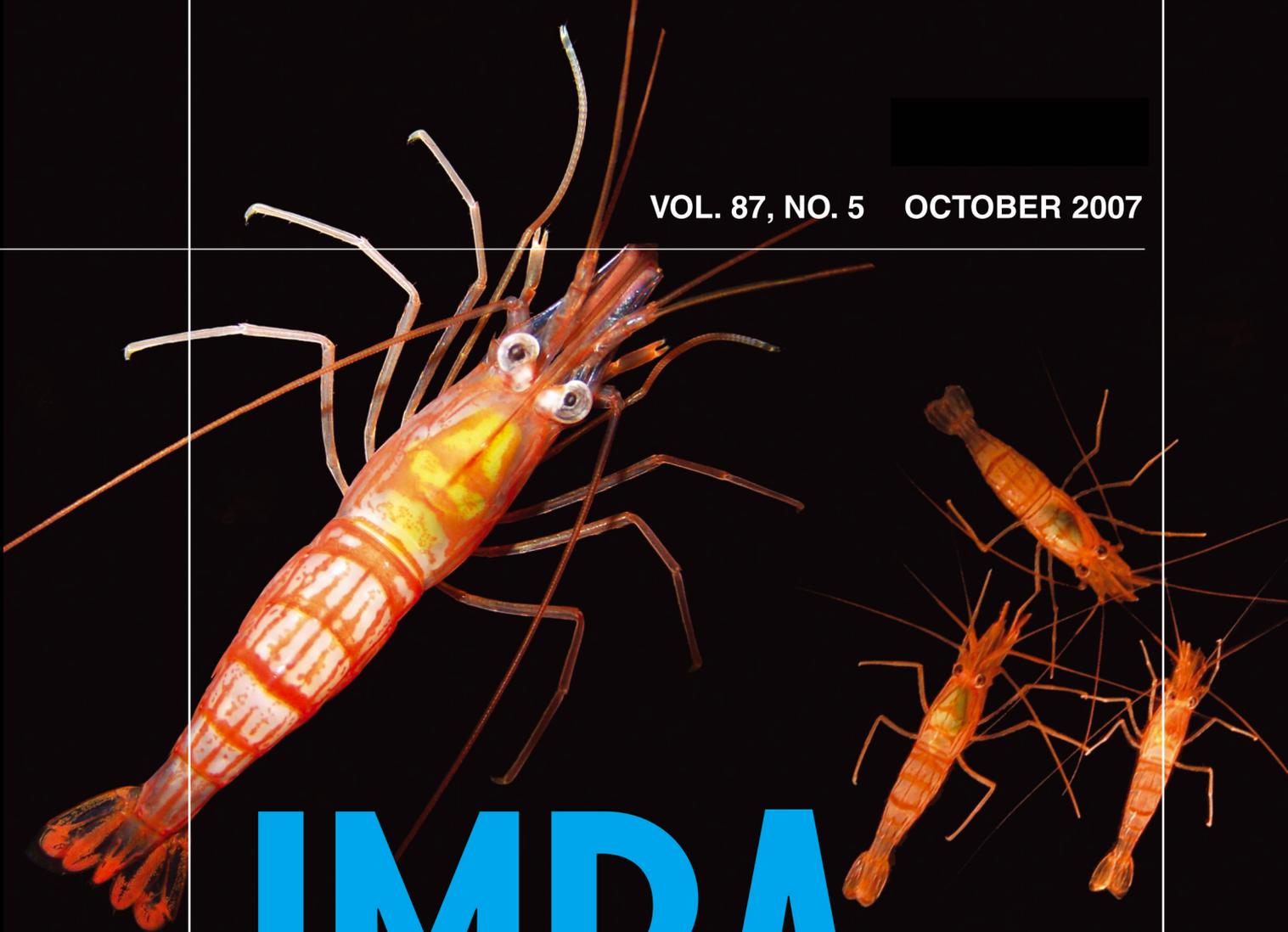


VOL. 87, NO. 5 OCTOBER 2007



JMBA

**Journal of the Marine Biological
Association of the United Kingdom**

**CAMBRIDGE
UNIVERSITY PRESS**

ISSN: 0025-3154

No effect of group size on sex allocation in a protandric-simultaneous hermaphroditic shrimp

