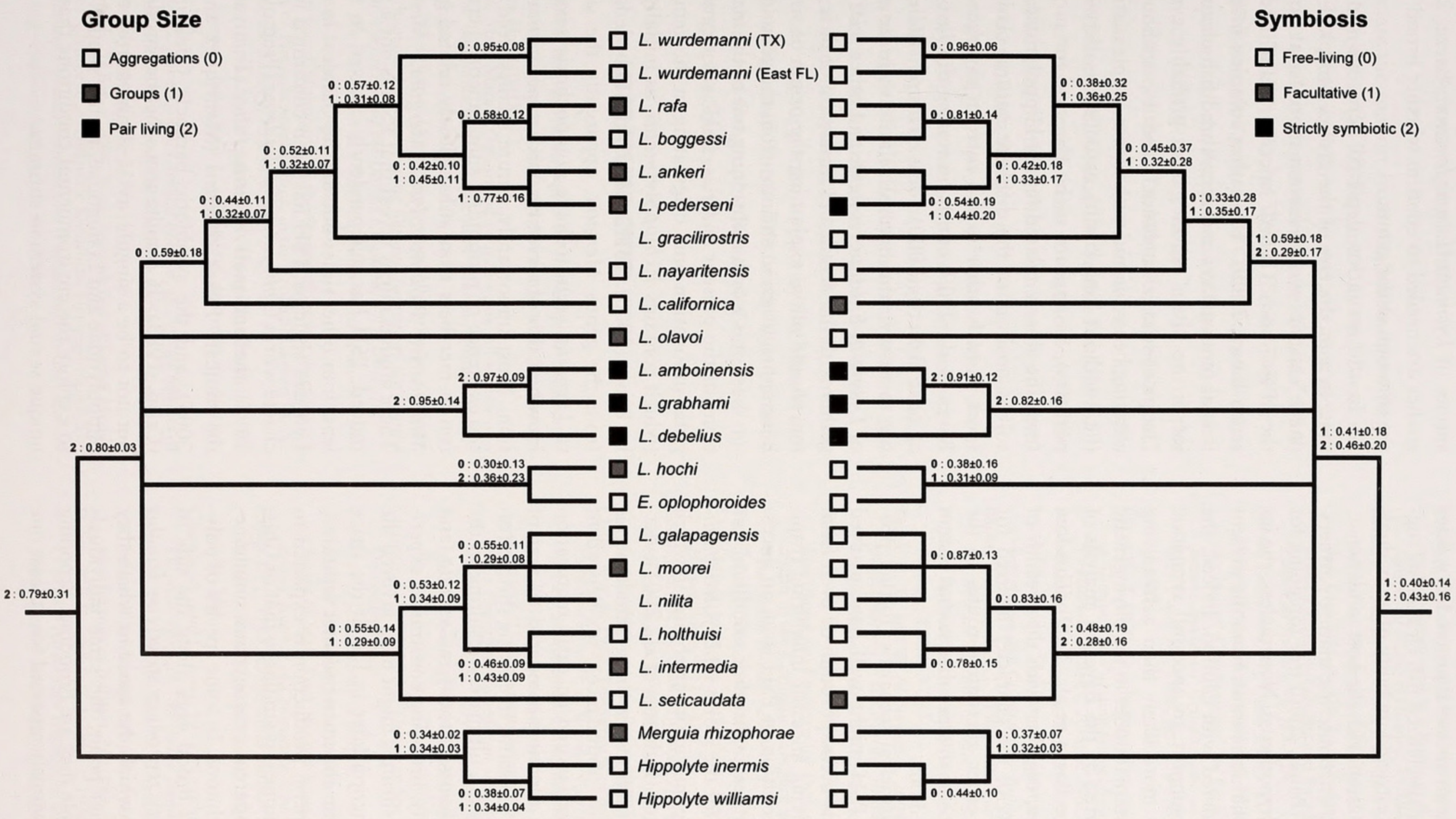


FIGURE 4. A 50% majority-rule consensus tree obtained using Bayesian inference phylogenetic methods showing the posterior densities of the reconstructed ancestral states (symbiosis and group size) at different nodes. For each node, the posterior probability for group size (left tree) and symbiosis (right tree) obtained when reconstructing the ancestral state of the most recent common ancestor to different clades in each tree is shown.

