

Cost of maleness on brood production in the shrimp *Lysmata wurdemanni* (Decapoda: Caridea: Hippolytidae), a protandric simultaneous hermaphrodite

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Individuals of *Lysmata wurdemanni* first mature in a male phase (MP) and then change to the external phenotype of females (female-phase=FP). The FPs retain the male gonadal system and function both as male and female (simultaneous hermaphrodites). The cost of maleness to FPs on fecundity was estimated with an experiment in which the social environment (FP opportunity to function as a male) was varied. The effect of maleness on brood size (number of embryos brood⁻¹) and frequency of spawning (interspawn interval in days) was measured in FPs maintained in different social environments (treatments) over two complete spawning cycles. In treatment 1 (isolated FP) and 2 (1 FP, 1 MP), FPs could only function as females. In treatments 3 (2 FPs) and 4 (5 FPs, 5 MPs), FPs could breed both as male and female.

Baseline brood size was described for FPs with a regression equation of brood size on FP body size (carapace length). Brood size is positively and isometrically related to FP size. Brood sizes, adjusted for FP body size using the baseline regression equation, were compared among treatments 2–4 (isolated FPs in treatment 1 did not produce fertile broods). Brood sizes were significantly greater in FPs in treatment 2 (only female breeding) than in treatments 3 and 4 (both male and female sexual function possible). However, spawning was less frequent (longer interspawn intervals) in treatments 1 and 2 than in treatments 3 and 4. Total fecundity over a four-month breeding period was estimated with a model using mean treatment brood sizes and interspawn intervals. Estimates of total fecundity in FPs functioning both as male and female were much lower, in spite of somewhat more frequent spawning, than those in which male function was not allowed. The ‘price’ (cost) of maleness on fecundity appears to be compensated by the high selective advantage of male mating ability in the simultaneous hermaphrodite FPs of *Lysmata* species.

INTRODUCTION

During part of its life, the marine caridean shrimp *Lysmata wurdemanni* (Gibbes, 1850) is a functional simultaneous hermaphrodite, an unusual reproductive system for a decapod crustacean. Hermaphroditism is rare in the Decapoda (e.g. shrimps, crayfish, lobsters, crabs). However, there are at least 40 species, mainly caridean shrimps, in which functional hermaphroditism has been demonstrated (Bauer, 2000). Most hermaphroditic caridean shrimps are protandric sex changers that first function as males (male-phase=MP) before changing to females (female-phase=FP) (Bauer, 2000, 2004).

Recently, simultaneous hermaphroditism has been documented and investigated in the hippolytid caridean genus *Lysmata* (Bauer & Holt, 1998; Fiedler, 1998; Bauer, 2000, 2002a,b; Lin & Zhang, 2001; Baldwin & Bauer, 2003; Udekem d’Acoz, 2003; Baeza & Bauer, 2004; Bauer & Newman, 2004). In *Lysmata* spp., individuals first function sexually as males (MPs) and then when larger (older) moult into a female-phase. Female-phase individuals have an external phenotype typical, except for male gonopores, of a caridean female, without male sexual appendices and with the caridean female ‘breeding dress’ (Bauer, 2004). Although *Lysmata* FPs spawn eggs and brood embryos, they produce sperm in the ovotestes, mate as males, and can non-reciprocally inseminate newly moulted

prespawning (receptive) FPs copulating as females. To date, self-insemination has not been demonstrated (Bauer & Holt, 1998; Fiedler, 1998; Bauer & Newman, 2004). Thus, FPs of *Lysmata* spp. are functional outcrossing simultaneous hermaphrodites. Although other terminology has been reasonably applied to the simultaneous hermaphrodite FPs of *Lysmata* spp. (Lin & Zhang, 2001; Calado & Narciso, 2003), the use of ‘FP’ is preferred here because the FP of *Lysmata* has the external phenotype of a caridean female and incubates the embryos. It is developmentally analogous and probably homologous with the FPs of purely protandric species (Bauer, 2000).