J. Antonio Baeza*†

*Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Ancón, Republic of Panama. †Smithsonian Marine Station at Fort Pierce, 701 Seaway Drive, Fort Pierce, Florida 34949, USA. E-mail: baezaa@si.edu

Lysmata wurdemanni is a protandric-simultaneous hermaphroditic shrimp. Individuals reproduce as males first and late in life as simultaneous hermaphrodites. I examined whether sex allocation (resources devoted to ova vs sperm) varies with group size in shrimps that have just matured as hermaphrodites. Focal males were reared with different numbers of hermaphrodites (1, 2, 5 or 10). Sperm stored in the ejaculatory ducts and eggs brooded underneath the abdomen were retrieved and weighted immediately after focal shrimps matured as hermaphrodites. Hermaphrodites should invest more into sperm with increasing group size to cope with more intense sperm competition. The proportion of focal shrimps that lost their first clutch of eggs after maturing as hermaphrodites increased with group size. This suggests male gender preferences by hermaphrodites experiencing large group sizes. No differences in sex allocation among group sizes were recorded for shrimps that did not lose their first clutch of eggs. Thus, group size does not affect sex allocation in terms of ova and sperm mass. This lack of phenotypic plasticity might be explained if sperm competition is not important in *L. wurdemanni*. It should not pay in terms of fitness for shrimps to produce and inseminate female-role hermaphrodites with large amounts of sperm when full paternity is assured in the absence of multi-male mating. In agreement with this idea, a second experiment demonstrated that female-role hermaphrodites invariably mated only once with a single other shrimp.

INTRODUCTION

For hermaphrodites, sex allocation theory predicts adjustments in allocation to the sex functions according to environmental, including social, conditions (Charnov, 1982). In sequential hermaphrodites, the timing of sex change should vary according to the relative abundance of individuals of the opposite sex. In simultaneous hermaphrodites, individuals should alter the amount of resources devoted to sperm and ova depending on group size (Charnov, 1982; Fischer, 1984). In agreement with these predictions, socially mediated shifts in sex allocation have been reported for both sequential and simultaneous hermaphrodites (Collin, 1995; Warner et al., 1996; Locher & Baur, 2000; Schärer & Ladurner, 2003; Tan et al., 2004; Collin et al., 2005; Lorenzi et al., 2005). Plastic adjustments in sex allocation should also occur in hermaphrodites with sequential-simultaneous sex allocation patterns (St Mary, 1994; Fiedler, 1998; Lorenzi et al., 2006).

Examples of sequential-simultaneous hermaphroditism include bidirectional sex change in fish (St Mary, 1994; Munday et al., 1998, 2006), size-dependent sex allocation in species originally reported as strict simultaneous hermaphrodites (Petersen & Fischer, 1996; Trouvé et al., 1999; Schärer et al., 2001), and protandric-simultaneous hermaphroditism. In protandric-simultaneous hermaphrodites, individuals invariably reproduce as males first and

later in life as simultaneous hermaphrodites. This sexual system has been confirmed in a polychaete worm (Premoli & Sella, 1995), a land snail (Tomiya, 1996), a tunicate (Manríquez & Castilla, 2005) and shrimps from the genus *Lysmata* (Baeza, 2006).

In protandric simultaneous hermaphrodites, adjustments in sex allocation should occur at two different levels. First, males should alter the timing of maturation as hermaphrodites according to male mating opportunities (Baeza 2007). This idea has received empirical support from some studies (in *Lysmata wurdemanni*—Baeza, 2007; Baeza & Bauer, 2004) but not from others (in *Ophryotrocha diadema*—Lorenzi et al., 2006).

