Same sexual system but variable sociobiology: evolution of protandric simultaneous hermaphroditism in *Lysmata* shrimps

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Synopsis The sexual system of the decapod (caridean) shrimp *Lysmata* is protandric simultaneous hermaphroditism (PSH). Individuals first mature as males (male phase = MP) and then when older (larger) change to the external phenotype of female carideans (female phase = FP). However, unlike purely protandric carideans, *Lysmata* FPs retain reduced male gonadal tissues and ducts, and are able to mate nonreciprocally as males as well as to reproduce as females. Thus, FPs of *Lysmata* species are functional simultaneous hermaphrodites although most reproductive effort is devoted to embryo production and incubation. The question explored here is, given the propensity of carideans to protandry, the apparent low cost, and high reproductive advantage of PSH, why has not PSH evolved more frequently? The mating systems and sexual selection of caridean shrimps, the original sex of protandric individuals, the cost of maleness, and sex allocation theory are discussed in relation to protandry and PSH. None of these factors adequately explains the evolution of PSH of *Lysmata* species. *Lysmata* has at least 2 species groups with very different sociobiologies; these groups do not appear to share current selective pressures that would explain PSH in both. A historical contingency hypothesis, testable in part with a phylogenetic analysis, may explain the evolution of PSH in *Lysmata*.

Introduction

Shrimps of the caridean genus *Lysmata* are decapod crustaceans that have received considerable attention from both professional and amateur biologists because of their often bright coloration (Debelius 1999) and interesting fish cleaning behaviors (Limbaugh and others 1961; Bauer 2004). These shrimps, one of the groups termed "ornamental" species in the pet aquarium industry (Calado and others 2003), have received much attention from divers, aquarium enthusiasts, and aquaculturists. As a result, considerable observations made on living specimens gave rise to anecdotal reports of "females mating with females" indicative of simultaneous hermaphroditism. Detailed studies on the sexual morphology and mating behavior of *Lysmata amboinensis* (Fiedler 1998) and *Lysmata wurdemanni* (Bauer and Holt 1998) revealed that indeed "females," that is, individuals with an external female phenotype that incubate embryos, are also capable of successfully mating as males. As in purely protandric species, individuals first pass through a male phase (MP) before changing to a female phase (FP) in which, unlike other protandric shrimps, the male ducts and male mating abilities are retained. This sexual system, termed "protandric simultaneous hermaphroditism" or PSH (Bauer, 2000) apparently confers a considerable

reproductive advantage on the individual compared to gonochory and pure protandry, the other 2 common sexual systems which occur in the Caridea. In this article, 2 related questions about PSH are addressed (Bauer 2000, 2006). First, given the apparent individual reproductive advantage of PSH, why has it not evolved more frequently in caridean shrimps, given the tendency of this group to protandry, an obvious precursor to PSH? Second, what explains the occurrence of 2 very different sociobiologies among *Lysmata* spp. with the same sexual system (PSH) that is rare, if not unique, among caridean and other decapod crustaceans?