Bauer (2000) termed the sexual system of *Lysmata* ‘protandric simultaneous hermaphroditism’ (PSH) because there is a functional male phase before the simultaneous hermaphrodite female phase. He proposed that PSH has evolved in *Lysmata* from a protandric ancestor by retention of the male ducts and gonopores after sex change instead of the complete loss of the male system, which occurs in purely protandric shrimps (Bauer, 2000).

Why is PSH or even complete simultaneous hermaphroditism not more common in caridean shrimps? The PSH of *Lysmata* spp. appears to bestow a very high reproductive fitness on FPs compared with females of gonochoristic species or the FPs of purely protandric species, which can only breed as females. In *L. wurdemanni*, competitive mating experiments between MPs and FPs mating as

males showed that FPs are just as capable as MPs in copulating with and inseminating prespawning FPs (Bauer, 2002a). The benefit of male function to FPs of *Lysmata* spp. is clear. However, is there a significant cost to maleness, physiological or behavioural, that accounts for the apparent rarity of simultaneous hermaphroditism in caridean shrimps? The FPs must expend at least some metabolic energy on male ducts and sperm as do MPs. In addition, FPs acting as males pursue receptive FPs and compete, at least indirectly, with other MPs and FPs seeking to mate (as males) with the same receptive FP. Thus, both the physiological and behavioural costs of maleness may detract from the energy put into female function (fecundity) measured in terms of size of broods (number of embryos) and frequency of brood production.

The purpose of this study was to test the hypothesis that male function has a significant cost to female fecundity in the simultaneously hermaphroditic FPs of *Lysmata wurdemanni*. The prediction was that FPs allowed to function as males would have lower brood production than those that could not. This prediction was tested with an experiment in which male-mating opportunity of FPs was varied among treatments.

MATERIALS AND METHODS

Field sampling

Live specimens of the shrimp *Lysmata wurdemanni* were collected with dipnets at night during spring and summer 2001 at the rock jetty at Mustang Island, Port Aransas, Texas (27°50'N 97°03'W). Shrimps were maintained at the University of Louisiana at Lafayette (ULL) aquatics laboratory in aquaria and water tables with recirculating seawater. As in Bauer (2002a), shrimps were maintained before and during experiments at water temperatures of 25–28°C, salinities of 33–36 ppt, and a 14 h:10 h day–night photoperiod. Shrimps were fed daily with Wardley® Shrimp Pellets (1/2 pellet individual⁻¹, 0.06–0.08 g pellet⁻¹).

Analysis of brood size with FP body size

Baseline variation in brood size (number of embryos incubated) with FP body size was measured. Thirty FPs with embryos in early stages of development (Bauer, 1991) were selected at random from population samples reported in Bauer (2002b). Body size was measured as carapace length (CL) as in Bauer & Holt (1998). All embryos were removed from below the abdomen and counted.

A simple linear regression of brood size (number of embryos brood⁻¹) on FP body size (carapace length = CL) was calculated for the baseline brood measures as well as for experimental treatments 2–4. Additionally, an allometric analysis of brood size on FP carapace length was performed using log-transformed measures (Bauer, 1991). Brood size, measured as number of embryos, approximates a volume measure (Bauer, 1991). In allometric analysis with log-transformed measures, where y is a volume and x is a linear measure, a slope of 3 indicates isometry, significantly >3 positive allometry, and significantly <3 negative allometry (Gould, 1966; Bauer, 1991).

Experiment on the effect of male function on FP brood production

The null hypothesis in this experiment was that there is no effect of FP male-mating opportunity on FP fecundity (brood production). The prediction tested was that the size and number of broods produced by the hermaphroditic FPs do not vary with their opportunity to function as males. The alternative hypothesis is that FPs not allowed to mate as males will produce a greater number of embryos per brood and/or a greater number of broods than FPs that have the opportunity to act as males.

