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Experimental test of socially mediated sex change in a protandric simultaneous hermaphrodite, the marine shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae)

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Abstract In *Lysmata wurdemanni*, individuals begin benthic life in a male phase (MP) but later change to a female phase (FP) with female external morphology, but with both male and female reproductive capacity (protandric simultaneous hermaphroditism). Previous studies have demonstrated that the size (timing) of sex change varies considerably in natural populations. We experimentally tested for social mediation of sex change by rearing male-phase individuals (MPs) in both large and small social groups with different sexual and size composition. In the “large group” experiment, speed of sex change was inversely related to the abundance of female-phase individuals (FPs) in the group (sex-ratio induction). Increased allocation to female function (more rapid change to FP) may occur when male mating opportunities are lower because the simultaneous-hermaphrodite FP can immediately reproduce as a female while maintaining male mating capacity. When FPs are abundant, delayed sex change might be adaptive because the costs of female reproduction are considerable. An MP may gain reproductively by increased growth before changing to FP at a larger size (fewer but much larger broods). Size-ratio induction of sex change by small MPs was suggested but not confirmed. Experimental results from “small groups” (1–2 individuals) were qualitatively similar but not as conclusive as those from large groups. The number and complexity of social interactions in large groups may be necessary to stimulate labile sex change in this species. In *L. wurdemanni*, sex change may be influenced not only by abiotic factors related to breeding [Bauer (2002) Biol Bull 203:347–357] but also by social factors in certain demographic situations.

Keywords Hermaphroditism · Sex allocation theory · Sex change · Sex determination · Social mediation

Introduction

Many marine invertebrates and fishes are sequential hermaphrodites, first developing as one sex before later changing to the other (Ghiselin 1969; Charnov 1982; Policansky 1982; Chan and Yeung 1983; Bauer 2000). Among decapod crustaceans, hermaphroditism is mainly found in caridean shrimps and is protandric (male to female sex change) (Bauer 2000). The direction of sex change in carideans is rather well explained by sex-allocation theory, particularly the size-advantage model (Ghiselin 1969; Warner 1975). In caridean species in which males do not guard females, male reproductive fitness does not increase with increasing size (age) but female fecundity does, as in all carideans (Bauer and Abdalla 2001). Thus, it is not surprising that protandry has evolved in approximately 40 species (Bauer 2000).

The time spent as one sex before change to the other in sequential hermaphrodites is a form of sex allocation, an adaptive response of considerable interest in hermaphrodites that are strictly sequential (e.g., protandric pandalid shrimps: Charnov 1982; protogynous and protandric fishes: Chan and Yeung 1983; Shapiro 1987; Warner 1988), simultaneous (e.g., a serranid fish: Petersen and Fischer 1996; a cestode worm: Schärer et al. 2001), or sequential-simultaneous (e.g., a polychaete worm: Sella 1990; a gobiid fish: St. Mary 1997). Studies on a variety of marine invertebrates and fishes have shown that timing of sex change may be socially mediated (e.g., the gastropods *Crepidula norrisiarum*, Warner et al. 1996, and *Coralliophila violacea*, Chen et al. 1998; fishes, e.g., Fishelson 1970, Robertson 1972; Fricke and Fricke 1977; Chan and Yeung 1983; Nemtsov 1985; Ross 1990; Warner and Swearer 1991). Evidence from size–frequency distributions of fished populations of protandric pandalid carideans suggested that labile sex change was presumably mediated by social interactions in different

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demographic situations (“environmental sex determination” or ESD, Charnov et al. 1978; Charnov 1981, 1982; Charnov and Anderson 1989). However, socially mediated change in pandalid shrimps has not been empirically demonstrated (Marliave et al. 1993; Bergström 1997, 2000).