Hermaphroditism in decapod crustacea and caridea

Hermaphroditism is relatively rare in most decapods but protandry is not uncommon in caridean shrimps (Bauer 2000). In protandric carideans, an individual first matures as a male, with external male phenotype and male reproductive function. However, the gonads are ovotestes with functional male and rudimentary female portions. With increasing age and size, the external phenotype changes to female, the gonad becomes completely ovarian, and the individual reproduces as a female. The individual before the sex change is often termed male and after sex change
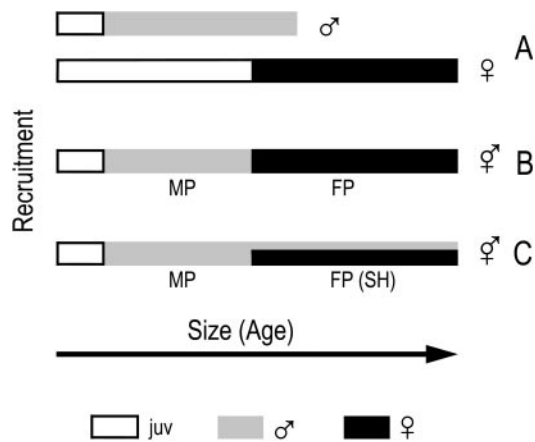
Fig. 1 Diagram of size (age) ontogeny of (**A**) gonochoristic species with small males, large females; (**B**) purely protandric (male to female sex change) species; (**C**) protandric simultaneous hermaphroditism (PSH) in *Lysmata* species in which the FP individuals have a primarily female phenotype but retain male gonadal tissue, spermatogenesis, and the ability to mate as male as well as female (functional simultaneous hermaphrodites). Unfilled bars represent the sexually immature (juvenile) phase; gray fill, male function; black fill, female function. MP, male phase; FP, female phase; FP (SH) female phase (functional simultaneous hermaphrodite).

female, but this terminology implies 2 different individuals. It is more appropriate and indicative of the individual's ontogeny to use male phase and female phase instead of male and female.

In a purely protandric caridean species, all individuals undergo male to female sex change (for example, *Pandalus goniurus*, Bergström 2000) (Fig. 1B). However, in several "protandric" species, the population is composed of protandric sex changers and individuals that do not change sex (primary females or primary males (PMs)). In most *Pandalus* spp., large commercially important shrimps from boreal waters, varying proportions (up to 50%) of individuals either mature only as females ("primary females") or go through a brief but nonfunctional MP before maturing as females ("early maturing females"). Primary females occur in other protandric caridean shrimp species as well, such as *Crangon crangon* (Bodekke and others 1991) and *Processa edulis* (Noël 1976). In *Thor manningi*, 50% of the population are protandric hermaphrodites and the other 50% are PMs, that is individuals that never change sex (Bauer 1986). In the alpheid *Athanas kominatoensis*, symbiotic with sea urchins, all individuals begin benthic life as MPs and all are capable of sex change (Nakashima 1987). However, only part of a cohort will change to the embryo-producing FPs; other MPs will remain

male and grow to the large MPs characteristic of the species. In *A. indicus*, the population is a mix of PMs, primary females, and sex changers (Gherardi and Calloni 1993).

Mating systems, sexual selection, and sexual systems in caridean shrimps

The 2800 species of caridean shrimps show a considerable ecological and morphological diversity (Bauer 2004). It is not surprising that a variety of mating systems have evolved in shrimps (Correa and Thiel 2003; Bauer 2004); some of them are more conducive to classical sexual selection (Darwin 1871; Thornhill and Alcock 1983) than others. The type and intensity of sexual selection may have influenced the evolution of gonochoristic versus hermaphroditic sexual systems in carideans.

In temporary mate guarding (Bauer 2004), breeding males are larger than females and are equipped with enlarged chelipeds or other weaponry (Ridley 1983; Bauer 2004). Such males seek females nearing the parturial molt (or are sought out by such females) and guard them aggressively for one to several days prior to the female parturial molt. As in all carideans, copulation and spawning take place shortly after the female molt, spermatophores are deposited externally, and there is no sperm storage. Spawning takes place soon after mating, and the male abandons the female and seeks other pre-parturial females.

In extended mate guarding (social monogamy; "pair living")(Wickler and Seibt 1981), a male is paired with the female for a long period, as in alpheids such as snapping shrimps (*Alpheus, Synalpheus* spp.) and many pontoniines (Bauer 2004). However, strict sexual fidelity is usually found lacking when the mating system is well studied (Seibt and Wickler 1979; Knowlton 1980). The individuals of a pair tend to be similar in size and cheliped weaponry, with well-developed chelipeds in both sexes.