Female-phase individuals of *Lysmata wurdemanni* usually produce successive broods, as do FPs of many purely protandric carideans or females of gonochoristic species. The interspawn interval is defined as the number of days from one spawning to the next. Brood size (the number of embryos FP brood⁻¹) and frequency of brood production (interspawn interval in days) were measured in focal FPs maintained in four treatments: (1) a single FP; (2) 1 FP, 1 MP (male-phase individual); (3) 2 FPs; (4) a group of 5 FPs and 5 MPs. In treatments 1 and 2, FPs could only reproduce as females, while in treatments 3 and 4, they could produce broods as females and also interact and mate as males. In treatment 1, only interspawn interval could be measured because isolated FPs can not mate and do not self-inseminate; after spawning, the unfertilized eggs are either not attached or are attached briefly and then are lost within a day (Bauer & Holt, 1998).

Because sufficient FPs were not available from collecting to begin all treatments simultaneously, individual treatments were set up when sufficient FPs were obtained. The experiment was conducted in 38-l aquaria with recirculating seawater. For treatments 1–3, the aquaria were divided by perforated partitions into five compartments, each with 1 FP in treatment 1, 1 FP and 1 MP in treatment 2, and 2 FPs in treatment 3. For treatment 4, there was no subdivision of the aquaria in which 5 FPs and 5 MPs were placed. Only data for FPs that survived through two full interspawn intervals were used in the analysis. Mortality, especially during moulting, and the failure of some FPs to go through two interspawn intervals during the time course of the experiment, led to final sample size of N=27 in treatment 1, N=30 in treatment 2, and N=29 in treatment 4. For treatment 3, data from 30 focal FPs that completed the experiment were selected at random so that sample size was similar to that of other treatments for statistical analyses. In treatments 3 and 4, FPs had to be identified individually using internal coloured elastomer tags (Baldwin & Bauer, 2003); FPs of treatments 1 and 2 were similarly tagged for experimental consistency.

Observations on focal FPs were made on a daily basis: degree of ovarian maturation in the ovotestes, prespawning moult (exuvium present), and presence/absence of embryos. All FPs began the experiment with a brood of previously spawned embryos. The first interspawn interval began after this initial brood hatched and the FP moulted and spawned. The FPs that spawned unsuccessfully were identified by an empty gonad and an absence of embryos. The FPs were followed through two complete interspawn intervals. After their third spawning, FPs were removed, anaesthetized by chilling, preserved in seawater–formalin, and later washed with water before storage in 70% ethanol. Those MPs that changed sex or died during the

experiment were replaced. In treatment 3, where only a pair of FPs were present, any FP that died was replaced with another so that the remaining FP could have a male-mating opportunity as planned in this treatment.

RESULTS

Baseline brood size

In a sample from a natural population, fecundity of female-phase individuals (FP) increased with body size (Figure 1). The relationship of brood size with FP size is described by the linear regression equation $y=448.3x-2750.8$ where y =the number of embryos brood⁻¹ and x is FP carapace length (CL in mm) ($R^2=0.82$, $F_{1,28}=126.5$, P of nonsignificant regression <0.001). Allometry of brood size with FP sized was analysed by calculating the regression equation of log transformed brood size on log CL values ($\log y=3.16x-0.05$; $R^2=0.87$; $F_{1,28}=189$, $P<0.001$). With 95% confidence limits of 2.69 and 3.6, the slope of 3.16 was not significantly different from 3.0, the slope of no allometry (isometry) when y is a volume (or an approximation of a volume) and x is a linear measure (Gould, 1966; Bauer, 1991).

Comparison of brood size among experimental treatments

Brood sizes from final (third) spawnings of treatments 2 (1 FP, 1 MP), 3 (2 FPs) and 4 (5 FPs and 5 MPs) were compared (Figure 2); treatment 1 (1 FP) was not included because isolated FPs spawn but do not brood the unfertilized eggs. There was much variation in brood size within treatments; a simple linear regression of brood size on FP CL was not significant (P of $\beta=0$) in treatments 2 ($F_{1,28}=3.3$, $P=0.08$) and 3 ($F_{1,28}=2.48$, $P=0.11$) but was in treatment 4 ($F_{1,27}=6.9$, $P=0.01$). An analysis of covariance (ANCOVA), using log transformed (brood size + 1) and CL values, was attempted to compare brood sizes among treatments 2–4. However, the assumption of similarity (homogeneity) of slopes was not met ($F_{2,83}=3.4$, P of equal $\beta=0.036$).

