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SIMULTANEOUS HERMAPHRODITISM IN CARIDEAN SHRIMPS: A UNIQUE AND PUZZLING SEXUAL SYSTEM IN THE DECAPODA

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ABSTRACT

The sexual system of the caridean genus Lysmata has been described until recently as protandric hermaphroditism, in which individuals change sex from male to female with increasing size. However, recent studies by Bauer and Holt (1998) and Fiedler (1998) have shown that female-phase individuals of at least two species are outcrossing simultaneous hermaphrodites, a sexual system described here as protandric simultaneous hermaphroditism (PSH). There is considerable variation in the ontogeny of protandric carideans, revealing an underlying flexibility in sex determination and development which has made PSH possible in at least some *Lysmata* spp. Possible costs and benefits of retention of male reproductive function in female-phase hermaphrodites are proposed. The PSH appears to be unique (to date) within the Decapoda and other Malacostraca to the caridean genus *Lysmata* and perhaps the related genus *Exhippolysmata*. It is puzzling that PSH has evolved in a group with such considerable variation in socio-ecological attributes; some *Lysmata* species are warm temperate, highly aggregated, with unspecialized (facultative) fish-cleaning behavior while others are tropical species, occur at low density in hermaphrodite pairs associated with sea anemones, and are specialized fish cleaners. Description of sexual systems, costs/benefits of PSH, and socio-ecological attributes of *Lysmata*, considered in the context of a phylogeny of the group, will be necessary to understand how PSH evolved in *Lysmata* and why it has not evolved in other groups of protandric carideans.

Although most species of decapod crustaceans have separate sexes (gonochorism), sex change from male to female (protandry) is not uncommon, especially in some families of caridean shrimps. Protandry has been reported in 37 decapod species, most of which are carideans (see next section for references). Simultaneous hermaphroditism has only been suggested in a few species of decapods on the basis of reproductive morphology (Buchanan, 1963; Kagwade, 1982). Recently, functional simultaneous hermaphroditism has been confirmed, with breeding observations and experiments, in two species of caridean shrimps, the hippolytids *Lysmata wurdemanni* (Gibbes, 1850) by Bauer and Holt (1998) and *L. amboinensis* (De Man, 1888) by Fiedler (1998). Evidence is presented in this paper that this unique sexual system may be widespread in the tropical and subtropical genus *Lysmata*. The existence of this previously unknown mode of reproduction in the Caridea raises new questions and directs attention to still unresolved problems about hermaphroditism in caridean shrimps and other decapods. The objective of this report is to analyze information on sexual and social systems of *Lysmata* in order to propose hypotheses on the evolution of simultaneous hermaphroditism in this genus. Costs and benefits of sequential and simultaneous hermaphroditism will be evaluated in order to address the question of why simultaneous hermaphroditism has not evolved more often from protandric caridean species.

PROTANDRIC HERMAPHRODITISM IN THE CARIDEA

Of 37 species of decapods known to have protandric sexual systems, 31 are caridean shrimps, 1 is an axiid thalassinid, 1 is a parastacid crayfish, 2 are hippid anomurans, and 2 are penaeoid shrimps [Table 1 in Brook *et al.*, 1994, plus the alpheid shrimp *Athanas indicus* (Coutière, 1903) in Gherardi and Calloni (1993); the pandalid shrimps *Pandalus gracilis* Stimpson, 1860, in Hayashi (1988) and *P. nipponensis* Yokoya, 1933, in Tamura (1950); the parastacid crayfish *Parastacus nicoleti* (Philippi, 1882) in Rudolph (1995); and *Melicertus kerathurus* (Forskål, 1775) in Heegaard (1971)]. In several protandric caridean species, all individuals of the population mature first as males and then become females as they increase in size and age, e.g., *Pandalopsis dispar* Rathbun, 1902; *Pandalus platyceros* Brandt, 1851; *Pandalus hypsinotus* Brandt, 1851; *Pandalus goniurus* Stimpson, 1860 (Butler, 1964, 1980) (Fig. 1B). However, there are life history variations on this simple case of obligatory sex change (Fig. 1C–E). In one such variation, most individuals are protandric, but primary females are present in the population, as demonstrated in *Processa edulis* (Risso, 1816) by Noël (1976) (Fig. 1C). This mixture of life histories has also been reported in *Crangon crangon* (Linnaeus, 1758) by Boddeke *et al.* (1991) and is indicated in the crangonid *Argis dentata* (Rathbun, 1902) from the work of Fréchette *et al.* (1970). Protandry has been rather well-documented in the caridean family Pandalidae (e.g., Butler, 1964, 1980) in which 12 of the 31 protandric caridean species are found. In several species of *Pandalus*, some variable portion (< 50%) of the population either go through a brief, nonfunctional male-phase before maturing into the female-phase ("early maturing females") or mature directly into females (Fig. 1D). It is still not clear whether these latter are "primary females," i.e., genetic females as in gonochoristic species; whether they are the same genotype as protandric individuals but in which the male-phase is repressed completely by environmental (social) control, as indicated by the work of Charnov *et al.* (1978) and Charnov (1981); or whether there is a mixture of genotypes involved (Bergström, 1997).