Second, hermaphrodites should adjust the proportion of resources allocated to sperm vs ova according to group size (number of male competitors in the population) (Charnov 1982; Fischer, 1984; Schärer & Ladurner, 2003). In small groups, i.e. monogamous pairs, hermaphrodites should produce the smallest amount of sperm necessary to fertilize their partner's eggs; there is no risk of losing paternity due to multi-male mating. In aggregations, hermaphrodites should invest more into sperm to cope with greater sperm competition (Charnov, 1982). This idea relies on the rarely tested assumption that female-role hermaphrodites mate with multiple male-role hermaphrodites once they become receptive (Petersen, 1991). Increased allocation to sperm with group size has been demonstrated in various hermaphroditic spe-

cies, including the protandric-simultaneous hermaphroditic worm *Ophryotrocha diadema* (Lorenzi et al., 2006). Whether a single species of protandric-simultaneous hermaphrodite has the ability to shift its sex allocation at different levels (i.e. behaviourally, physiologically) needs investigation (see Lorenzi et al., 2006).

The shrimp *L. wurdemanni* represents a model system to test the effect of group size on sex allocation at multiple levels. Protandric-simultaneous hermaphroditism in this shrimp is a consequence of sex-dependent energetic costs and reproductive time commitments (Baeza, 2006). In the field, shrimps live between 1 and 1.5 y, and may remain as males between one-quarter and two-thirds of their life (see Baldwin & Bauer, 2003). Hermaphrodites consistently go through successive cycles of moulting (10–15 d), mating in the female role, spawning, and brooding of spawned embryos. Usually, less than a day after hatching embryos, hermaphrodites with mature oocytes filling the ovarian part of the ovotestes moult to reproduce again as females (Bauer & Holt, 1998). After becoming hermaphrodites, individuals do not revert to males, and no self-fertilization has been demonstrated (Bauer, 2002a).

In *L. wurdemanni*, the time that shrimps spend as males before maturing as hermaphrodites varies notably in natural populations (Baldwin & Bauer, 2003). The moment at which males become hermaphrodites is influenced by both abiotic and biotic (social) conditions (Bauer, 2002a; Baeza & Bauer, 2004; Baeza, 2007). Males delay maturation as hermaphrodites in environments with a hermaphrodite-biased sex ratio compared to environments with an even sex ratio (Baeza & Bauer, 2004). Also, males delay the timing of maturation in a large group compared to a small group of hermaphrodites (Baeza, 2007). This behavioural plasticity is adaptive as males are more successful in the male role than hermaphrodites (Baeza, 2007; Zhang & Lin, 2005 but see Bauer, 2002b).

In this study, I used the shrimp *L. wurdemanni* to determine if hermaphrodites alter sex allocation in terms of male and female gametes. I examined whether sex allocation (resources devoted to ova vs sperm) varies with group size in shrimps that have just matured as hermaphrodites. Hermaphrodites should increase allocation to sperm with increasing group size as sperm competition should increase accordingly. I also tested whether the risk of sperm competition is important in the mating system of this shrimp.

MATERIALS AND METHODS

Collection and maintenance of shrimps

Individuals of *Lysmata wurdemanni* were collected from the rock jetty at Port Aransas, Mustang Island, Texas (27° 50' N 97° 03' W) between July and September, 2003 and June and September, 2004. Specimens were collected with long-handled dipnets under rock ledges at night during low tides (below zero mean sea levels). Collected shrimps were placed in large plastic bags with aerated seawater and transported to the laboratory. Shrimps were maintained in 114-l recirculating aquaria at a water temperature of 24°C, 34–35 ppt salinity, and a light:dark cycle of 14 h:10 h and were fed daily (½ food pellet per shrimp, Wardley® Shrimp Pellets).

Food was provided *ad libitum* (more than half a food pellet per shrimp per day) during experiments to avoid increasing food depletion with group size. This food regime helped to control for any potential confounding effect (suboptimal food conditions) on sex allocation other than the population size of hermaphrodites (Baeza, 2007). Concrete blocks were placed in each aquarium as a perch for shrimps. Shrimps were observed roaming and foraging on the surface of these concrete blocks. The food gathered from the blocks most probably served as complementary nutrition to shrimps helping with the *ad libitum* food regime. Notwithstanding the food regime, the growth rate of focal males maintained with 10 hermaphrodites was lower than that recorded for focal males maintained with a single other hermaphrodite (Baeza, 2007).