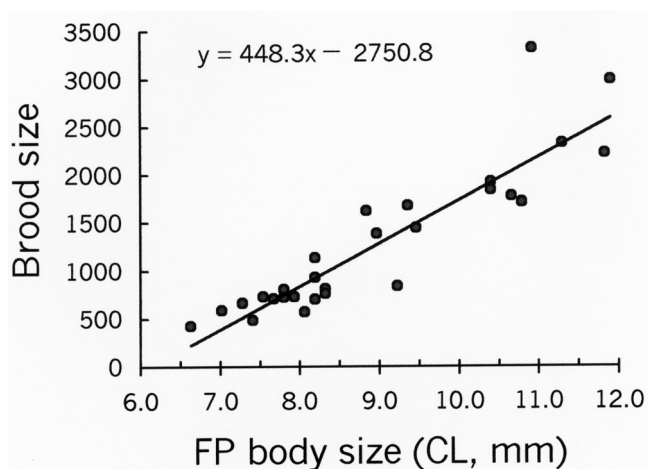


Figure 1. Variation of brood size (number of embryos brood⁻¹) with FP (female-phase hermaphrodite) body size (carapace length=CL, in mm) in *Lysmata wurdemanni*.

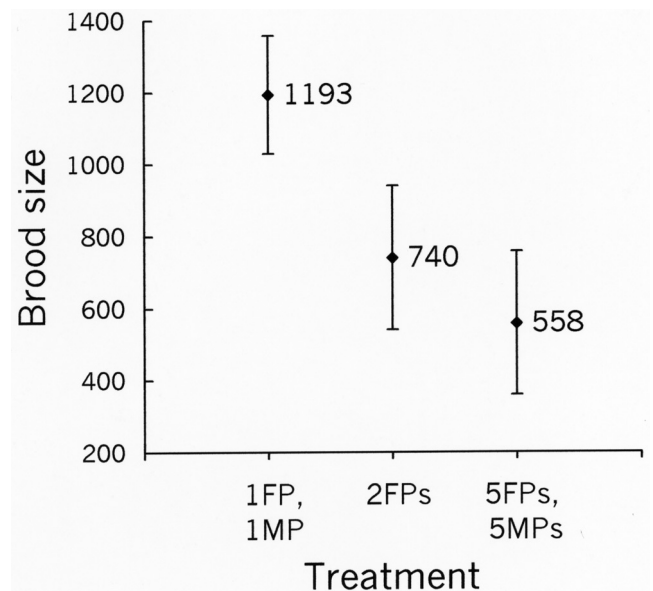


Figure 2. Brood size (number of embryos brood⁻¹; means and 95% confidence limits) of FPs in treatments 2 (1 FP, 1 MP; N=30), 3 (2 FPs; N=30) and 4 (5 FPs, 5 MPs; N=29).

Given the ANCOVA results, another comparison of brood sizes among treatments was done by calculating the differences (deviations) of observed brood sizes from those predicted (expected) by the baseline regression of brood size on body size (Figure 1). Adjustment for differences in FP body size (CL) was done for comparison of brood sizes among treatments because brood size is positively correlated with body size (Figure 1). The same deviation in brood size, in number of embryos, from that predicted from the baseline brood size regression, is relatively unequal in FPs of different body size. There were significant body size differences among treatments (Figure 3) (analysis of variance [ANOVA] of log transformed FP carapace lengths; $F_{3,112}=4.0$, $P=0.009$). Although there were no significant size differences among treatments 1–3 (adjusted Bonferroni $P>0.05$), the FPs of treatment 4 were significantly smaller than those of treatment 3 ($P=0.008$) although not from treatment 2 ($P=0.067$) or treatment 1 ($P=0.587$). Therefore, brood size deviations (observed brood size – expected brood size) for treatments 2–4 were adjusted for body size by dividing by the expected brood size for a given FP body size (CL).