Another permutation in protandry (Fig. 1E) was first indicated by Chace (1972) and then fully described by Bauer (1986) in the hippolytid *Thor manningi* Chace 1972, a species named for Raymond B. Manning, the honoree of the symposium for which this paper was written. In this species, half of the population is composed of primary males, i.e., individuals which remain small, have hypertrophied male appendices and prehensile third pereiopods. The rest of the population are protandric hermaphrodites, with individuals first exhibiting relatively small male appendices, non-prehensile third pereiopods, and gonads which produce sperm conducted via vasa deferentia terminating in typical male ejaculatory ducts. With increasing size (age), the male characters diminish and are lost completely at the molt at which the gonad is first full of vitellogenic oocytes, at which time the first mating and spawning as a female occurs. However, *Thor dobkini* Chace, 1972, and *T. floridanus* Kingsley, 1878, which occur in shallow-water seagrass habitats like those inhabited by *T. manningi*, are completely gonochoristic (Bauer and VanHoy, 1996). A situation somewhat similar to that of *T. manningi* occurs in the alpheids *Athanas kominatoensis* Kubo, 1942, and *A. indicus* (Nakashima, 1987; Gherardi and Calloni, 1993) except that the primary males grow as large or larger than female-phase hermaphrodites.

A major unsolved question about protandric hermaphroditism in carideans has to do with the original sexual genotype of hermaphroditic individuals: Are they male or female? Resolution of this issue will be important in understanding the evolution of protandry in its various forms and simultaneous hermaphroditism in *Lysmata* (see below). Given the relative rarity of hermaphroditism in the Decapoda, it is reasonable to assume that gonochorism, or separate sexes, is ancestral. Hoffman (1972) proposed that, in *Pandalus platyceros*, the hermaphroditic genotype arose in females. In studies on gonad histology, he found that oogenesis occurred before spermatogenesis in immature shrimps. Primary spermatocytes were unusually large for a caridean, and Hoffman proposed that they were oocytes masculinized into spermatocytes by secretions of the androgenic (male) gland, the anlage of which occurs both in male and female decapods and other malacostracans. On the other hand, Charniaux-Cotton and Payen (1985) postulated that protandry in pandalids evolved in male genotypes by an early degeneration of the androgenic gland, which produces male hormone in malacostracans, allowing later maturation as female. However, in populations of the hippolytid *Thor manningi*, Bauer (1986) found that the population consisted of 50% primary males, 49% protandric hermaphrodites, and a very few primary females which did not go through a male-phase. He argued that protandry must have evolved in primary females of a gonochoristic ancestor of *T. manningi*, given the "size-advantage" hypothesis of Ghiselin (1969), amplified by Warner (1975). According to this hypothesis, in species in which male reproductive advantage is greater at small size and female reproductive advantage is higher at

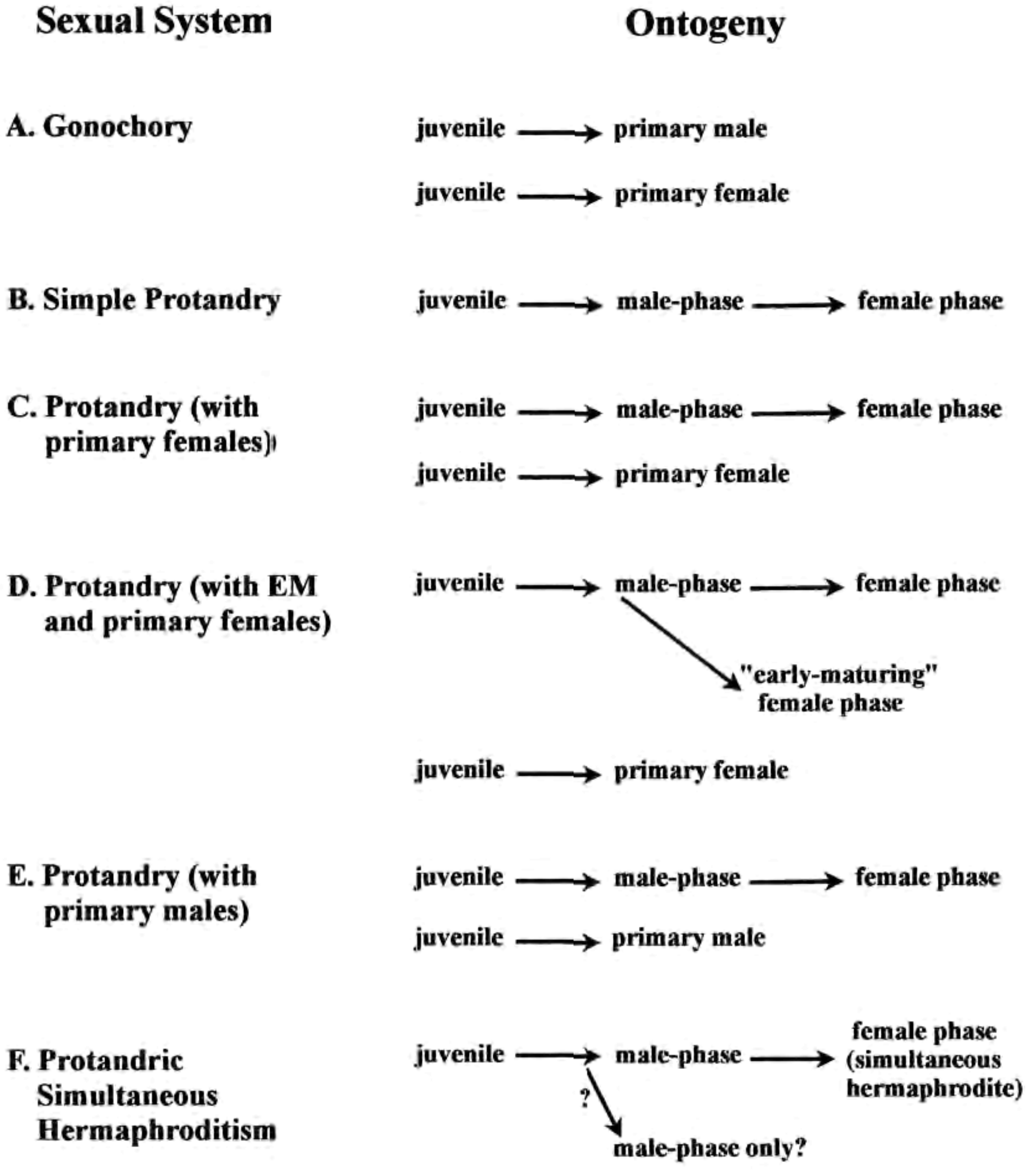

Fig. 1. Ontogeny of sexual morphs in gonochoristic and hermaphroditic reproductive systems described in the Caridea.