In many other caridean species, males do not seek out females to guard or defend them from other males for copulatory privileges. Instead, they frequently make contact with other conspecifics, often with the long antennal flagella. If the encountered individual is a newly molted parturial female, copulation takes place after which the male immediately abandons the mated female. Such a seemingly random mating system ("pure searching," Wickler and Seibt 1981) may evolve when the opportunity for an encounter with a receptive female is relatively high. As might be expected, pure-searching mating systems are found in the many species of gonochoristic caridean shrimps in

which conspecifics occur in mobile aggregations or schools (Bauer 1996; Bauer and Abdalla 2001). A correlate of a pure-searching mating system is that on average males are smaller than females (Fig. 1A), and there is no sexual dimorphism in cheliped weaponry. In protandric carideans, MPs are smaller than FPs (Fig. 1B), and, as expected, the male mating system appears to be pure searching (Bergström 2000 for pandalids; Bodekke and others 1991 for *Crangon crangon*; Bauer and Holt 1998; Bauer 2002a for *Lysmata wurdemanni*).

Sexual selection for large male size and appendage weaponry has obviously occurred in the many caridean species with temporary mate guarding and pair living. The mechanisms involved may be intrasexual selection (for example, male-male competition in *Macrobrachium rosenbergii*; Ra'anan and Sagi 1985) and/or female choice (epigamic or intersexual selection, Thornhill and Alcock 1983), as observed in *Alpheus* spp. (Knowlton 1980; Rahman and others 2002) and *Rhynchocinetes typus* (Thiel and Hinojosa 2003). The similarity of body size in pair-living species, in which sexual selection is strong, may be explained by size-assortative pairing driven by female-female competition and female choice in *Alpheus heterochelis* (Rahman and others 2002). However, Schein (1975), working with the same species, earlier proposed that heterosexual pairing of similar-sized individuals was due to an "agonistic" balance established during initial contacts. In the many gonochoristic caridean species with pure-searching, large male size and enhanced weaponry have not been selected for. Males of such mobile species do not establish or defend territories to attract or defend females. In these species, male reproductive success is not strongly correlated with male size. This sets the stage for protandry, in which individuals reproduce as male when smaller and female when larger.

In caridean females (and FP protandric hermaphrodites), as with many organisms, fecundity is strongly correlated with size (Bauer 2004). This explains well the direction of sex change in caridean shrimps, that is, from male to female, rather than the reverse (Size Advantage Model; Ghiselin 1969; Warner 1975; Charnov 1982). This is not to say that there is absolutely no correlation of male size and reproductive success in pure-searching species. Although not conclusive, the observations of Chiba and others (2003) on *Pandalus latirostris* suggest that larger males have some mating advantage over smaller ones. Likewise, in *Lysmata wurdemanni*, larger MPs were significantly more successful in obtaining copulations than smaller ones (Bauer 2002a). However, compared to species with temporary mate guarding or pair living, male mating success is at best weakly correlated with male size. Thus, the Size Advantage Model appears valid in explaining the direction of sex change in caridean shrimps.

PSH

As in protandric carideans, individuals of *Lysmata* spp. develop an external male phenotype soon after settlement from the plankton. Their gonads are ovotestes, with a well-developed testicular portion, vasa deferentia, ejaculatory ducts with sperm, and a rudimentary ovarian portion. During this MP, corresponding to that of protandric species, the individual can only function sexually as a male. As the MP grows larger, the ovarian portion of the gonads increases in relative size and, when reaching sex change molt, the oocytes are large and full of yolk (vitellogenic). At this molt, the female breeding dress appears, and mating as a female, spawning, and incubation of embryos occurs for the first time. In a purely protandric species, FPs lose all male characters, both external and gonadal, after the sex change molt. However, in *Lysmata* spp., FPs retain the testicular portion of the gonads, the male ducts, and the male gonopores.