The adjusted brood size deviations (Figure 4) were compared among treatments with ANOVA after log transformation (2 was added to all adjusted brood size deviations, usually negative, to make these values positive and >1 for log transformation). The null hypothesis of no difference among treatments was rejected ($F_{2,86}=12.5$, $P<0.001$). Comparison of pairs of means shows that treatments 3 and 4 are both significantly different from treatment 2 (adjusted Bonferroni $P<0.001$) but not from each other ($P=1.0$). Therefore, brood size, adjusted for body size differences among treatments, was lower in treatments 3 (2 FPs) and 4 (5 FPs, 5 MPs) than in treatment 2 (1 FP, 1 MP).

Comparison of interspawn intervals among experimental treatments

The frequency of brood production, measured in interspawn intervals, was compared among treatments 1–4.

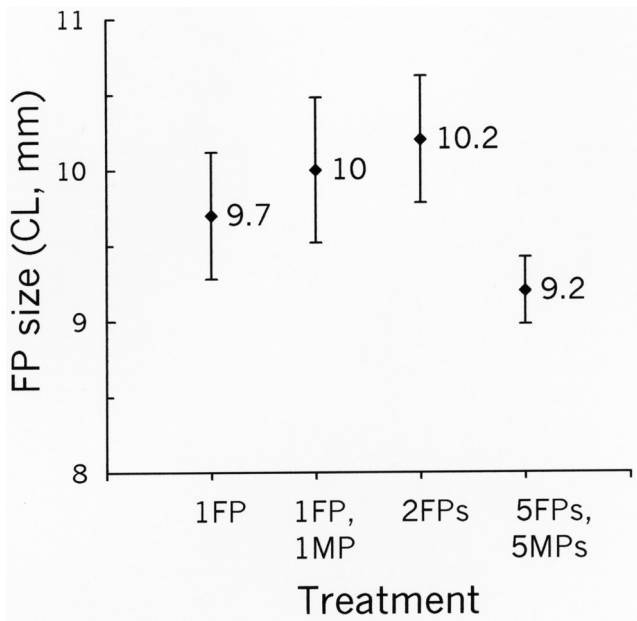


Figure 3. FP body size (carapace length=CL, in mm; means and 95% confidence limits) in treatments 1 (1 FP; N=27), 2 (1 FP, 1 MP; N=30), 3 (2 FPs; N=30) and 4 (5 FPs, 5 MPs; N=29).

Interspawn intervals 1–2 and 2–3 were both shorter in treatments 3 and 4, in which FPs could act as males, than in treatments 1 and 2, in which FPs could not do so (Figure 5A,B). Prior to a statistical comparison of interspawn intervals among treatments, it was found that incubation period was significantly (positively) correlated with FP body size (CL) in treatments 2 and 3 for both interval 1 (Pearson correlation coefficient $r=0.425$ and 0.523 ; $P=0.039$ and 0.006 , respectively; $N=30$ treatment⁻¹)