larger body sizes, selection for protandry can occur. Large size is advantageous to females because egg production shows a high positive correlation with body size in carideans and other decapods (Jensen, 1958; Bauer, 1991). Since sperm production takes so little energy compared to egg production in decapods, small male size is advantageous when the mating system does not involve precopulatory mate guarding, in which large males have an advantage. In many gonochoristic caridean taxa with small males and larger females, males do not guard females, instead expending energy in searching for and contacting many females in order to meet and mate with a receptive one ("pure searching" mating tactic, Wickler and Seibt, 1981; see Bauer, 1996). Small males are also more cryptic than the larger females, and thus have an advantage in avoiding detection by predators and, additionally, put less energy into growth. A female caridean, however, must grow to a greater size in order to produce the large, energetically-expensive, vitellogenic oocytes. They must grow through a size range at which males can produce sperm and reproduce. Development of a male-phase during this juvenile female growth period would certainly be adaptive, even if successful reproduction during the male-phase occurs only once. Thus, evolution of protandric individuals from genetic females seems plausible.

However, arguments for evolution of protandric individuals from genetic males, as proposed by Charniaux-Cotton and Payen (1985), based on premature degeneration of the male androgenic glands and subsequent maturation as females, are also persuasive. Given the flexibility of sex determination in malacostracans (Rigaud *et al.*, 1997), the two hypotheses are not exclusive; in some caridean species, protandry may have developed from genetic females, but in others from genetic males. If there were recognizable sex chromosomes in carideans, and control of sex was strictly under the genes on heterochromosomes, it might be possible to karyotype different sexual morphs to answer questions about the original sexual genotype of protandric individuals. Unfortunately, heteromorphic sex chromosomes are rare or recognized with difficulty in the Decapoda (Nakamura *et al.*, 1988; Lécher *et al.*, 1995). Even if heterogametic karyotypes could be perceived, sex determination in crustaceans is usually not a simple matter of sex genes located on dimorphic chromosomes (see below).

The questions posed above might be solved when the mechanisms of sex determination are well understood in gonochoristic species with hermaphroditic relatives. Unfortunately, little progress on the control of sex determination by genetic, environmental, or cytoplasmically-inherited factors has been made in the Decapoda, unlike that accomplished in peracarids (Legrand *et al.*, 1987; Rigaud *et al.*, 1997). Charniaux-Cotton, along with various colleagues, made pioneering efforts in this field with amphipods and in the caridean shrimp *Lysmata seticaudata* (Risso, 1816), considered a species with protandric hermaphroditism. Masculinization of females and feminization of males by implantation and extraction of the male androgenic glands, respectively, have shown the important role of these glands in sex determination of amphipods (Charniaux-Cotton, 1965, 1975). Similar results, however, have not been obtained in gonochoristic decapods (Charniaux-Cotton and Payen, 1985). A generalization that may be made for malacostracans is that an allele of a male gene, promoting development of the androgenic gland, is a key in sex determination. In the absence of the allele or its inhibition by a female gene, the androgenic gland does not develop and individuals are female, the "default" sex. All individuals of malacostracan crustaceans thus have the potential to differentiate as males or females (Charniaux-Cotton and Payen, 1985). All individuals appear to have the embryonic rudiments for the androgenic glands, and the gonads may become either testes or ovaries, depending on the presence or absence of androgenic hormone. Studies on the genetic control of metabolic pathways leading to male or female development ("genetic architecture," Marin and Baker, 1998) need to be resolved in order to determine the sexual genotype in which sex change evolved in gonochoristic ancestors of hermaphroditic carideans.

FUNCTIONAL SIMULTANEOUS HERMAPHRODITISM IN *LYSMATA*

The sexual system of shrimps in the hippolytid genus *Lysmata* has been described as protandric hermaphroditism by investigators during most of this century. Spitschakoff (1912) described the gonads of *Lysmata seticaudata*. Individuals of all sizes had paired ovotestes which showed ovarian characteristics anteriorly but testicular features posteriorly, with two pairs of ducts corresponding to oviducts and sperm ducts (vasa deferentia). In younger (smaller) individuals, the relative size of the testicular portion of these ovotestes was about equal to that of the ovarian portion. In larger individuals reproducing as females, the ovarian portion became greatly enlarged. Spitschakoff concluded that individuals of *L. seticaudata* were protandric hermaphrodites, first acting as males and then changing sex to female with increasing size and age. However, he noted and illustrated that the "females" retained a small testicular portion of the gonad, complete with vasa deferentia. Although the relative size of the testicular portion was quite small compared to that of the ovarian portion in these females, its absolute size remained about that of the male-phase, when the individual was smaller in body size.

Dohrn (1950) examined the reproductive biology of *Lysmata seticaudata* from samples of a population taken throughout the year. He found younger (smaller) individuals with male secondary characteristics, with larger (older) individuals serving as breeding females. He also concluded that this species is a sex-changer. Like Spitschakoff, he found ovotestes in individuals of all sizes, without disappearance of the testicular portion or male ducts during the female-phase. Berreur-Bonnenfant and Charniaux-Cotton (1965) studied the histology of the gonads of *Pandalus borealis* Krøyer, 1838, and *L. seticaudata* in both male- and female-phase individuals. In both species, both spermatogenesis and oogenesis occurred in the gonads of male-phase individuals, although oocytes did not progress past primary vitellogenesis (Charniaux-Cotton and Payen, 1985). After sex change, spermatogenesis ceased in *P. borealis* and only vestiges of male ducts remained. On the other hand, in *L. seticaudata* spermatogenesis and sperm production continued, although less actively, in the testicular part of the ovotestes, and the male ducts were retained (Berreur-Bonnenfant and Charniaux-Cotton, 1965). However, the possibility that such sperm-producing "females" might be able to mate as males was not addressed.