Mating experiments (Bauer 2002a) have shown that FPs of *Lysmata wurdemanni* are just as capable as MPs in obtaining copulations with prespawning FPs. Copulation between 2 FPs is not reciprocal; one individual acts a male and the other as a female after which they interact no further. Although mechanically possible, self-fertilization does not take place in FPs (Bauer and Holt 1998; Fiedler 1998; Bauer and Newman 2004). Bauer (2000) termed this sexual system "PSH" (Fig. 1C).

Various terms could be used to describe the individual after sex change, such as "euhermaphrodite phase" (Lin and Zhang 2001) or "simultaneous hermaphrodite phase" (Calado and Narciso 2003). However, because of the FPs' primarily female phenotype and its developmental similarity (and probable homology) with FPs of protandric species, I prefer the term "FP," used in the majority of papers on the sexual systems of *Lysmata* (Bauer and Holt 1998; Fiedler 1998; Bauer 2000, 2001, 2002a, 2002b, 2005; Baldwin and Bauer 2003; Baeza and Bauer 2004; Bauer and Newman 2004).

As in protandric species such as *Pandalus* shrimps (Charnov 1982), there is considerable variation in the size (age) of sex change in *Lysmata wurdemanni* (Bauer 2000, 2001, 2002a) and perhaps other *Lysmata* spp. Laboratory experiments and observations on population structure of natural populations have shown that environmental factors influence the timing of sex

change, both the demographic environment ("socially mediated sex change") (Bauer 2002a; Baeza and Bauer 2004) and abiotic ones related to the seasonality of reproduction (Bauer 2002a; Baldwin and Bauer 2003). The role of sex allocation on the timing of sex change in *Lysmata* continues to be of considerable interest and published work to date has been covered in depth elsewhere (Bauer 2006).

Original sex of carideans with protandry and PSH

An important question in understanding the evolution of protandry and PSH is "What is the original sex of the sex changer?"(Bauer 2000). In gonochoristic species with small males and larger females, juvenile females are similar in size to mature males. In a "female origin" of protandric individuals, male sexual characters would develop in the juvenile female growth phase on the way to the larger sexually mature female (Fig. 2A). Just a single successful mating as an MP would give such individuals increased reproductive fitness compared to pure female genotypes. In a "male origin," the FP would have to be added to the end of the life history of a male (Fig. 2B). This would entail both added growth to the larger size needed by females to produce vitellogenic oocytes and an extension of the normal male lifespan. Heterogametic sex chromosomes, which might identify the sexual origin of hermaphrodites, are either rare or difficult to recognize by karyotyping in decapod crustaceans (Bauer 2000).

In decapod and other malacostracan crustaceans, all individuals have the potential to become males or females (Charniaux-Cotton and Payen 1985). Gonads of developing immature individuals become testes if exposed to androgenic (male) hormone, ovaries if not. Rudiments of the androgenic glands are present during embryonic development in both males and females. Development of the androgenic glands depends on the presence and expression of a specific allele in genotypic males. In genotypic females, the "androgenic" allele is absent or is inhibited by another "female" allele. In either case, androgenic glands do not develop, embryonic gonads become ovaries, and the individual develops as a female, the "default" sex (Bauer 2000).