Recently, a variation of caridean protandry, protandric simultaneous hermaphroditism (PSH) (Bauer 2000), has been described in the shrimp genus *Lysmata* (Caridea: Hippolytidae) (Bauer and Holt 1998; Fiedler 1998; Bauer 2000; Bauer and Newman 2004). In purely protandric carideans, individuals mature sexually first as “males” (male-phase individuals=MPs) with typical caridean male sexual characters. Later in life, MPs change into “females” (female-phase individuals=FPs), with typical caridean female morphology and reproductive behavior (Bauer 2000). In *Lysmata* spp., individuals also develop first as MPs before changing into typical female external morphology. However, unlike purely protandric carideans, the female-phase individuals retain testicular tissue, sperm production, male ducts and gonopores. These female-like individuals can and do mate as both male and female (Bauer and Holt 1998; Fiedler 1998; Bauer 2002a; Bauer and Newman 2004) and thus are functional simultaneous hermaphrodites. Individuals in this female-like phase are termed FPs, as in Bauer and Holt (1998), Bauer (2000, 2002a, 2002b) and Baldwin and Bauer (2003), because they are developmentally analogous (and probably homologous) to FPs of purely protandric carideans. Unlike some sequential/simultaneous hermaphrodites (e.g., gobiid fish *Lythrypnus* spp., St. Mary 1994, 1996), sex change occurs only once, i.e., FPs do not revert back to MP (Bauer 2002a).

The basic reproductive biology of the “red cleaning” or “peppermint” shrimp *Lysmata wurdemanni* from the Gulf of Mexico was described by Bauer and Holt (1998), Bauer (2002a, 2002b), and Baldwin and Bauer (2003). FPs go through successive cycles of vitellogenesis, molting, mating (as female), spawning, brood incubation and hatching. FPs can mate as a male at any time, but copulation with another FP is not reciprocal, i.e., a newly molted prespawning FP copulates as a female, with the other FP serving as male. Adhesive spermatophoric masses are attached to the underside of the prespawning FP by its male mating partner (either an MP or FP) during the single copulation lasting few to several seconds. Sperm from a mating is used to fertilize only the spawning that occurs about 2 h later; there is no long-term sperm storage. FPs do not fertilize themselves. Thus, FPs are outcrossing simultaneous hermaphrodites, while MPs only mate as males. In this species, in which individuals occur in loose aggregations in rocky bottom marine habitats, there are no obvious precopulatory behaviors or interactions, although potential male mating partners do appear to recognize a prespawning FP about an hour before its molt (Bauer 2002a). No aggressive interactions among potential male mating partners are apparent, similar to the caridean *Palaemonetes pugio* (Bauer and Abdalla 2001) and unlike carideans in which

males defend and guard females (e.g., *Macrobrachium rosenbergii*, Ra’anan and Sagi 1985; alpheid shrimps, e.g., Schein 1975; Nakashima 1987).

In this report, *L. wurdemanni* serves as a model system to examine social control of sex change. Studies on its population biology (Bauer 2002b; Baldwin and Bauer 2003) show that the size of MP to FP change is variable. Bauer (2000, 2002a) proposed that delayed sex change might be reproductively advantageous under certain demographic situations (e.g., abundant FPs in the population). If large MPs (delayed sex changers) were better at male mating than the simultaneous-hermaphrodite FPs, a longer period as MP might be adaptive. However, extensive laboratory mating experiments showed that MPs, large or small, are no more successful than FPs (mating as males) in inseminating prespawning FPs. Furthermore, it was observed that large MPs (delayed sex changers) were more frequent in the autumn and winter than in the spring and summer (Bauer 2002a, 2002b; Baldwin and Bauer 2003). In the laboratory, MPs changed to FPs more slowly when maintained under suboptimal (autumn/winter) than under optimal (spring/summer) breeding conditions. Abiotic factors related to breeding were thus suggested as an explanation for the delayed sex change in MPs reaching potential sex-change size in the autumn (Bauer 2002a). On the other hand, limited experiments by Lin and Zhang (2001) demonstrated some social influence on sex change.

In this study, we directly tested the hypothesis of social mediation of sex change in *L. wurdemanni* with experiments on the rate of sex change in different demographic environments. Hypotheses about size-ratio and sex-ratio induction of sex change (Ross 1990) were tested by rearing MP sex-change candidates within large and small social groups composed of conspecifics of different sexual composition and body size.