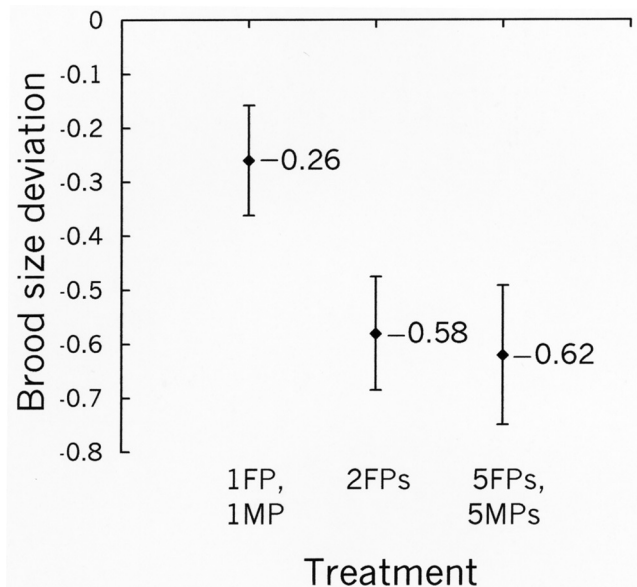


Figure 4. Brood size deviation (means and 95% confidence limits) from that expected, based on baseline brood size on FP body size regression equation (Figure 1), for a given FP body size (carapace length=CL). Brood size deviations, including adjustment for FP body size, were calculated as: [(observed FP brood size) – (expected brood size for FP of CL 'x')] divided by [expected brood size]. Treatment 1, (1 FP; N=27); 2 (1 FP, 1 MP; N=30); 3 (2 FPs; N=30); and 4 (5 FPs, 5 MPs; N=29).

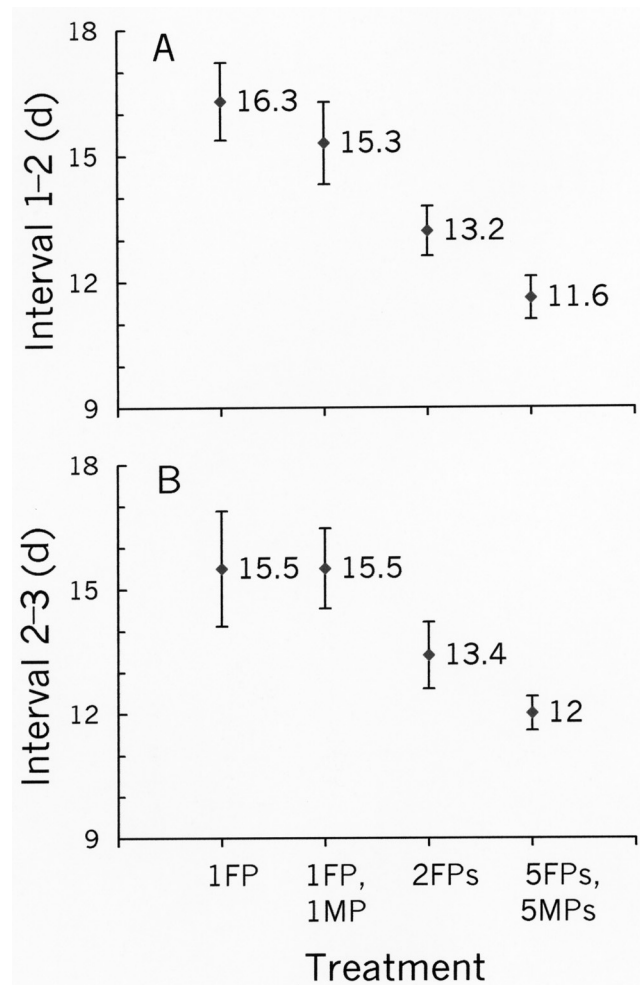


Figure 5. Interspawn interval 1–2 (A) and 2–3 (B) (in days; means and 95% confidence limits) of FPs in treatments 1 (1 FP; N=27), 2 (1 FP, 1 MP; N=30), 3 (2 FPs; N=30) and 4 (5 FPs, 5 MPs; N=29).

and interval 2 ($r=0.456$ and 0.465 ; $P=0.023$ and 0.019 , respectively). Because treatments differed in FP carapace length (Figure 3), an adjustment for body size was made by dividing observed interspawn intervals by individual carapace length (CL), the measure of FP body size. Arcsine transformation of this ratio data (Sokal & Rohlf, 1995) was done by taking the arcsine (degrees) of the square root of incubation time (d) divided by CL (mm \times 10). An ANOVA showed significant differences for interspawn intervals 1–2 and 2–3 among treatments (interspawn interval 1–2, $F_{3,112}=29.9$, $P<0.001$; interspawn interval 2–3, $F_{3,112}=12.4$, $P<0.001$). In both interspawn intervals, the mean interspawn periods of treatments 3 and 4 were significantly different (shorter) from treatments 1 and 2 (adjusted Bonferroni $P\leq 0.001$) but not from each other ($P\gg 0.05$). Treatments 1 and 2 means were not statistically different in either interspawn interval 1 (but $P=0.053$) or interval 2 ($P\gg 0.05$).