Both a female and a male origin of protandric individuals have been proposed by different investigators working on different species of the caridean genus *Pandalus*. Hoffman (1972) cited histological evidence from the gonads in support of a female origin for protandric individuals. In MPs of *P. platyceros*, oogenesis occurs before spermatogenesis. The primary spermatocytes of MPs in this species are unusually large compared to males of gonochoristic carideans.
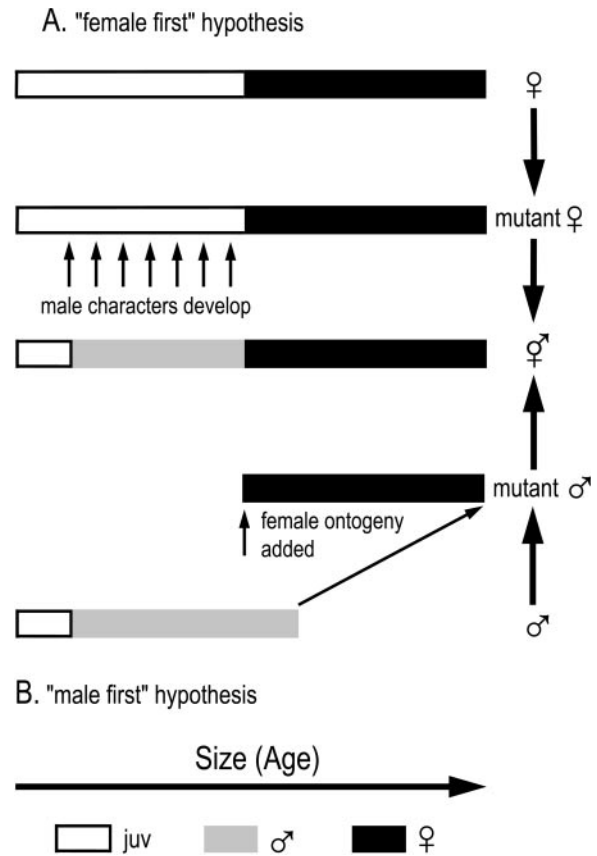

Fig. 2 Two hypotheses on the original sex of protandric individuals: (**A**) "Female first" hypothesis: male characters develops in juvenile female stage of mutant female individuals; (**B**) "Male first" hypothesis: in mutant of original male genotype, androgenic degenerates, female characters develop, and life span is extended.

Hoffman proposed that they are oocytes transformed into spermatocytes by secretions of the androgenic glands. Protandry could arise in an ancestor by a mutation triggering the transitory development of the androgenic gland during the development of a genotypic female. Instead of passing through a juvenile FP, the individual would go through a male phase during the same size and growth period. This would be possible because of the apparently small energetic investment into male appendices and gamete production in males from "small-male" caridean species. Degeneration of the androgenic glands later in development would allow reversion (sex change) to female.

Alternately, Charniaux-Cotton and Payen (1985) proposed, working with *Pandalus borealis*, that the original sex of protandric individuals was male. A mutation in males of a gonochoristic ancestor resulted in early degeneration of the androgenic gland, resulting in sex change to female.

In the hippolytid caridean *Thor manningi*, Bauer (1986) found a novel mix of sexual

morphotypes: primary males (PMs) and protandric hermaphrodites. In the same size range as MPs, PMs have much larger male sexual appendices than MPs. Additionally, PMs have prehensile first walking legs, possibly an adaptation for grasping FPs during copulation. Thus, PMs are "supermale" compared to the MPs of the same species. Bauer (1986) proposed that protandry developed in females of a gonochoristic ancestor of *T. manningi*, as described above in the "female origin" hypothesis. However, unlike other protandric species, PMs have not been selected against and eliminated in *T. manningi* because of their "supermale" characteristics, which perhaps give them a male mating advantage over MPs. These features may be fortuitous preadaptations because they are also found in males of gonochoristic *Thor* species (Bauer and VanHoy 1996).

Evolution of PSH in *Lysmata* shrimps

The evidence to date favors a female origin of protandric individuals in carideans, including those of *Lysmata* spp. It seems most probable that PSH in *Lysmata* shrimps evolved directly from protandry, given that the difficult step of sex change had already evolved. Retention of male gonopores and male ducts in a protandric FP is a small evolutionary step compared to the evolution of sex change. Protandry has evolved in a number of unrelated caridean taxa (Bauer 2000). Given the propensity of carideans to protandry and the relative small evolutionary step from protandry to PSH, it is puzzling that PSH has not evolved more often in caridean shrimps.

Costs of Maleness in PSH

One hypothesis on the rarity of PSH is that the costs of maleness in FP simultaneous hermaphrodites are high, representing a barrier to PSH. However, in *Lysmata* FPs, there is negligible male external morphology. Internally, the testicular portion of the FP ovotestes is small relative to the ovarian; the mass of sperm produced by FPs is small compared to that of vitellogenic oocytes.