Methods

Collection and maintenance of shrimps

Individuals of *L. wurdemanni* were collected from the rock jetty at Port Aransas, Tex. (27°50’N, 97°03’W) and rock groins at Galveston, Tex. (29°18’N, 94°47’W) between June and August, 2002. Specimens were collected with long-handled dipnets under rock ledges during low tides (below zero mean sea level) and at night, when the habitat was accessible and shrimps became active, respectively. After collection, specimens were placed in sealed large plastic bags containing oxygenated seawater for transportation to the aquatics laboratory at the University of Louisiana at Lafayette (ULL). In the laboratory, individuals were maintained prior to experiments in 114 l recirculating aquaria at a water temperature of 24°C, 34–35 ppt salinity, a 14:10-h light:dark cycle and were fed daily (1/2 food pellet per shrimp, Wardley Shrimp Pellets). Partial change of aquarium water and removal of obvious wastes and debris was done weekly.

Experiment on social mediation of sex change in “large groups”

The null hypothesis of no social mediation of sex change was tested in large social groups ($n=10$ individuals) maintained in 38 l aquaria

Table 1 Mortality of focal male-phase individuals (*MPs*) in the large-group experiment. Given for each treatment is the percentage of replicates with focal-*MP* mortality, the mean (*c*) frequency \pm

Treatment	% Replicates	$c \pm SD$	Min., max.	<i>n</i>
5 focal <i>MPs</i> + 5 <i>MPs</i>	20.0	0.20 \pm 0.41	0, 1	15
5 focal <i>MPs</i> + 5 <i>FPs</i>	33.3	0.47 \pm 0.64	0, 2	15
5 focal <i>MPs</i> + 4 <i>MPs</i> + 1 <i>FP</i>	20.0	0.20 \pm 0.41	0, 1	15
5 focal <i>MPs</i> + 5 small <i>MPs</i>	6.7	0.13 \pm 0.52	0, 2	15
All replicates	21.7	0.25 \pm 0.51	0–2	60

under similar environmental conditions (except for a higher water temperature of 26–28°C), feeding, and aquarium maintenance as described above. Each aquarium contained a rectangular piece of concrete block, approximately 10 \times 20 \times 2 cm, which served as a shelter and perch. Male-phase individuals are capable of changing to the simultaneous-hermaphrodite *FP* at 6 mm carapace length (CL), and a majority do so by 8 mm CL (Baldwin and Bauer 2003). Accordingly, we considered *MPs* of 6–8 mm CL as sex-change candidates (termed here “*MP* candidates”). In each replicate of this experiment, we measured the time to sex change in five *MP* candidates (“focal *MPs*”) reared with five other conspecifics. To examine the effect of the sexual and body-size composition of groups on sex change, the experiment was composed of four treatments in which five focal *MPs* were maintained either with: (1) five nonfocal *MPs* in the same size range as the focal *MPs* or (2) five *FPs* (incubating embryos at the beginning of the experiment) or (3) four nonfocal *MPs* in the same size range as the focal *MPs* plus one *FP* incubating embryos or (4) five nonfocal *MPs* smaller (<6.0 mm CL) than focal *MPs*. A total of 15 replicates per treatment were conducted using a total of 300 focal *MPs*, 210 nonfocal *MPs* and 90 *FPs*. Nonfocal individuals were identified and distinguished from focal *MPs* by a colored elastomer tag injected into their abdominal musculature (Northwest Marine Technology, USA; Godin et al. 1996). The CL of focal *MPs* was measured just prior to the start of the experiment. Carapace length is the standard measure of body size in carideans and is defined as the distance from the posterior edge of the eye orbit to the mid-dorsal posterior edge of the carapace (Bauer and Holt 1998). There was no significant differences among treatments in mean CL of focal *MPs* (one-way ANOVA, $F_{3,56}=1.7$, $P=0.171$). The duration of the experiment was 50 days, a time period permitting up to several molts at which a candidate may change sex (Bauer and Holt 1998; Bauer 2002a; Baldwin and Bauer 2003).