The effect of group size on sex allocation

The null hypothesis of no effect of group size on sex allocation of *L. wurdemanni* was tested when single focal males were reared with a variable number of hermaphrodites. In replicates of this experiment (N=15 per treatment), a single small focal male (5.0 <carapace length, CL [mm] <7.0) capable of maturing as a hermaphrodite in a short period of time (because of its relatively large size), was maintained in a 38-l aquarium either with 1, 2, 5, or 10 hermaphrodites. Hermaphrodites were distinguished from focal males in each aquarium by a coloured elastomer tag injected into their abdomen as in Baeza & Bauer (2004).

Observations on maturity of each focal male as a hermaphrodite were recorded daily. When males mature as hermaphrodites, they moult, mate as females for the first time, and spawn embryos to underneath the abdomen (Bauer & Holt 1998). The time (in days) that each focal male took from the start of the experiment up until maturation as a hermaphrodite was recorded and reported in Baeza (2007). Immediately after the focal shrimps matured as hermaphrodites, the sperm mass contained in their ejaculatory ducts was retrieved. Short electric shocks at 10–12 volts and 1.5 amps were applied (repeatedly) for about 2–5 s each time near the male gonopores until no more sperm was retrieved. The procedure above does empty all of the sperm stored in the ejaculatory ducts, and thus, represents a reliable way of obtaining all the sperm stored by shrimps (Baeza, 2006). Next, the embryo mass deposited in the abdomen was gently collected with forceps. Then, focal shrimps (that die minutes after electro-ejaculation because of the trauma caused by this procedure) and their embryo and sperm masses were dried for 48 h at 70°C in an oven (Grieve Co., LO–201C), and weighed to the nearest 0.01 mg with an analytical balance (Mettler AE163).

From the measurements above, I calculated four different estimates of reproductive allocation. Allocations to female and male function were estimated as the dry weight of embryos and sperm contained in the ejaculatory ducts, respectively. Total reproductive investment was estimated as the sum of the male and female allocations and represents the absolute amount of resources invested in reproduction. Sex allocation was estimated as the ratio of female to male allocation and represents the proportion of resources that individuals invest in functioning as the different sexes.

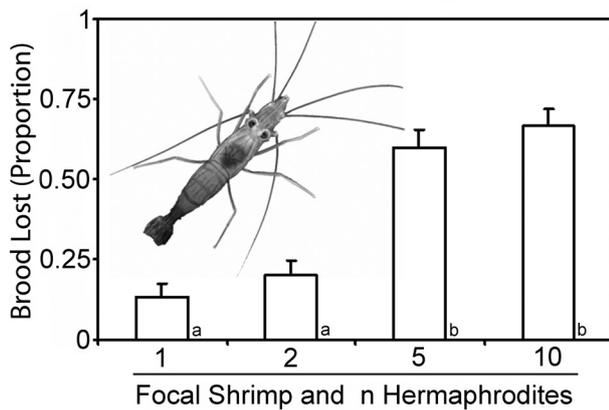


Figure 1. The frequency of occurrence of brood lost in focal shrimps of *Lysmata wurdemanni* immediately after maturation as hermaphrodites. Bars represent standard error bars. Treatments labelled with different letters are significantly different ($P < \text{sequential Bonferroni } \alpha$).

Comparisons among treatments on male allocation, female allocation, sex allocation and total allocation of focal shrimps were conducted with different analyses of covariance (ANCOVA) using the generalized linear model procedure (GLM) as implemented in the software SAS (SAS Institute, 2004). In this analysis, treatment (group size) was used as an independent factor and the mass (dry weight) of shrimps achieved after maturation as hermaphrodites as the covariate. Evaluation of assumptions of normality, homogeneity of variances and homogeneity of slopes were checked and found to be satisfactory for each independent ANCOVA. The power of each ANCOVA was calculated with the macro %POWER (SAS Institute, 2004).