One indication that the male system is not physiologically expensive to *Lysmata* FPs comes from the Calado and others' (2005) study of parasitized FPs of *L. seticaudata*. Carideans are frequently parasitized by bopyrid isopods. The large female parasite (with attached dwarf male) lives either within the gill chamber or under the abdomen of the host shrimp. Parasitized female shrimps are unable to produce vitellogenic oocytes and embryos; that energy goes to brood production of the parasite female (Beck 1980; O'Brien and Van Wyk 1985). Calado and others (2005) found that FPs of *L. seticaudata* did not produce broods;

however, they were able to mate as males and inseminate broods of nonparasitized FPs.

There are also behavioral costs to consider. The only male behavior that FPs exhibit in *L. wurdemanni* is the brief precopulatory chase of prespawning FPs just after their molt. Because the number of prespawning FPs available is low on any given day, this is probably not a frequent behavior, at least compared to female incubation behavior (frequent beating of pleopods to circulate water among the embryos; grooming of embryos).

Whatever the total and type of costs of maleness, how significant are they in terms of FP fecundity, a function of brood size and interspawn interval? Bauer (2005) compared the fecundity of FPs of *Lysmata wurdemanni* in treatments in which the opportunity for the FP to mate as a male was varied. The brood sizes of FPs without male mating opportunities were indeed significantly larger than those of FPs that could mate as males. Interestingly, the interspawn interval was significantly shorter in FPs that could mate as males. However, a model of fecundity showed that this would not compensate for the reduction of brood size over the course of a breeding season. Thus, there is a significant cost of maleness on brood production, at least in these laboratory experiments, in FPs of *L. wurdemanni* and perhaps other *Lysmata* spp.

However, has the cost of maleness observed in *Lysmata* FPs been a barrier to the evolution of PSH in other carideans? The FPs of *Lysmata* are quite capable of mating as male and in competing with MPs for copulations with prespawning FPs (Bauer 2002a). The loss in female fecundity in one FP spawning cycle would be more than made up with a single insemination of another FP's brood of embryos. Potentially, an FP mating as male could inseminate several other broods. The details of the costs of maleness on brood production versus the benefits of male function need to be quantified. Presumably, the benefits outweigh the costs in *Lysmata*, otherwise PSH would not adaptive. If the benefits of maleness do outweigh their costs in *Lysmata* FPs, why has not PSH evolved more often? Perhaps one has to look at the sociobiology of *Lysmata* and the role of historical processes to answer this question.

The comparative method and the sociobiology of *Lysmata* spp.

The use of the comparative method to search for the selective pressures responsible for an adaptation has been quite productive for evolutionary biologists (Thornhill and Alcock 1983; Harvey and Pagel 1991). One searches for an environmental trait, abiotic or biotic, common to the taxa with the adaptation in

question. Is there some common feature of the habitat, ecology, or social organization of *Lysmata* species that might suggest the selective pressures that resulted in the evolution of PSH in *Lysmata* and not other caridean taxa?

The general socioecological characteristics are known for several of the 30+ *Lysmata* species (Bauer 2000, 2006). Instead of revealing some environmental feature common to all, the sociobiology of *Lysmata* species shows a distinct dichotomy. In one group of species, such as *Lysmata wurdemanni, L. seticaudata,* and *L. californica,* individuals live in aggregations, often large, of MPs and FPs. I have termed these "Crowd" species (Bauer 2000). The mating system appears to be pure searching (for example, Bauer 2002a), similar to that found in protandric species and small-male/large-female gonochoristic carideans, both of which tend to occur in high density aggregations. "Crowd" species of *Lysmata* are nocturnal, generalized foragers. They will feed on or "clean" the surface of other organisms, especially fishes, if the recipient allows them to do so. However, this facultative fish cleaning is unspecialized and does not involve the behavioral displays or coloration used by specialized cleaner shrimps to attract fish clients (Limbaugh and others 1961; Bauer 2004). The coloration of "Crowd" species is subdued, consisting of reddish "peppermint" stripes and reddish antennal flagella. This group of species occurs in tropical and warm temperate waters around the world.