Cost of maleness on FP fecundity

A simple model (Figure 6) was constructed depicting the potential costs of maleness on total fecundity (number of embryos produced) in FPs living in social environments

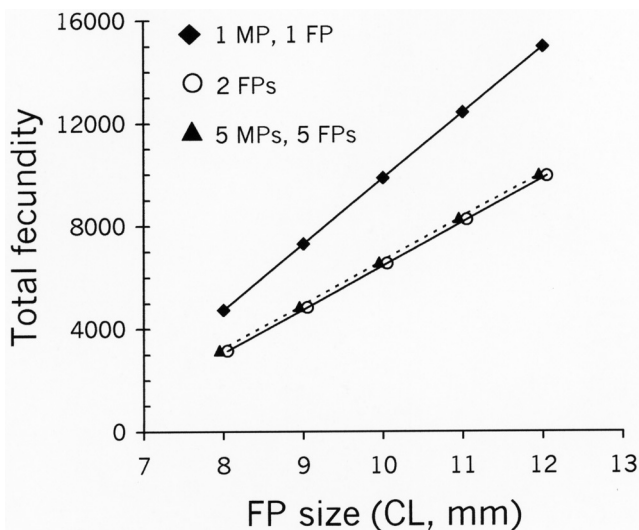


Figure 6. Model depicting cost of maleness on total fecundity (number of embryos produced) in FPs in social environments varying in opportunities for the FP hermaphrodites to function as males. Hypothetical embryo production over a four-month period was based on brood size and interspawn interval 2–3 data from treatments 2 (1 FP, 1 MP), 3 (2 FPs), and 4 (5 FPs, 5 MPs). For each treatment carapace length, total fecundity was estimated by multiplying estimated brood size by the estimated number of spawnings over a four-month (120 d) period.

varying in potential FP male function. For the purposes of the model, a four-month (120 d) period of FP brood production was considered a reasonable approximation based on life history information in Baldwin & Bauer (2003). For each of the treatments (2–4) in which broods were produced, an estimate of brood size (number of embryos) was made for five FP body sizes (CL) based on the mean treatment brood size deviation (Figure 4) from that expected from the baseline brood size on body size regression (Figure 1). The estimate of brood size for a particular CL was calculated as: [(mean treatment brood size deviation)(expected brood size) + expected brood size]. The number of successive spawnings (broods) for each treatment was estimated by dividing 120 d by the treatment mean for interspawn interval 2–3 (Figure 5B). For each treatment and CL, total fecundity (number of embryos) (Figure 6) was estimated by multiplying the estimate of brood size by the number of spawnings. Total fecundity in the model was much higher in treatment 2 (no FP male function possible) than that of treatments 3 and 4 (FPs may function both as female and male). Estimates of fecundity in the model are essentially identical in treatments 3 and 4.

DISCUSSION

Fecundity, a function of brood size and interspawn interval (frequency of spawning), of female-phase hermaphrodites (FPs) appears to be affected by their social environment in the shrimp *Lysmata wurdemanni*. In this study, an experiment was performed in which the male-mating opportunity of FPs was varied. In experimental treatments 1 (isolated FPs) and 2 (1 FP, 1 MP), FPs had no opportunity to act as males, i.e. to pursue and inseminate other FPs acting as females. In treatment 3

(2 FPs), an FP could and did copulate as a male, inseminating the other FP with which they cohabited. In treatment 4 (5 FPs, 5 MPs), an FP had to compete with several MPs and other FPs to copulate with any receptive, prespawning FP. In *L. wurdemanni*, this competition involves swimming and chasing a newly moulted prespawning FP prior to copulation. For this species, in which FPs and MPs occur in aggregations on rocky or coral substrates (Bauer, 2000), treatment 4 most approaches the natural social environment.