Observations on sex change of focal *MPs* were recorded daily. Focal *MPs* that changed sex were removed from aquaria and replaced by nonfocal *MP* candidates. This procedure provided similar social conditions (composition of groups) in replicates. Any nonfocal *MP* in treatments 1, 3, and 4 that became “transitional” (presence of vitellogenic oocytes in the gonads signaling sex change at the next molt) was immediately removed and replaced by a *MP* of similar size. Any nonfocal individual found dead was replaced by another nonfocal individual of similar size and sexual phase. Focal *MPs* missing or found dead during the first 2 weeks were replaced by other focal *MPs*. However, after 2 weeks, focal *MPs* missing or dead were replaced by nonfocal *MPs*. We presumed that social conditions differentially affected *MPs* placed later in the experimental aquaria compared to *MPs* at the beginning or early in the experiment. The mortality of focal *MPs*, chiefly by conspecific predation on newly molted individuals, is shown in Table 1. There was no significant difference among treatments in the total number of dead or missing focal *MPs* per replicate (one-way ANOVA, $F_{3,57}=1.3$, $P=0.288$).

Comparisons in the timing of sex change of *MP* candidates (focal *MPs*) were made among treatments with a modified version of Cox’s maximum partial likelihood regression (Lee et al. 1992), a survival analysis technique. For each focal *MP*, the time from the start of the experiment until change to the female phase was measured during a period of 50 days. Also included in the analysis as right-censored data points were those focal *MPs* that suffered

standard deviation (*SD*), and the minimum (*min.*) and maximum (*max.*) number of focal *MPs* dying per replicate. Female-phase individuals is denoted by *FPs* and *n* is the number of replicates

mortality before sex change (time from start of experiment to death) and those that never changed sex (50 days) (Lee et al. 1992). Curves were plotted for each treatment using estimates of the proportion of focal *MPs* remaining as *MPs* (not changing sex to *FP*) using procedure PHREG as implemented in SAS (SAS Institute, 2001). We tested the null hypothesis of no difference in “sex-change” curves among treatments by testing for homogeneity of treatment curves with the Wald chi-square method (Allison 1995). Upon rejecting homogeneity of curves, unplanned comparisons between pairs of curves were conducted using the Wald chi-square method adjusting for the standard alpha level of 0.05 with the sequential Bonferroni correction (Rice 1989). The sequential Bonferroni correction was chosen over the standard Bonferroni correction because the former has been shown to be more powerful (Rice 1989).

In survival analysis, failure-time observations on members of the same group (replicate) are considered correlated (dependent) (Lee et al. 1992). Likewise, in this study, the sex-change measurements (failure-time observations) on focal *MPs* in the same aquarium (replicate) were not treated as independent. The possible dependence among failure-time observations was included in the modified Cox’s regression analysis by clustering failure-time observations of focal *MPs* from the same aquarium. In addition, we employed the COVSANDWICH option of PHREG to test for homogeneity of sex-change curves because it generates robust standard errors for nonindependent observations (Lee et al. 1992).

Experiment on social mediation of sex change in “small groups”

In this experiment, the null hypothesis of no social mediation of sex change was also tested. Our rationale for this experiment, in which focal *MPs* were reared alone or with one other individual of different size and sexual phase, was two-fold. First, we tested for sex-ratio and size-ratio induction in an environment in which the number and complexity of possible social interactions, such as competition for food or dominance/subordination, were reduced by the small group size. Secondly, with this group size, we could examine the effect of male mating opportunity (which could be measured in this experiment) on the speed of sex change. In four treatments, a single sex-change candidate (focal *MP*) was reared (1) with one nonfocal *MP* of similar size, or (2) one *FP* incubating embryos, or (3) alone, or (4) with one nonfocal *MP* smaller (<6.0 mm CL) than the focal *MP*. The treatment with a solitary *MP* candidate (3) was included to observe a “default” sex change, i.e., speed of *MP* to *FP* change in the absence of other individuals. Replicates of these four treatments were conducted in 5 l plastic buckets with a plastic mesh for shelter and were maintained under similar environmental conditions and feeding regimes as in the large-group experiment. A total of 20 replicates per treatment were conducted using 80 focal *MPs*, 40 nonfocal *MPs*, and 20 *FPs*. There was no significant difference among treatments in the body size (CL) of focal *MPs* (one-way ANOVA, $F_{3,76}=1.2$, $P=0.316$).