The first published report on simultaneous hermaphroditism in a caridean was that of Kagwade (1982) on *Exhippolysmata ensirostris* (Kemp, 1914), a member of a genus taxonomically close to *Lysmata* (Chace, 1972). Male ducts and sperm, as well as male sexual appendices on the pleopods, were found in "females." Kagwade concluded, based on this morphological evidence, that these individuals were simultaneous hermaphrodites. However, no mating experiments were performed to confirm this view, which was opposed by Sukumaran (1982), who supported the view of strict protandry. From this time until 1998, an unpublished thesis, abstracts from scientific meetings, unconfirmed statements in the literature, and anecdotal observations in aquarium magazines strongly indicated simultaneous hermaphroditism in the female-phase of some *Lysmata* spp. (see Bauer and Holt, 1998).

Recently, two studies have confirmed simultaneous hermaphroditism in "females" of two species of *Lysmata*. Fiedler (1998) followed 4 pairs of female-phase individuals (FPs) of *L. amboinensis*, an Indo-Pacific species, through cycles of molting and spawning, until each shrimp spawned clutches of viable embryos. Two pairs were separated and followed as isolated individuals; although they continued to spawn, eggs were inviable and were discarded. Individuals of the remaining two pairs continued to spawn eggs which developed as embryos. Copulation between FPs was observed twice by Fiedler, who presented histological evidence confirming the presence of vitellogenic oocytes and sperm in the same gonad (ovotestes).

Bauer and Holt (1998) studied the population structure and reproductive morphology of *Lysmata wurdemanni* from the Gulf of Mexico. They observed copulation between female-phase individuals in 17 pairs recorded with time-lapse video and evidence of successful mating (viable spawns) in five others. In this species, the smaller individuals are male-phase (MP), with typical male appendices masculinae on endopods of the second pleopods, cincinnuli (coupling hooks) on endopods of the first pleopods (a male character), and ovotestes with both male and female ducts, similar to that illustrated for *L. seticaudata* by Spitschakoff (1912) and Berreur-Bonnenfant and Charniaux-Cotton (1965), and illustrated here for *Lysmata californica* (Stimpson, 1866) (Fig. 2A–E). Female-phase individuals, i.e., those carrying broods of developing embryos, lacked appendices masculinae (Fig. 2I), although vestiges could be observed in some individuals, and cincinnuli on pleopod 1 were absent (Fig. 2H). However, the gonad of these individuals, as described in *L. seticaudata* and shown here for *L. californica* (Fig. 2F, G), had a distinct testicular portion with vasa deferentia, in addition to an anterior ovarian portion, distended with vitellogenic oocytes as spawning approached. The vasa deferentia led to fully developed, typical male ejaculatory ducts which opened to the outside via gonopores on the coxae of the fifth pereiopods (8th thoracic segment, as in all malacostracan males). Material squeezed from the ejaculatory ducts of FPs, including those incubating embryos, contained typical caridean sperm cells in *L. wurdemanni*. There were a few medium-sized