Brood sizes were significantly smaller in treatments 3 and 4, in which FPs could act both as male and female, than in treatment 2, in which the FP cohabited with an MP. Treatment 1 could not be included in the brood size analysis because isolated FPs cannot produce fertile broods; they do continue to go through ovarian maturation and spawning cycles. However, the period between spawns (interspawn intervals) was shorter in treatments 3 and 4 than in treatments 1 and 2. Thus, FPs in treatments in which male function could be expressed produced smaller brood sizes but at more frequent intervals than in treatments in which only female function could be expressed. In terms of the costs of maleness to FPs on fecundity, these are contradictory trends.

A simple model of total FP fecundity (Figure 6) shows that increased frequency of spawning (shorter interspawn intervals of treatments 3 and 4) does not greatly compensate for the decreased brood production that FPs would experience over a reproductive season or lifetime. In the model, FPs with no potential to act as males (treatment 2) demonstrate a significantly higher total fecundity. In nature, FPs live in groups with other FPs and MPs (Bauer & Holt, 1998; Bauer, 2000), so that FPs generally do have male-mating opportunities, as in treatments 3 and 4. Thus, there is a significant cost to FPs, in terms of brood production, in retaining male gonadal tissues, sperm production, and male function after changing from the male phase (external male phenotype and male function only) to the simultaneous hermaphrodite female phase (external female phenotype, but both male and female reproductive capacity). However, this cost of maleness is potentially compensated by the capability of FPs to function as males and to inseminate the broods of other FPs acting as females.

The reduction in brood size in FPs of *Lysmata wurdemanni* due to male function may represent energetic costs that are both physiological and behavioural in nature. The testicular tissue, sperm ducts, and sperm mass of the male system of FPs are small in size and presumably in energetic costs compared with the ovarian tissue and large mass of yolky oocytes of the female system prior to spawning. However, the ejaculatory ducts, which store sperm, are nearly as large in relative size in FPs as in MPs [Bauer & Holt, 1998; Bauer & Newman, 2004 for *L. californica* (Stimpson, 1866)]. The emission, depletion, and subsequent replacement of spermatophores (sperm masses) during and after copulation must have some energetic cost. There are also behavioural costs to consider. About an hour before a prespawning FP moults and is receptive to mating, other FPs behave as do MPs in approaching and remaining near the premoulted FP. After the prespawning FP moults, FPs and MPs vigorously swim after and chase the newly moulted FP until one of them

copulates with it. Although this activity appears to be energetically expensive, there were no significant differences in fecundity measures between treatments 3 (2 FPs) and 4 (5 FPs, 5 MPs). However, each FP in treatment 4 had more opportunities to mate as male. Additionally, the possibility for 'intramale' competition for an FP (receptive as a female) was nonexistent in treatment 3 but high in treatment 4. This might indicate that costs of maleness to FPs are mainly physiological and that the behavioural costs of 'intramale' competition are negligible.

In this study, it has been demonstrated that when FPs are allowed to act as male as well as female, the usual condition in nature, brood production is reduced relative to that of FPs that can not reproduce as males. Is this cost of maleness, somehow overcome by the *Lysmata* ancestor, so significant that it is a barrier to attainment of FP simultaneous hermaphroditism in other caridean species? Bauer (2000) proposed that perhaps the key to the evolution of *Lysmata*'s unusual sexual system is its unresolved evolutionary history. Simultaneous hermaphroditism may have evolved under a unique combination of environmental circumstances (a historical contingency hypothesis; Bauer, 2000). The cost of maleness on brood production in FPs, observed here in *L. wurdemanni* and presumably other *Lysmata* species, might be viewed as an evolutionary 'price' paid by individuals of the *Lysmata* ancestor for the high selective advantage of functional simultaneous hermaphroditism.

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