evolved in the tropics from an ancestral protandric species of *Lysmata* that became a specialized fish cleaner, as suggested by Bauer (2000). Restricted mobility of individuals resulting from their association with the host, and, hence, the reduced probability of encountering mating partners, would have favored PSH (Bauer, 2000) (see foregoing for further details about this hypothesis). Nonetheless, the inferences about ancestral character states from the present analysis need to be considered with caution. Indeed, the present analysis did not support an ancestral symbiotic condition as significantly more likely than a free-living condition. Also, several internal nodes in the phylogenetic tree were not well supported by the Bayesian analysis of phylogenetic inference (see Baeza et al., 2009). This low support for internal nodes, together with the breadth of the posterior distributions of the character inferred for these nodes, means that other alternative routes to the evolution and maintenance of this peculiar sexual system in *Lysmata* cannot be ruled out.

Among alternative historical scenarios (to that proposed by Bauer, 2000), PSH might well have evolved from a strict simultaneous hermaphrodite or even from a strict gonochoric free-living ancestor inhabiting tropical environments. The evolution of PSH from an ancestral strictly simultaneous hermaphroditic condition has been reported previously for the worm *Ophryotrocha diadema*, one of the few other marine invertebrates in which PSH has been demonstrated (Dahlgren et al., 2001). Acting together with the conditions favoring simultaneous hermaphroditism (i.e., low abundance), sex-dependent energetic costs might have favored an early maturation of the male reproductive function compared to that of the female function in the ancestral free-living shrimp (regardless of its sexual system), ultimately resulting in the evolution of PSH as we observe it today in *Lysmata* (and *Exhippolysmata*). Similarly, brooding constraints experienced by hermaphroditic shrimps might have favored the retention of the male function later in life. If the space for brooding embryos in the abdomen becomes saturated, allocation of energy to sperm production is expected to maximize fitness. This argument is similar to that of Ghiselin (1987) to explain apparent protogynous simultaneous hermaphroditism in chitons. In some species of polyplacophorans, individuals brood eggs along the side of the body. Early in life, they reproduce strictly as females until they reach a size at which the space in which they brood is saturated. At that point, the same individuals start producing sperm while they are brooding. Brooding constraints have been previously reported for at least one species of *Lysmata* (*L. wurdemanni*; Baeza, 2006). New studies are needed to confirm whether brood constraints are common in the genus.

In the scenarios depicted here, we should expect that, in a phylogeny of the group, "tropical–low abundance" species would have a more basal position than the "Pair" and "Crowd" species ("Pair" and "Crowd" sensu Bauer, 2000). The rather complex mating system (social monogamy) and specialized fish-cleaning behavior of the "Pair" species most probably evolved from "tropical–low abundance" species without complex cleaning behavior and with rather simple mating systems (i.e., without long-lasting associations between mating partners), as appears to be the case for most shrimps from the closely related family Hippolytidae. The unresolved position of the different natural clades with respect to each other in the current phylogeny (see also Baeza et al., 2009) constrain testing this last hypothesis against Bauer's (2000) ideas. Future studies attempting to resolve the natural relationships among species of *Lysmata*, *Exhippolysmata*, and other related taxa together with the detailed examination of their sexual system should allow explaining the origin of simultaneous hermaphroditism in shrimps from the genus *Lysmata*.

Last, it is worth mentioning one of the main assumptions of the present analysis. PSH was treated as a singular innovation only originating in the genus *Lysmata* (which contains *Exhippolysmata*), as initially suggested by Bauer (2000). To the best of my knowledge, shrimps from the genus *Merguia*, apparently the sister group to *Lysmata*, seem to have a gonochoric sexual system. However, this observation needs experimental confirmation. Most importantly, future studies need to test for the existence of protandric simultaneous hermaphroditism in members from other closely related genera (i.e., *Mimocaris*, *Parahippolyte*, *Merguia*, *Merhippolyte*). These studies might reveal that PSH is not a singularity. Indeed, PSH has independently evolved in the past at least four other times outside the Caridea. In addition to *Lysmata* shrimps, PSH has been confirmed in the polychaete worm *Ophryotrocha diadema* (Premoli and Sella, 1995), the land snail *Achatina fulica* (Tomiyama, 1996), the tunicate *Pyura chilensis* (Manríquez and Castilla, 2005), and the symbiotic barnacle *Chelonibia patula* (Crisp, 1983). If simultaneous hermaphroditism turns out not to be a singularity in shrimps from the families Hippolytidae and Lysmatidae, then it should be possible to explore the environmental conditions that favor this unique sexual system in shrimps.