The rationale for this experiment was to subject focal males to increasing male mating opportunities and more intense sperm competition with increasing group size (number of hermaphrodites). This experiment did not control for the potential confounding effect of density. However, density does not affect sex allocation in other hermaphroditic species (Schärer & Ladurner, 2003; Lorenzi et al., 2005).

The risk of sperm competition due to multiple inseminations

I examined the null hypothesis that there is no multiple mating when shrimp are maintained in aggregations. I recorded the number of times a 'parturial' hermaphrodite was inseminated by different shrimps acting as males. 'Parturial' hermaphrodites are pre-spawning hermaphrodites close to moulting and reproducing as females (Bauer, 2002a). During the main reproductive season of *L. wurdemanni*, the relative proportion of small males (shrimps <6.0 mm carapace length, CL) to large males (shrimps >6.0 mm CL) to small hermaphrodites (shrimps <9.0 mm CL) to large hermaphrodites (shrimps >9.0 mm CL) is 4:3:2:1, respectively (see Bauer, 2002b). This ratio was reproduced in the laboratory by placing a combination of 10 shrimps of the different sizes and sexual phases (4:3:2:1) into 20-l aquaria (40×20×25 cm). After an initial acclimatization period of at least 8 h, one 'parturial' hermaphrodite was introduced into the same aquarium. Moulting and the subsequent number of inseminations experienced by this 'parturial' hermaphrodite

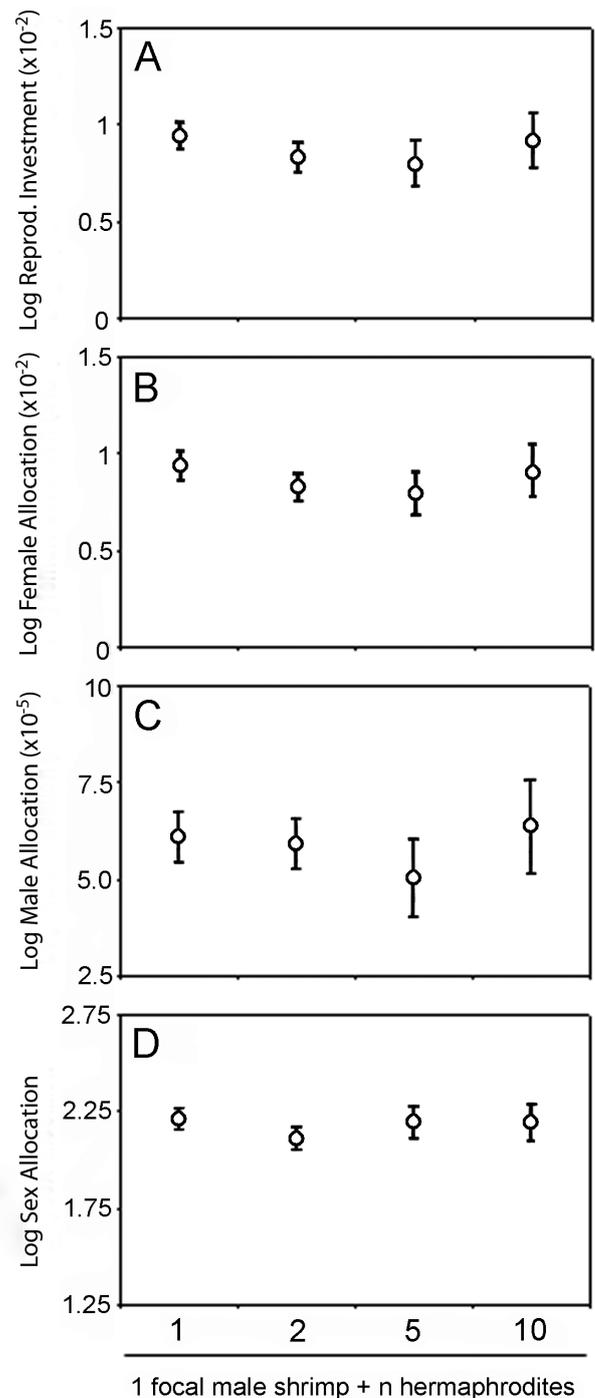


Figure 2. The effect of group size on reproductive allocation of *Lysmata wurdemanni* focal shrimps after maturation as hermaphrodites. Least square means \pm standard errors are shown for each one of the variables. (A) Total reproductive investment; (B) female allocation; (C) male allocation; (D) sex allocation. All measurements are in grams (g) of dry mass. See Methods for further details.

were counted in each of 10 replicates. Recording was conducted with time-lapse video as in Baeza (2007).