In contrast, in another group of *Lysmata* species, individuals are brightly colored with stripes and spots of white color strongly contrasting with a darker reddish background color. The antennal flagella are a bright white. During the day, these shrimps, which are often reported as living in pairs (Bauer 2000), display themselves to fishes by lashing the antennal flagella and swaying the body. Fish clients arrive and perform a characteristic submissive display, after which the shrimps hop on the client and forage on materials on their surface. At least some individuals of these species live in FP (simultaneous hermaphrodite) pairs (for example, Wirtz 1997). Although a thorough investigation of these FP pairs is warranted, the mating system appears to be extended mutual mate guarding. Population density of "Pairs" species, unlike that of "Crowd" species, is low. Thus, "Pairs" species such as *Lysmata grabhami, L. amboinenesis,* and *L. debelius* are obligate, specialized fish cleaners with very different socioecological traits from those of "Crowd" species (Bauer 2000). There is no current environmental trait apparent in both groups of species that suggests the selective pressure responsible for the unique sexual system (PSH) shared by both groups.

A historical contingency hypothesis

Current selective pressures do not explain the PSH of *Lysmata* species. Sex allocation theory (Charnov 1982) is important in explaining the direction and, in part (Bauer 2002a; Baeza and Bauer 2004; Bauer 2006), the timing of sex change in species with protandry and PSH. Certainly, further detailed examination of sex allocation in *Lysmata* species will shed light on the sociological and ecological conditions under which hermaphroditism can evolve in caridean shrimps and perhaps other organisms. However, as pointed out by Gould (1989), unique adaptations evolve under the general background of natural selection but often owe their existence to a cascade of unpredictable historical events, each event dependent on a previous one (historical contingency). The existence of PSH in 2 groups of *Lysmata* species living under such different socioecological conditions may point to the role of history in the evolution of PSH in *Lysmata* and its apparent absence, or at least rarity, in other caridean shrimps, in which protandric hermaphroditism is somewhat common.

The evolution of sex change in individuals, male or female, of a gonochoristic species is a difficult evolutionary step (Charnov 1982). By comparison, retention of a reduced testicular portion of the gonad and male ducts in protandric caridean, already sex changers, appears to be a much smaller evolutionary change. In a historical contingency hypothesis on the evolution of PSH in *Lysmata* (Bauer 2000, 2006), a protandric ancestor of *Lysmata* species is proposed as most likely. As in modern protandric species, this would have been an aggregated species living at high density, with frequent contact among MPs and FPs and a pure-searching mating system. The first historical event necessary for PSH would have been an invasion of a population of this species into another habitat or a habitat change that resulted in a reduction of density and/or mobility of individuals. The former could come about with a reduction of resources (food, foraging space, shelter) and the latter by increased predation pressure (cf. *Alpheus* species, Knowlton 1980). The result would be infrequent contact between potential mating partners. This would be the selective pressure favoring both PSH and pair living, so that the individual always has both a male and female mating partner. The mating system would thus change from that of pure searching in the protandric *Lysmata* ancestor to extending mate guarding in the new species with PSH and pair living. This represents the ancestral "Pairs" species of *Lysmata*. In "Pairs" species, specialized fish cleaning behavior evolved as a primary feeding adaptation in shrimps with reduced mobility.