ACKNOWLEDGMENTS

I appreciate the support from the Smithsonian Tropical Research Institute (STRI, Panama City and Bocas del Toro, Panama) Marine Fellowship and the Smithsonian Marine Station at Fort Pierce (Fort Pierce, Florida, USA) Fellowship. I thank Dr. Rachel Collin for inviting me to join the 2007 Research Cruise to La Coiba Island and Las Perlas Archipelago, off the Pacific coast of Panama, aboard the R/V *Urraca* (STRI), during which a portion of this study was conducted. I thank Dr. Klaus Ruetzler (National Museum of Natural History, Smithsonian Institution), Dr. Anson (Tuck) Hines (SERC) and Dr. Valerie Paul (SMSFP) for funding various research visits to Carrie Bow, Belize, during which a major portion of this manuscript was completed. I also thank Paula Rodgers and Rafael Lemaitre for their support during my visit to the National Museum of Natural History. The comments by two anonymous referees substantially improved this manuscript. This work is contribution number 776 of the Smithsonian Marine Station at Fort Pierce and contribution number 840 of the Caribbean Coral Reef Ecosystems Program (CCRE), Smithsonian Institution, and supported in part by the Hunterdon Oceanographic Research Fund. This study was partially funded by a National Geographic Research Grant from the National Geographic Society, USA.

LITERATURE CITED

Baeza, J. A. 2006. Testing Three Models on the Adaptive Significance of Protandric Simultaneous Hermaphroditism in a Marine Shrimp. *Evolution*, 60:1840–1850.

———. 2007a. Male Mating Opportunities Affect Sex Allocation in a Protandric Simultaneous Hermaphroditic Marine Shrimp. *Behavioral Ecology and Sociobiology*, 61:365–370.

———. 2007b. No Effect of Group Size on Sex Allocation in a Protandric-Simultaneous Hermaphroditic Shrimp. *Journal of the Marine Biological Association of the United Kingdom*, 87:1169–1174.

———. 2007c. Sex Allocation in a Simultaneously Hermaphroditic Marine Shrimp. *Evolution*, 61:2360–2373.

———. 2008a. Social Monogamy in the Shrimp *Pontonia margarita*, a Symbiont of *Pinctada mazatlantica*, in the Tropical Eastern Pacific Coast. *Marine Biology*, 153:387–395.

———. 2008b. Protandric Simultaneous Hermaphroditism in the Shrimps *Lysmata bahia* and *L. intermedia*. *Invertebrate Biology*, 127:181–188.

Baeza, J. A., and A. Anker. 2008. *Lysmata hochi* n. sp., a New Species of Hermaphroditic Shrimp from the Southern Caribbean. *Journal of Crustacean Biology*, 28:148–155.

Baeza, J. A., and R. T. Bauer. 2004. Experimental Test of Social Mediation of Sex Change in a Protandric Sequential Hermaphrodite; The Marine Shrimp *Lysmata wurdemanni* (Crustacea: Caridea). *Behavioral Ecology and Sociobiology*, 55:544–550.

Baeza, J. A., J. Reitz, and R. Collin. 2008. Protandric Simultaneous Hermaphroditism and Sex Ratio in the Shrimp *Lysmata nayaritensis*. *Journal of Natural History*, 41:2843–2850.

Baeza, J. A., C. D. Schubart, P. Zillner, S. Fuentes, and R. T. Bauer. 2009. Molecular Phylogeny of Shrimps from the Genus *Lysmata* (Caridea: Lysmatidae): The Evolutionary Origins of Protandric Simultaneous Hermaphroditism and Pair-Living. *Biological Journal of the Linnaean Society*, 96:415–424.

Baeza, J. A., and M. Thiel. 2007. "The Mating System of Symbiotic Crustaceans: A Conceptual Model Based on Optimality and Ecological Constraints." In *Evolutionary Ecology of Social and Sexual Systems: Crustaceans as Model Organisms*, ed. J. E. Duffy and M. Thiel, pp. 250–267. Oxford, UK: Oxford University Press.

Bauer, R. T. 2000. Simultaneous Hermaphroditism in Caridean Shrimps: A Unique and Puzzling Sexual System in the Decapoda. *Journal of Crustacean Biology*, 20(Spec. No. 2):116–128.

———. 2006. Same Sexual System but Variable Sociobiology: Evolution of Protandric Simultaneous Hermaphroditism in *Lysmata* Shrimps. *Integrative and Comparative Biology*, 46:430–438.