Observations of focal *MP* sex change, replacement of dead or missing individuals, marking of nonfocal individuals were the same as in the large-group experiment. Only one focal *MP* (a replicate with another *FP*) suffered mortality during the experiment. The experiment terminated after all *MP* candidates had changed sex (63 days).

As in the large-group experiment, the Cox maximum partial likelihood regression was used for the analysis of sex-change measurements on focal MPs. However, in contrast to the first experiment, each failure-time observation was independent because there was only one focal MP in each replicate. Therefore, we employed the default COVS option of PHREG (Allison 1995).

Reproductive condition (prespawning molt and brood production) of FPs in treatment 2 was recorded throughout to determine if and how frequently mating opportunities were available to focal MPs (with possible effect on speed of sex change).

Results

Experiment on social mediation of sex change in large groups

The proportion of focal MPs (MP candidates) not changing sex to FPs over time is plotted for each treatment (Fig. 1). Qualitatively, the curves show a gradient of more rapid sex change in treatments in which 5 focal MPs were maintained with: (1) 5 small MPs > (2) 5 MPs > (3) 1 FP+4 MPs > (4) 5 FPs (Fig. 1). The hypothesis of no difference in sex-change curves among treatments was rejected (Wald chi-square test, $\chi^2_1=19.99$, $P<0.001$). Focal MPs reared with 5 small MPs changed significantly faster than focal MPs reared in the treatments with either 1 FP+4 MPs (a posteriori Wald chi-square test, $\chi^2_1=6.27$, $P=0.0123$; sequential Bonferroni $\alpha=0.0125$) or with 5 FPs ($\chi^2_1=20.98$, $P=0.0001$, $\alpha=0.0083$). Focal MPs reared with 5 other MPs of similar size changed more quickly than focal MPs reared with 5 FPs ($\chi^2_1=10.12$, $P=0.0015$; $\alpha=0.01$) but not more quickly than focal MPs reared with 1 FP+4 MPs ($\chi^2_1=0.8$, $P=0.3708$, $\alpha=0.0125$). Sex change in the two treatments in which focal MPs were reared with 5 small MPs or 5 MPs of similar size was not significantly different

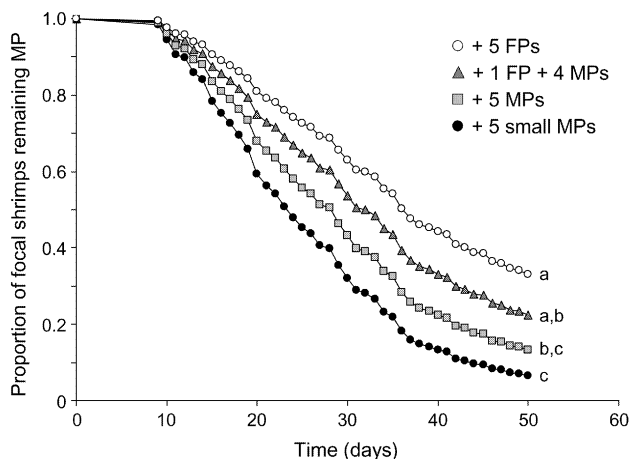


Fig. 1 “Large group” sex-change experiment. Curves denote the proportion of male-phase (MP) candidates (focal shrimps) not changing to female-phase (FP) individuals over time (days). Points on curves were estimated for each treatment with a modified Cox’s maximum partial likelihood regression method (see Methods for details). Treatment curves labeled with different letters are significantly different ($P<$ sequential Bonferroni α)