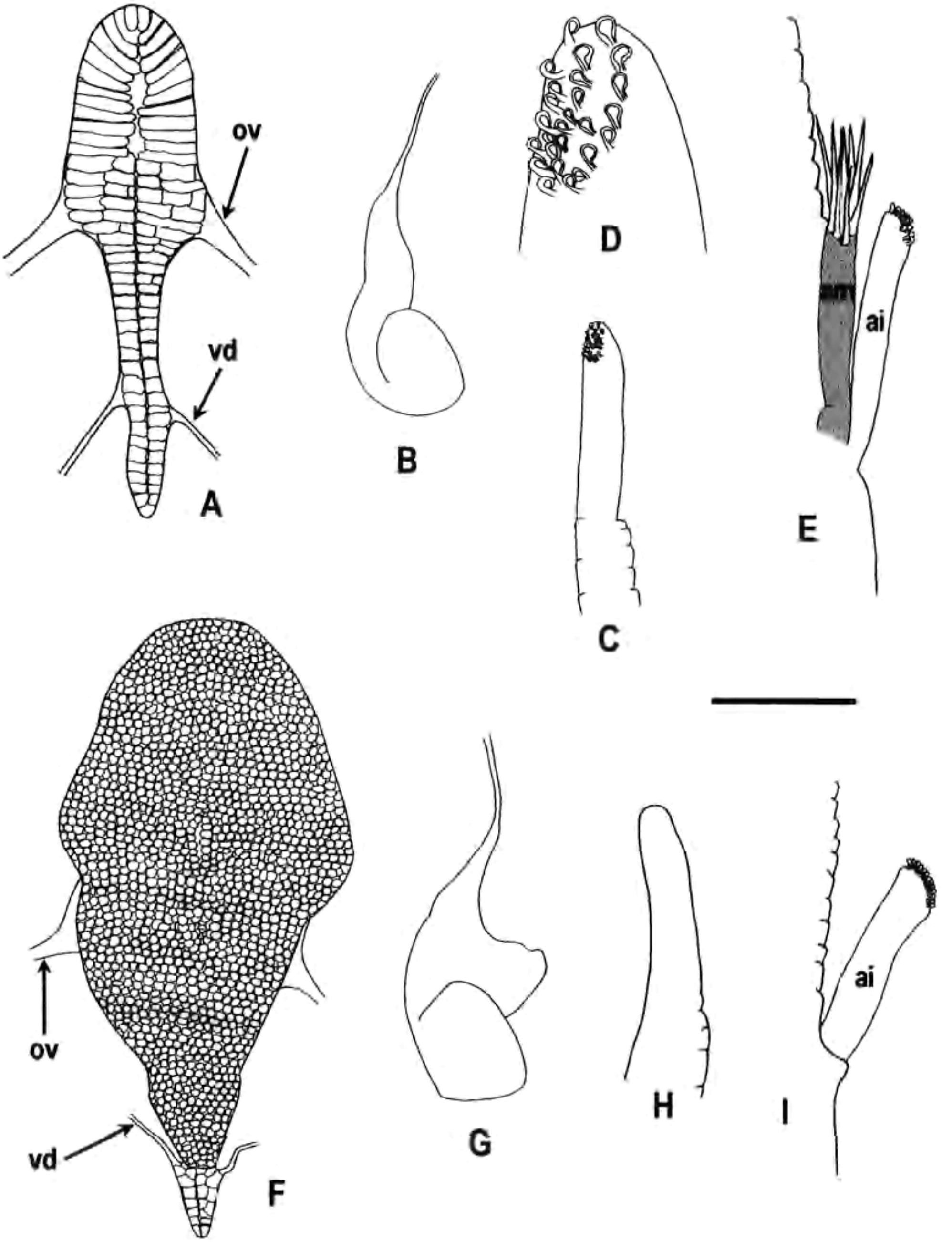

Fig. 2. *Lysmata californica*, gonads and other sexual characters in a male-phase (MP) individual 11.3 mm carapace length (CL) (A–E) and in an ovigerous (embryo-incubating) female-phase (FP) individual 21.2 mm CL (F–I). A, MP gonad, with oviducts (ov) and vasa deferentia (vd); B, MP ejaculatory duct; C, tip of endopod of MP pleopod 1, with cincinnuli (coupling hooks) illustrated in greater detail in D; E, medial border of endopod of MP pleopod 2, with appendix masculina (am, shaded) and appendix interna (ai); F, FP gonad with large anterior ovarian part distended by vitellogenic oocytes, distinct from smaller posterior testicular part from which vasa deferentia (vd) extend; ov, oviducts. G, FP ejaculatory duct; H, tip of endopod of FP pleopod 1, completely lacking cincinnuli; I, medial border of FP pleopod 2, equipped only with appendix interna (ai). Scale bar represents 1.5 mm in A, 2.7 mm in B, 590 µm in C, 120 µm in D, 650 µm in E, 4.4 mm in F, 2.9 mm in G, 1.2 mm in H, and 1.4 mm in I.

Table 1. Emerging patterns of association among sexual system, social organization, fish-cleaning behavior, and biogeographic distribution in *Lysmata* species. Details and supporting references given in text. PSH = protandric simultaneous hermaphroditism.

Species	Sexual system	Social organization of breeding adults	Fish-cleaning behavior	Biogeographic distribution
L. seticaudata	protandry or PSH?	"crowds"	unspecialized	warm temperate
L. nilita	protandry or PSH?	?	?	warm temperate
L. wurdemanni	PSH	"crowds"	unspecialized	tropical, warm temperate
L. californica	protandry or PSH?	"crowds"	unspecialized	warm temperate
L. amboinensis	PSH	pairs at low density	specialized	tropical
L. grabhami	protandry or PSH?	pairs at low density	specialized	tropical
L. debelius	PSH	?	specialized?	tropical

to larger individuals with typical male appendices but in which the ovarian portions of the ovotestes were full of large vitellogenic oocytes. It was proposed that these "transitionals" would mate and spawn as FPs just after the next molt, when male appendices would be lost.

Mating experiments were conducted in which only FPs which had spawned at least once as "females" were used (Bauer and Holt, 1998). After the molt of a prespawning FP (an individual with ovotestes distended by vitellogenic ooctyes), the other FP of the pair usually mated as a male with the molter. Successful broods were produced in the majority of these matings. In two pairs, both FPs were near spawning when paired; both subsequently molted and spawned on the same evening within a few hours of each other. In both cases, each FP served as a male mating partner when the other molted but copulated as a female after molting itself. The broods produced by these reciprocal matings were all viable. However, prespawning FPs maintained in isolation spawned, but their broods were not viable, i.e., self-fertilization did not take place.

Thus, a FP of *L. wurdemanni* may function as male and female within the space of a few hours, i.e., they are outcrossing functional simultaneous hermaphrodites. Individuals first develop into a male-phase and then are capable of "changing sex" or entering a female-phase with both male and female function (Fig. 1F). This sexual system might be termed "protandric cosexuality," following a suggestion in Policansky (1982); however, I prefer the more obvious "protandric simultaneous hermaphroditism" (PSH).

In the population sampled by Bauer and Holt (1998), the considerable overlap in size between MPs and FPs indicated that many MPs do not make the change from MP to FP, although all are morphologically capable of it. Alternatively, the change to FP may be delayed in some MPs until they are much older (larger) than the minimum size at which such change in sexual type can take place.