Bauer, R. T., and G. J. Holt. 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 W. A. Newman. 2004. Protandric Simultaneous Hermaphroditism in the Marine Shrimp *Lysmata californica* (Caridea: Hippolytidae). *Journal of Crustacean Biology*, 24:131–139.

Braga, A. A., L. S. López-Greco, D. C. Santos, and A. Fransozo. 2009. Morphological Evidence for Protandric Simultaneous Hermaphroditism in the Caridean *Exhippolysmata oplophoroides*. *Journal of Crustacean Biology*, 29:34–41.

Bruce, A. J. 1983. *Lysmata debelius*, New Species, a New Hippolytid Shrimp from the Philippines. *Revue Francaise d'Aquariologie et Herpetologie*, 4:115–120.

Burukovsky, R. N. 2000. *Lysmata splendida* sp. nov., a New Species of Shrimp from the Maldives (Crustacea: Decapoda: Hippolytidae). *Senckenbergiana Maritime*, 30:223–227.

Chace, F. A. Jr. 1972. *The Shrimps of the Smithsonian–Bredin Caribbean Expeditions with a Summary of the West Indian Shallow-Water Species*. Smithsonian Contributions to Zoology, No. 98. Washington, D.C.: Smithsonian Institution Press.

———. 1997. *The Caridean Shrimps (Crustacea: Decapoda) of the Albatross Philippine Expedition, 1907–1910, Part 7: Families Atyidae, Eugonatonotidae, Rhynchocinetidae, Bathypalaemonellidae, Processidae, and Hippolytidae*. Smithsonian Contributions to Zoology, No. 587. Washington, D.C.: Smithsonian Institution Press.

Charnov, E. L. 1982. *The Theory of Sex Allocation*. Princeton: Princeton University Press.

Correa, C., J. A. Baeza, E. Dupré, I. A. Hinojosa, and M. Thiel. 2000. Mating Behavior and Fertilization Success of Three Ontogenetic Stages of Male Rock Shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *Journal of Crustacean Biology*, 20:628–640.

Crisp, D. J. 1983. *Chelonobia patula* (Ranzani), a Pointer to the Evolution of the Complemental Male. *Marine Biology Letters*, 4: 281–294.

Crosnier, A., and J. Forest. 1973. "Les Crevettes Profondes de l'Atlantique Oriental Tropical." In *Faune Tropicale 19*. Paris: O.R.S.T.O.M.

Dahlgren, T. G., B. Åkesson, C. Schander, K. M. Halanych, and P. Sundberg. 2001. Molecular Phylogeny of the Model Annelid *Ophryotrocha*. *Biological Bulletin*, 201:193–203.

Dohrn, P. F. R., and L. B. Holthuis. 1950. *Lysmata nilita*, a New Species of Prawn (Crustacea Decapoda) from the Western Mediterranean. *Pubblicazioni della Stazione Zoologica di Napoli*, 22:339–347.

d'Udekem d'Acoz, C. 2002. *Lysmata seticaudata* (Risso, 1816) and *L. nilita* Dohrn and Holthuis, 1950 Are Protandrous Simultaneous Hermaphrodites (Decapoda, Caridea, Hippolytidae). *Crustaceana*, 75:1149–1152.

Espinoza-Fuenzalida, N. L., M. Thiel, E. Dupre, and J.A. Baeza. 2008. Is *Hippolyte williamsi* Gonochoric or Hermaphroditic? A Multi-Approach Study and a Review of Sexual Systems in *Hippolyte* Shrimps. *Marine Biology*, 155:623–635.

Fiedler, G. C. 1998. Functional, Simultaneous Hermaphroditism in Female-Phase *Lysmata amboinensis* (Decapoda: Caridea: Hippolytidae). *Pacific Science*, 52:161–169.

Fransen, C. H. J. M. 1991. *Lysmata olavoi*, a New Shrimp of the Family Hippolytidae (Decapoda, Caridea) from the Eastern Atlantic Ocean. *Arquipelago-Life Marine Sciences*, 9:63–73.

Ghiselin, M. T. 1974. *The Economy of Nature and the Evolution of Sex*. Berkeley: University of California Press.

———. 1987. "Evolutionary Aspects of Marine Invertebrate Reproduction." In *Reproduction of Marine Invertebrates: General Aspects: Seeking Unity in Diversity*. Volume 9, ed. A. C. Giese, J. S. Pearse, and V. B. Pearse, pp. 609–665. Pacific Grove, Calif.: The Boxwood Press.