The evolutionary scenario proposed above could explain the evolution of "Pairs" species with PSH and pair living. But in "Crowd" species, the selective pressure of infrequent contact with mating partners, which may have selected for PSH and pair living in "Pairs" species, does not exist. Individuals of these species live in aggregations at relatively high density with a pure-searching mating system. There is no lack of male mating partners for a prespawning FP, because both MPs and FPs can mate as males. In a historical contingency hypothesis of PSH, a second historical event must have taken place to explain the presence of PSH but the absence of pair living in "Crowd" species. I propose that another habitat change (or invasion), resulting in high resource availability and/or lower predation pressure, allowed individuals of this *Lysmata* species to live again in the aggregated, high density populations the *Lysmata* ancestor and of extant "Crowd" species. Pair living would be selected against because of its costs (for example, agonistic interactions with and defense of the pair partner; reduced opportunities for extra-pair copulations). The PSH inherited from the "Pairs" species ancestors would be retained, once evolved, because of its high reproductive advantage and relatively low cost. However, PSH (and pair living) could not have evolved in an aggregated, high density protandric ancestor without the selective pressure of limited mating opportunities that appeared because of historical events (habitat change).

How can this historical explanation of PSH be tested? One important test must come from a phylogeny of *Lysmata* species. According to the above hypothesis, "Pairs" species must be ancestral to "Crowd" species (Fig. 3). The "Pairs" species should form a single clade from which all "Crowd" species descend, either from a single "Pairs" species (Fig. 3A) or perhaps pair living was lost independently in several "Pairs" species to give rise to the several "Crowd" species (Fig. 3B). In either case, 2 habitat changes (unpredictable historical events) would be necessary: the first on the protandric ancestor giving rise to a "Pairs" ancestor with PSH and pair living, and the second giving rise to "Crowd" species from a "Pairs" ancestor. The likelihood of multiple episodes of coevolution of pair living and PSH seems less likely than the loss of pair living with the retention of PSH in "Crowd" species. However, if the phylogeny reveals that "Crowd" species are ancestral to "Pairs" species, then the historical contingency hypothesis, as presented above, would be rejected.

The laborious task of gathering the evidence on *Lysmata* species required to test the above hypothesis needs to be done. The ecology, social organization, and mating systems of the majority of *Lysmata* species are
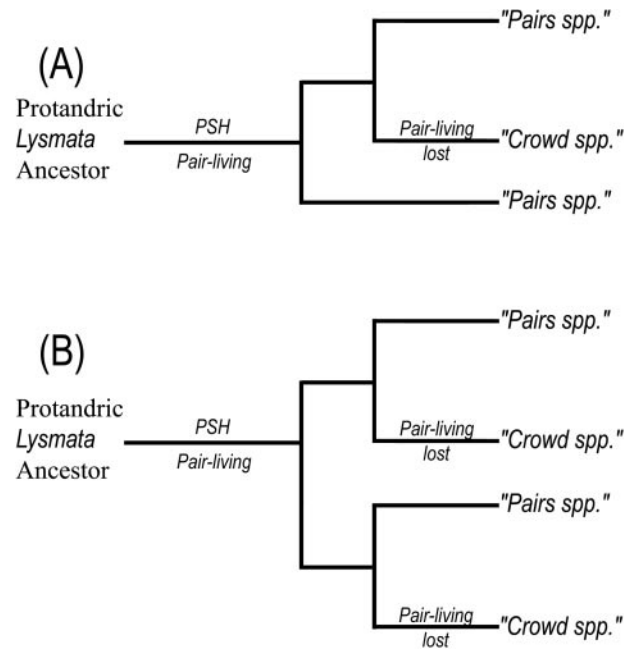

Fig. 3 Possible phylogenies supporting a historical contingency hypothesis on the evolution of protandric simultaneous hermaphroditism (PSH) and pair living in a protandric *Lysmata* ancestor, with either a single (**A**) or multiple (for example, double, **B**) origin of "Crowd" species by loss of pair living in "Pairs" species.

still unknown or poorly known. The distribution of these socioecological traits on a *Lysmata* phylogeny, as yet not determined, will be essential in testing historical hypotheses on the evolution of PSH. Testing of models on the hypothesized selective pressures leading to PSH and to different lifestyles (pair-living versus aggregations) will be useful in understanding the evolution of PSH.

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