Thus, in both *L. wurdemanni* and *L. amboinensis*, mating experiments have confirmed male reproductive capability in FPs. Other species of *Lysmata* with similar ovotestes are likely to have a comparable sexual system (Table 1). The presence of ovotestes in all individuals and retention of male ducts has been well-documented in the *L. seticaudata* (above) and reported by Dohrn and Holthuis (1950) in *Lysmata nilita* Dohrn and Holthuis, 1950. Preliminary observations reported in this paper reveal similar ovotestes in male- and female-phase individuals in *L. californica* from southern California (Fig. 2); *Lysmata grabhami* (Gordon, 1935) from the Atlantic appears to have a similar reproductive morphology (personal observation by author reported in Wirtz, 1997). Preliminary observations by Fletcher *et al.* (1995) and Simoes *et al.* (1998) have indicated simultaneous hermaphroditism in the Indo-Pacific *Lysmata debelius* Bruce, 1983 as well (Table 1). Based on these observations, it seems that this unusual sexual system is widespread in the genus *Lysmata*, which has at least 24 species (Chace, 1997). It may well occur in species of *Exhippolysmata*, given Kagwade's (1982) report on ovotestes and male ducts in female-phase individuals in *E. ensirostris*. Certainly, other genera closely related to *Lysmata* should be investigated in this regard.

COSTS AND BENEFITS OF PROTANDRIC SIMULTANEOUS HERMAPHRODITISM

Given the increase in reproductive fitness to an individual which can function simultaneously as male and female, it is puzzling that simultaneous hermaphroditism has not evolved more frequently in carideans. Phylogenetic constraints on evolution of PSH should not be readily invoked since protandry, the first step to PSH, has evolved in various caridean families. The necessary genetic potential and developmental flexibility necessary for PSH seems to be present in the various species of sex-changing carideans. Why has not PSH evolved more frequently in the Caridea? The answer to this question may lie in the reproductive costs and benefits of maintaining male sexual capacity after change to the female-phase. Actual measurement of reproductive costs and benefits may also help to explain the broader question of why there are not more species with simple protandry among the Caridea, especially those species with small males and larger females.

Gains and losses in the number of offspring produced are the most direct measures of the benefits and costs of male and female function. In species with simple protandry, the smaller MP is capable of emitting several spermatophores in a short period of time, i.e., is capable of fertilizing broods of eggs from several females with a day or two (benefit). However, there is competition from other MPs for any sexually receptive FPs (cost). When switching to an FP, an individual gives up the possibility of fertilizing several broods in a short time (cost) for producing one to only several batches of eggs over the rest of its lifetime. However, all of these broods will normally be assured of fertilization (benefit), because the ratio of MPs to receptive FPs is so high. In *Lysmata* species with PSH, such as *L. wurdemanni*, an individual changing to an FP does not give up male function and resulting offspring, which is presumably the reproductive gain which explains the evolution of PSH. However, it is not known how much benefit male function really is in this group. When an FP becomes receptive to mating as a female after a pre-spawning molt, are MPs and FPs (acting as males) equally competitive in fertilizing the receptive FP? Experiments need to be conducted to determine the comparative mating success of MPs and FPs (acting as males). If MPs are better male mating partners than FPs, or if larger MPs are better than smaller MPs, it might be advantageous in some demographic situations (abundant FPs) for an individual to remain as an MP for a longer period or not to change to FP at all. The variable size of sex change in *L. wurdemanni* and the presence of large MPs indicates that this indeed may take place in this species. Thus, the increase in reproductive fitness gained by an individual which retains male function as an FP may easily be outweighed by the possibly low effectiveness of the FP as a male mating partner. In addition, the behavioral and physiological costs of maleness may detract from the number and size of broods an FP produces.

In addition to costs and benefits measured directly in numbers of offspring produced, what behavioral and physiological costs of sex change and retention of male-function in the female- phase might be measured in order to determine their magnitude and importance? In *L. wurdemanni* and other *Lysmata* species which occur in aggregations, the mating system appears to be a "pure searching" (Wickler and Seibt, 1981), similar to that of protandric species and gonochoristic species with small males and larger adult females. In this mating system, males do not guard females, but instead constantly search among the population for receptive females. The costs may be those of exposure to predation and the energy involved in searching. The FPs with male function may reduce their output as females because of such costs. On the other hand, in *L. grabhami*, which appear to have PSH (Table 1), FPs occur in pairs (Wirtz, 1997). It is not known whether members of the pair must guard against or compete with intraspecific intruders such as MPs and unpaired FPs which might come to mate when one of the pair is receptive as a female. If so, this would be a cost of maintaining male function in the female phase.

At least some of the morphological and energetic costs of sex change and retention of male reproductive function might be estimated or measured directly to help explain the evolution of PSH and protandric sexual systems in the Caridea. Morphometric analyses on sexual characters might be used to make approximations of the energetic costs of male or female function. For example, the relative sizes of the ejaculatory ducts with sperm in MPs and FPs of *L. wurdemanni* are nearly identical (Fig. 3A), indicating that the cost these structures to FPs is considerable (maintenance of previously formed ejaculatory duct, plus new growth, plus costs of new