Holthuis, L. B. 1948. Note on Some Crustacea Decapoda Natantia from Suriname. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series C, Biological and Medical Sciences*, 51:1104–1113.

Holthuis, L. B., and C. Maurin. 1952. Note sur *Lysmata uncicornis* nov. spec. et sur deux autres espèces intéressantes de crustacés décapodes macroures de la côte Atlantique du Maroc. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, 55:197–202.

Kagwade, P. V. 1982. The Hermaphrodite Prawn *Hippolysmata ensirostris* Kemp. *Indian Journal of Fisheries*, 28:189–194.

Kass, R. E., and A. E. Raftery. 1995. Bayes Factors. *Journal of the American Statistical Association*, 90:773–795.

Kemp, S. 1914. Notes on Crustacea Decapoda in the Indian Museum, V. Hippolytidae. *Records of the Indian Museum*, 10:81–129.

Limbaugh, C., H. Pederson, and F. A. Chace, Jr. 1961. Shrimps That Clean Fishes. *Bulletin of Marine Science*, 11:237–57.

Manríquez, P. H., and J. C. Castilla. 2005. Self-Fertilization as an Alternative Mode of Reproduction in the Solitary Tunicate *Pyura chilensis*. *Marine Ecology Progress Series*, 305:113–125.

Pagel, M., and A. Meade. 2006. Bayesian Analysis of Correlated Evolution of Discrete Characters by Reversible-Jump Markov Chain Monte Carlo. *The American Naturalist*, 167:808–825.

Pagel, M., A. Meade, and D. Barker. 2004. Bayesian Estimation of Ancestral Character States on Phylogenies. *Systematic Biology*, 53:673–684.

Policansky, D. 1982. Sex Change in Plants and Animals. *Annual Review of Ecology and Systematics*, 13:417–495.

Premoli, M. C., and G. Sella. 1995. Sex Economy in Benthic Polychaetes. *Ethology, Ecology, and Evolution*, 7:27–48.

Rathbun, M. J. 1906. South American Crustacea. *Revista Chilena de Historia Natural*, 11:45–50.

Rhyne, A. L., and A. Anker. 2007. *Lysmata rafa*, a New Species of Peppermint Shrimp (Crustacea, Caridea, Hippolytidae) from the Subtropical Western Atlantic. *Helgoland Marine Research*, 61:291–296, doi:10.1007/s10152-007-0077-4.

Rhyne, A. L., and J. Lin. 2006. A Western Atlantic Peppermint Shrimp Complex: Re-Description of *Lysmata wurdemanni*, Description of Four New Species, and Remarks on *Lysmata rathbunae* (Crustacea: Decapoda: Hippolytidae). *Bulletin of Marine Science*, 79:165–204.

Schatte, J., and R. Saborowski. 2006. Change of External Sexual Characteristics During Consecutive Moults in *Crangon crangon* L. *Helgoland Marine Research*, 60:70–73, doi:10.1007/s10152-005-0013-4.

Terossi, M., L. S. López-Greco, and F. L. Mantelatto. 2008. *Hippolyte obliquimanus* (Decapoda: Caridea: Hippolytidae): A Gonochoric or Hermaphroditic Shrimp Species? *Marine Biology*, 154: 127–135.

Tomiyama, K. 1996. Mate-Choice Criteria in a Protandrous Simultaneously Hermaphroditic Land Snail *Achatina fulica* (Férussac) (Stylommatophora: Achatinidae). *Journal of Molluscan Studies*, 62:101–111.

Wicksten, M. K. 2000. The Species of *Lysmata* (Caridea: Hippolytidae) from the Eastern Pacific Ocean. *Amphipacifica*, 2:3–22.

Williams, A. B. 1984. *Shrimps, Lobsters and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida*. Washington, D.C.: Smithsonian Institution Press.

Wirtz, P. 1997. Crustacean Symbionts of the Sea Anemone *Telmatactis cricoides* at Madeira and the Canary Islands. *Journal of Zoology*, 242:799–811.

Baeza, J. Antonio. 2009. "Protandric Simultaneous Hermaphroditism Is a conserved trait in Lysmata (Caridea:Lysmatidae): Implications for the Evolution of Hermaphroditism in the Genus." *Proceedings of the Smithsonian Marine Science Symposium* 38, 95–110.