RESULTS

The effect of group size on sex allocation

A total of 24 out of 60 (40%) focal shrimps lose their embryo masses immediately after they matured as hermaphrodites (after moulting and spawning eggs for the first time). It was

Table 1. The effect of group size and shrimp mass on the different dependent variables of reproductive allocation measured on *Lysmata wurdemanni* focal shrimps immediately after they mature as hermaphrodites. For each dependent variable, a one-way ANCOVA was performed using group size as fixed independent variable and shrimp mass as the covariate. Also, the power of each ANCOVA to detect significant differences in sex allocation among treatments when controlling for the covariate is shown.

Dependent variable	Model fit R ²	Factor: group size			Covariate: shrimp mass			Power
		F	df	P	F	df	P	
Total allocation	0.26	0.48	3,31	0.6959	6.46	1,31	0.0162	0.1362
Female allocation	0.26	0.48	3,31	0.6976	6.40	1,31	0.0167	0.1357
Male allocation	0.20	0.31	3,31	0.8157	3.88	1,31	0.0578	0.1023
Sex allocation	0.06	0.74	3,31	0.5344	0.03	1,31	0.8665	0.1851

not possible to observe if the shrimps that ‘aborted’ their newly spawned embryo mass consumed their eggs or if these eggs detached from the abdomen and fell down to the floor of the aquaria. The proportion of focal shrimps losing their embryos varied significantly among treatments (Pearson Chi-square exact test, $\chi^2_3=13.89$, $P=0.0031$) (Figure 1). Focal shrimps maintained with 1 and 2 hermaphrodites lost their brood significantly less frequently than focal shrimps maintained with 5 and 10 hermaphrodites (a posteriori subdivision of Pearson Chi-square exact test, $\chi^2_1=13.61$, $P=0.0002$, sequential Bonferroni corrected $\alpha=0.016$). No other significant differences among treatments were found ($P>0.05$ for the rest of the paired comparisons).

When only those focal shrimps that retained their embryo masses are considered, the different reproductive allocation measures studied did not vary significantly among treatments ($P>0.05$ in all cases, Figure 2; Table 1). Shrimp size affected total allocation and female allocation but not sex allocation ($P>0.05$). Male allocation was marginally affected by body size (Table 1). Thus, group size does not affect sex allocation in terms of gonad mass. The power of each ANCOVA was low because of the low number of replicates and their unbalanced distribution among treatments (Table 1).

The frequency of multiple mating and the risk of sperm competition

Sperm competition is absent in the mating system of *L. wurdemanni*. Shrimps roamed freely in the aquarium when maintained in aggregations. No agonistic interactions were observed among potential male mating partners. Parturial hermaphrodites appeared to be recognized when close to moulting. Some potential male mating partners started following and on occasion poking at these parturial hermaphrodites with their second antennae, third maxillipeds, and/or anterior pereopods ~1 h before they moulted. Parturial hermaphrodites usually escaped this ‘harassment’ by swimming haphazardly and/or roaming more actively the closer they became to moulting. In 5 out of the 10 replicates, insemination occurred at the moment of moulting, and in the remaining 5 replicates, while the parturial hermaphrodite was swimming (i.e. seconds after moulting). All pre-spawning hermaphrodites copulated only once with either a single male or hermaphrodite, in each of the 10 trials. These observations suggest that *L. wurdemanni*

features encounter-rate polygynandry as a mating system in which sperm competition is not relevant.