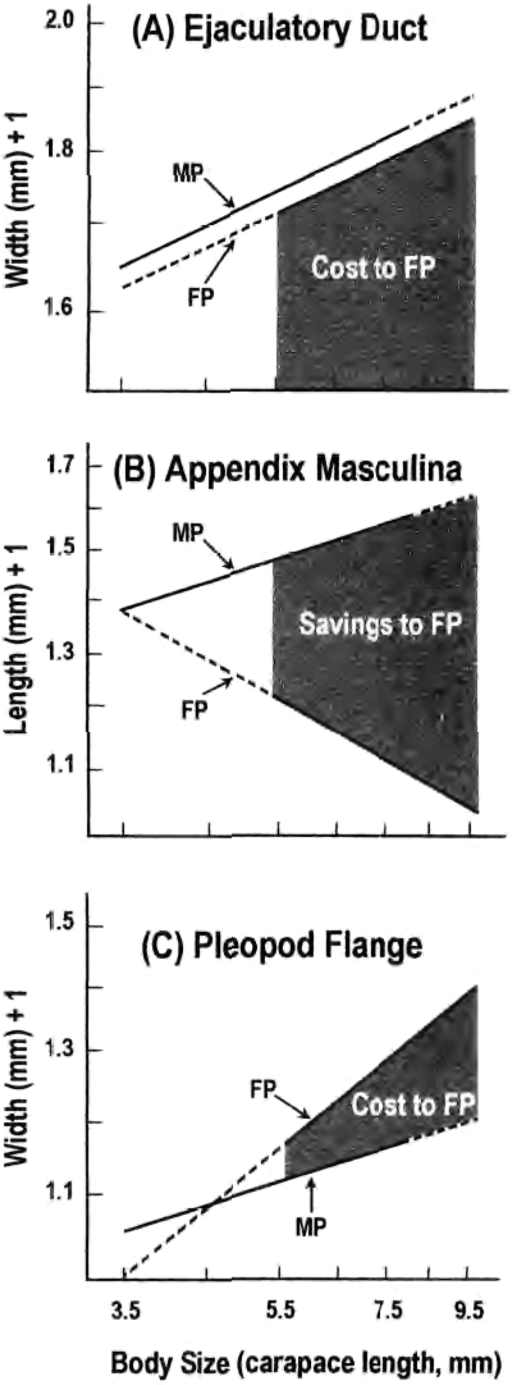

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Fig. 3. Diagrammatic representation of some of the morphological costs and benefits of sex change from a male-phase (MP) to a female-phase hermaphrodite (FP) in *Lysmata wurdemanni*, based on data given in Bauer and Holt (1998). Regression lines are calculated from allometric growth equations of the form $\log (Y + 1) = \beta \log X + \log \alpha$ where β = slope; α = Y-intercept; Y = ejaculatory duct width in (A), appendix masculina length in (B), and pleopod flange width in (C); X = body size (carapace length), with all measurements in millimeters (mm). The solid part of each line represents the size range of MP and FP individuals on which measurements were taken, and the dotted line is an extrapolation of the regression line beyond that size range. Shaded areas represent the morphological costs or savings to an individual which changes from an MP to an FP.

sperm and spermatophore material). A male feature, the appendix masculina on the second pleopods, is greatly reduced or absent in the female-phase, and savings in this "cost" to the female-phase might be indicated by the difference between allometric growth regression lines for MPs and FPs (Fig. 3B). Although the appendix masculina is small in size, the physiological and energetic costs of producing it at each molt could be quite high (e.g., underlying complex of hormones and associated biochemistry necessary for its formation), although these costs are as yet unknown. A cost of "femaleness," the relative increase in size of flanges on the pleopods, related to embryo incubation, might be similarly estimated (Fig. 3C). Direct measures of the energy content of male ducts and the testicular portion of the ovotestes might be made calorimetrically and compared between MP and FP individuals, using allometric growth regression equations as in Fig. 3, to estimate of the physiological costs of maleness. Energetic measures of the ovarian portion of the ovotestes might be compared between MPs and FPs. The hepatopancreas is an important organ in storage of reserves used for production of the energetically-expensive eggs in female decapods, as shown by Kyomo (1988) for the brachyuran *Sesarmops intermedium* (de Haan, 1835). The energy content of this organ should be included as part of a measure of the costs of femaleness. The physiological expense of maleness versus femaleness in MP and FP morphs in *Lysmata* species with PSH could be compared to that in protandric or gonochoristic *Lysmata* spp., if the latter two systems do exist in the genus. Such costs might also be measured in gonochoristic and protandric species of other carideans, not only to understand the evolution of PSH in *Lysmata* but also the evolution of sex change (protandry) in the Caridea.

SOCIO-ECOLOGICAL ATTRIBUTES AND SEXUAL SYSTEMS IN *LYSMATA* SPECIES

Although *Lysmata* spp. appear to possess the same unusual hermaphroditic reproductive biology, their social organization and ecology may differ greatly. There appears to be two groups of *Lysmata* spp. in terms of socialty, fish-cleaning behavior, and biogeographical distribution (Table 1). In "crowd" species (*L. seticaudata*, *L. wurdemanni*, and *L. californica*), individuals occur in aggregations at high density, especially in rocky crevices and caves over hard or heterogeneous bottom habitats. Dohrn (1950) collected rather large numbers of *L. seticaudata* in his seasonal samples, indicating high density, and Patzner (1982) reported *L. seticaudata* occurring in groups in shallow-water caves with moray eels. Aggregations of *L. californica*, composed of dozens to hundreds of individuals, can be observed in subtidal caves, often in association with morays (Limbaugh *et al.,* 1961; personal observation). *Lysmata wurdemanni* can occur in large numbers, with several individuals in small tidepools or captured in a single sweep of a dipnet from partially submerged boulders in the intertidal (Bauer and Holt, 1998). In aquaria, individuals of all sizes cluster closely together under rocks and stones (personal observation). On the other hand, breeding adults of *L. amboinensis* and *L. grabhami* occur in pairs in nature, usually in association with sea anemones (Limbaugh *et al.,* 1961; Criales and Corredor, 1977; Criales, 1979; Wirtz, 1997). Wirtz (1997) has shown that these pairs are composed of female-phase hermaphrodites in *L. grabhami*. Little is known about the juveniles and smaller adults (presumably male-phase). Anecdotal reports of aggregations of *L. amboinensis* (Debelius, 1984) may be referring to such individuals. However, this designation of *Lysmata* spp. into "crowd" vs. "paired" species needs to be verified with more information on the species discussed above.

"Crowd" species tend to have a warm-temperate distribution. *Lysmata seticaudata* is a Mediterranean species which extends north to the coast of France and southward to the Canary and Madeira Islands (Dohrn, 1950; Chace, 1997; Wirtz, 1997). *Lysmata californica* extends from southern California in the eastern Pacific down along the Baja California Peninsula (Chace, 1997). The distribution of *L. wurdemanni* ranges in the Western Atlantic from Virginia to Brazil, including the Gulf of Mexico and Caribbean (Williams, 1984; Chace, 1997), so that it may be characterized as warm-temperate/tropical. The "low density pairs" species are tropical: *L. amboinensis* and *L. debelius* in the Indo-Pacific, *L. grabhami* in the Western Atlantic (Chace, 1997), although the latter is abundant in the subtropical Madeira and Canary Islands as well (Wirtz, 1997).