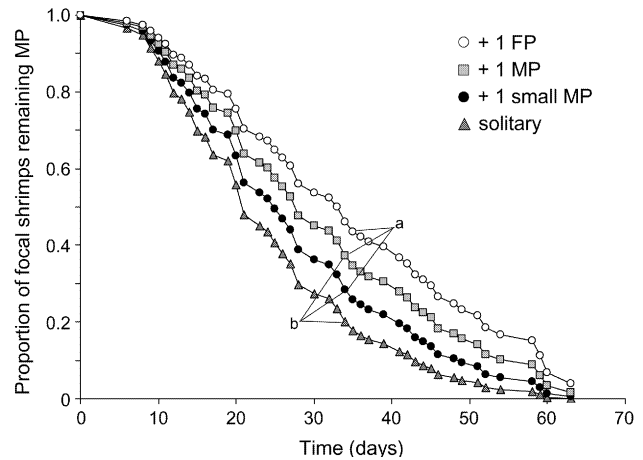


Fig. 2 “Small group” sex-change experiment. Curves denote the proportion of male-phase (MP) candidates (focal shrimps) not changing to female-phase (FP) individuals over time (days). Points on curves were estimated for each treatment with Cox’s maximum partial likelihood regression method (see Methods for details). Treatment curves labeled with different letters are significantly different ($P<$ sequential Bonferroni α)

($\chi^2_1=3.27$, $P=0.0707$; $\alpha=0.0125$). Similarly, there was no significant difference between the sex-change curves of the treatments in which focal MPs were reared with 1 FP+4 MPs or 5 FPs ($\chi^2_1=3.43$, $P=0.0639$; $\alpha=0.0125$).

Experiment on social mediation of sex change in small groups

The proportion of focal MPs (MP candidates) not changing sex to FPs over time is plotted for each treatment (Fig. 2). The curves show a qualitative gradient with more rapid sex change in treatments in which single focal MPs were maintained (1) alone > (2) with 1 small MP > with 1 MP > (4) with 1 FP. The hypothesis of no difference in sex-change curves among treatments was rejected (Wald chi-square test, $\chi^2_1=6.13$, $P=0.0133$) (Fig. 2). Focal MPs reared in isolation changed sex more quickly than those reared with 1 FP (a posteriori Wald chi-square test, $\chi^2_1=7.37$, $P=0.0066$; $\alpha=0.0083$). However, no other significant differences among treatments were found ($P>0.05$ in all cases).

In replicates of one treatment, a focal MP was maintained with an FP. Female-phase individuals went through spawning cycles, so that focal MPs could reproduce (mate as males). Eighteen of 19 focal MPs in this treatment inseminated the FP at least once, but most frequently three times (median=3; minimum=0, maximum=5) before changing sex to FP.

Discussion

In the large-group experiment, social environment affected the timing of sex change from the MP to the

simultaneous-hermaphrodite FP in the shrimp *L. wurdemanni*. Sex-change candidates changed more quickly in groups with fewer FPs, with the most rapid change in all-MP groups. Allocation to female function, in terms of time spent with female reproductive capacity, was lowest when MP candidates were reared in an environment with abundant FPs. However, in *L. wurdemanni*, an FP can mate as a male as successfully as an MP (Bauer 2002a) while also reproducing as a female. Why do MPs not change as quickly as morphologically possible to FP no matter what the social environment?

The adaptive advantage to rapid change is obvious in all-MP groups because there are no opportunities for mating, given the lack of FPs. An individual changing to FP as quickly as possible will reproduce immediately as female, while still retaining the capacity to mate as a male if the demographic environment changes. In groups with FPs, an MP candidate has opportunities to mate as a male, although there will be competition from other MPs as well as the hermaphroditic FPs. However, there are obvious and considerable energetic costs in the change from MP to FP. There is extensive change in the external morphology in body proportions and setation related to the female functions of spawning and embryo incubation (the "breeding dress," Höglund 1943). Production of the large yolky caridean eggs is a considerable energetic expense (Spaargaren and Haefner 1994). In caridean females, fecundity (brood size) varies with the cube of carapace length (Jensen 1958), and thus there is a significant increase in brood size with female size (Bauer 1991; Corey and Reid 1991; Calado and Narciso 2003 for *L. seticaudata*). By delaying sex change in an environment with FPs (mating opportunities present), an MP might channel energy into faster growth so that when it does change, it is a larger FP with greater fecundity. Having fewer but much larger broods as a larger FP would enhance the overall reproductive fitness of the individual. We believe that the stimulus, perceived perhaps by the number and kind of interactions with other members of an MP candidate's group, is the relative number of FPs and MPs in the group. This is sex-ratio induction of sex change (Ross 1990).

The rearing of sex-change candidates in small groups, that is, with one other individual (small MP, or another candidate MP, or an FP) or alone ("group" of one MP), allows some evaluation of group effects on social mediation of sex change. Our rationale was that sex allocation, in terms of time spent in the male phase versus the simultaneous-hermaphrodite female phase, might be more apparent in the small group environment because a much lower number and complexity of social interactions would occur in groups with just one (solitary MP candidate) or just two individuals (other three treatments). The overall trend in the sex-change curves is qualitatively similar to that of the large-group experiment. However, the results are statistically less conclusive. MP candidates reared individually with a single FP changed to the simultaneous-hermaphrodite female phase more slowly than MP candidates reared alone. This result might be

interpreted in terms of opportunities for reproduction, which, unlike the large-group experiments, were measured directly in the small-group experiments. MP candidates reared with an FP did reproduce (mated as male, inseminated broods) while the solitary MPs could not. It would make adaptive sense for a single MP (e.g., an MP in a low density situation) to change to FP as quickly as possible so that it could mate, as male or female, with the first other individual that it would meet within the environment. An MP reared with a single FP can reproduce, and, like MPs reared with FPs in the large-group experiment, might delay sex change in order to grow larger before changing to FP. However, although there were no reproductive opportunities in the two all-MP treatments, sex change of focal MPs in these treatments was not significantly faster than those reared with a single FP.

In both the large-group and small-group experiments, two treatments were designed to test size-ratio induction of sex change. In one all-MP treatment, focal (candidate) MPs were reared with small MPs, i.e., individuals too small to change sex. In the other all-MP treatment, focal MPs were reared with MPs of similar size. In both experiments, sex-change curves on focal MPs qualitatively indicated more rapid sex change in the treatment with small MPs. Although the hypothesis of no difference between these two treatments could not be rejected in either treatment, the same trend in both experiments is suggestive of size-ratio induction. If size-ratio induction does occur in *L. wurdemanni*, what might be its adaptive value? In the natural habitat of this shrimp, groups composed of small MPs and candidate MPs may occur in the spring, when the first major recruitment of the year occurs and when overwintering FPs have become rare or absent (Bauer 2002b; Baldwin and Bauer 2003). The presence of small MPs may be an additional and seasonal stimulus (a social signal) that FPs are rare or absent in the population, inducing rapid sex change in the candidate MP (size-ratio induction, as in some sequentially hermaphroditic fishes, Ross 1990).

An alternative explanation for the result indicating size-ratio induction in the experiments is that competition for food and space was responsible for the qualitatively more rapid change of candidate MPs reared with small MPs. Total food input was the same in both all-MP treatments, but in the treatment with small MPs, candidate MPs might have, by virtue of their larger size, been able to garner more food and better shelter, the latter perhaps important in molting. Similarly, sex change of MP candidates may have been slowed in treatments with FPs, producing apparent sex-ratio induction, if FPs were more competitive for food and shelter, a possibility that needs to be investigated.

The less conclusive results from the small-group experiment suggest that the numerous and complex interactions of large groups are necessary stimuli for expression of adaptive sex-change responses. A posteriori, perhaps it was to be expected, in this gregarious shrimp species, that adaptive responses in labile sex

change and sex allocation would be best expressed in the more natural setting of a large group. A sex-change candidate may require interactions with multiple individuals to “measure” the sex ratio and allocation potential of its environment.

Finally, we suggest that variability in the size (age) of sex change in *L. wurdemanni* may be influenced by both abiotic (Bauer 2002a) and biotic (social) factors. The size and sexual composition of groups (Raimondi and Martin 1991; Schärer and Wedekind 2001; Schärer and Ladurner 2003), the temporal stability of groups in nature, the degree of interchange of individuals among groups (“permeability,” Ross 1990), and the specific social interactions among individuals within groups must be analyzed to understand more completely the role of socially mediated sex change in *L. wurdemanni* and related species.

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