Lysmata shrimps are facultative or obligate fish "cleaners" that have been observed on the bodies of fishes, nipping and tugging on mucus, dead skin, and possibly parasites (Limbaugh *et al.,* 1961). Although there is some controversy as to exactly what takes place during this interaction with fishes (Poulin and Grutter, 1996; Spotte, 1996), there is no doubt that such an interaction does take place. Species reported here as living in pairs (Table 1) are considered specialized fish cleaners in which the relationship with fishes is highly evolved. *Lysmata grabhami* and *L. amboinensis* have conspicuous coloration and behavioral displays, such as antennal lashing and body swaying, which appear to attract diurnally active fish "clients" which respond with submissive behaviors and allow the shrimps to mount and pick at their bodies (Limbaugh *et al.,* 1961). Fish-cleaning behavior also occurs in "crowd" species but it is not as highly developed (Limbaugh *et al.,* 1961; Patzner 1982). Both *L. seticaudata* and *L. californica* occur with and pick at the bodies of moray eels and, in the case of *L. californica*, other fishes, as well as invertebrates such as spiny lobsters (Limbaugh *et al.,* 1961). There have been anecdotal reports of fish-cleaning behavior in *L. wurdemanni* (reported in Williams, 1984) and these shrimps, similar to other "cleaner" *Lysmata* shrimps, will seek out the fingers of an observer inserted into an aquarium, and pick and tug at dead skin and other material beneath fingernails (personal observation). None of these "crowd" species have conspicuous coloration as in specialized *Lysmata* cleaners, nor do they perform displays before mounting fish clients, which do not respond in highly stereotyped fashion. Crowd species (facultative fish cleaners) are most active at night (*L. californica*, Limbaugh *et al.* (1961); *L. seticaudata*, Dohrn, 1950; *L. wurdemanni*, personal observation), whereas specialized fish cleaners are active during the day. Limbaugh *et al.* (1961) considered *L. californica* to have an "imperfect" cleaning symbiosis with morays, because morays eat these shrimps, unlike fish clients cleaned by specialized cleaner shrimps. Additionally, fish cleaning appears to be but one food source, not necessarily the main one. In this primitive cleaning relationship, the shrimp is simply using the body of a cooperative fish as a substrate upon which to graze.

EVOLUTION OF PROTANDRIC SIMULTANEOUS HERMAPHRODITISM IN *LYSMATA*

What kinds of environmental conditions and demographic factors might have generated the selective pressures leading to the evolution of PSH in *Lysmata*? Scarcity of mating partners due to low population abundance is a selective pressure that may have led to simultaneous hermaphroditism in many invertebrate groups ("low density model," Ghiselin, 1969). One scenario that might be proposed using this hypothesis is that evolution of PSH took place in a protandric tropical *Lysmata* species that became a specialized fish cleaner, commensal with anemones. Wirtz (1997) has reported that if an individual of *L. grabhami* is separated from the shelter of its host anemone, it is quickly attacked by surrounding fishes. Although protection from the anemone is beneficial, restriction of the shrimp on or near its host reduces mobility, and in a species occurring at low densities, further reduces the probability of encountering a mating partner. Certainly, if both individuals of a pair were simultaneous hermaphrodites, the reproductive fitness of both would be enhanced over that of MP-FP pairs in a protandric species or male-female pairs of a gonochoristic species.

Under this scenario, the more ecologically generalized warm-temperate "crowd" species would have evolved from specialized tropical ones. The retention of PSH under the different ecological conditions and higher population abundances of the "crowd" species is not difficult to envision. There should be no selection against such a reproductively advantageous system, once evolved, provided its "cost" is not too high. However, most protandric carideans occur in high density groups, such as commercially-fished pandalids and crangonids, so that an ancestral protandric *Lysmata* species occurring in low density pairs and associated with anemones, required by this scenario, seems a bit unlikley. Additionally, the unspecialized fish-cleaning behavior of crowd species would have to be derived from the specialized fish-cleaning behavior of tropical "pairs" species such as *L. amboinensis* and *L. grabhami*, which seems improbable.

Alternatively, the evolutionary origin of PSH in a protandric "crowd" species might be considered. However, this seems quite unlikely, given the abundance of male-phase mating partners for female-phase individuals in species which live in high-density groups. There is no apparent selection pressure favoring simultaneous hermaphroditism under such circumstances. On the other hand, *Lysmata* spp. which form aggregations appear closer to the ancestral condition in terms of social organization and in their facultative, unspecialized fish cleaning behavior.

These evolutionary scenarios, examples of or attempts at "just-so stories" (Gould and Lewontin, 1979; Thornhill and Alcock, 1983), are proposed as preliminary hypotheses from which to consider the evolution of PSH in *Lysmata* and possibly other caridean taxa (e.g., *Exhippolysmata*). The reproductive biology of only 7 of 24 *Lysmata* spp. has been reported. The socio-ecological attributes and population biology of unstudied and understudied *Lysmata* spp. need to be described. A phylogeny of *Lysmata* species, based on morphological and molecular characters, must be constructed so that character states of features of interest, such as sexual system, social structure, ecological characteristics, distribution, etc., can be in displayed on a phylogenetic tree. The direction of evolution in these characters can then be analyzed, and points in the phylogeny at which probable advanced character states arose, such as PSH, pair-living, and specialized fish cleaning behavior, can be identified.

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