DISCUSSION

Individuals of *Lysmata wurdemanni* that have just matured as hermaphrodites lose their first batch of eggs more frequently when maintained in large than in small groups. This result suggests that, depending on social conditions, some shrimps might be selecting the male gender after maturing as hermaphrodites to improve their reproductive success. In turn, those shrimps that did not appear to prefer the male gender after maturing as hermaphrodites (i.e. did not lose their first batch of eggs) did not shift resources between the reproductive functions (in terms of gonad products) when subjected to different mating environments.

In the laboratory, males invariably mature as hermaphrodites regardless of the number of conspecifics with which they are reared (Baeza, 2007). Also, males almost never reach sizes as large as those reported for the largest hermaphrodites in the field (Baldwin & Bauer, 2003). Thus, maturing as a hermaphrodite appears to be an obligatory developmental pathway in *L. wurdemanni*. Young hermaphrodites might be selecting gender as a strategy to cope with changing social conditions after attaining certain size/age. Gender preferences have previously been reported for strict simultaneous hermaphrodites (female-role preference in *Navanax* slugs—Leonard & Lukowiak (1991); male-role preference in *Serranus* fishes—Petersen (2006)) and might occur in another protandric-simultaneous hermaphrodite (i.e. *Ophryotrocha diadema*—see Leonard, 2006). In *L. wurdemanni*, young hermaphrodites that appear to prefer the male role might be increasing their lifetime reproductive success if the cost of losing eggs is compensated by the benefits from increased male mating ability. It is unknown whether the male mating ability of non-brooding hermaphrodites is greater than that of brooding ones. However, male shrimps are more successful in mating with female-role hermaphrodites than brooding hermaphrodites acting as males (Baeza, 2006b; Zhang & Lin, 2005 but see Bauer, 2002b). Brooding hermaphrodites might be heavier than non-brooding hermaphrodites because of egg production and subsequent brooding (380 to 1500 eggs per female) (Baeza, unpublished data). The ability to chase and

grasp swimming female-role shrimps might decrease in non-brooding compared to brooding hermaphrodites. Future experiments examining gender preferences mediated by group size in hermaphrodites should test for: (1) the mating ability of brooding vs non-brooding hermaphrodites acting as males; and (2) determine whether brood lost by young hermaphrodites retrieved from the field occurs more frequently when maintained in large than in small groups.

The proportion of resources devoted to the sex functions (in terms of gonad mass) did not differ among shrimps that did not lose their embryo mass when reared with a different number of hermaphrodites. In contrast, plastic adjustments in sex allocation (in terms of gonad mass) with group size have been reported for the protandric-simultaneous hermaphroditic worm *O. diadema* (Lorenzi et al., 2005, 2006; Schleicherová et al., 2006) and for various strict simultaneous hermaphrodites (Locher & Baur, 2000; Schärer & Ladurner, 2003; Schärer et al., 2005; Tan et al., 2004; Trouvé et al. 1999; but see Schärer & Wedekind, 2001). Information gathering by individuals from the surroundings is relevant to respond optimally to the environment (Schleicherová et al., 2006; Shuker & West, 2004). Information constraints experienced by shrimps might explain the lack of phenotypic plasticity in *L. wurdemanni*. However, shifts in the timing of maturation as hermaphrodites by males reared with a different number of hermaphrodites have been previously demonstrated in this species (males delay maturation as hermaphrodites with an increasing number of hermaphrodites—Baeza, 2007) diminishing the importance of information constraints as a reason for the lack of plastic sex allocation (in terms of gonad mass) in this shrimp.

Alternatively, the lack of plastic sex allocation in *L. wurdemanni* (in terms of gonad mass) might be related to the absence of sperm competition. The single insemination by only one other shrimp experienced by female-role hermaphrodites contrasts with the polyandrous mating behaviour of females from gonochoric and protandric shrimps (Chiba et al., 2003; Correa et al., 2003), and other simultaneous hermaphrodites (Angeloni et al., 2003; Michiels, 1998). Notwithstanding the reasons for this monoandrous behaviour, it might not pay in term of fitness for shrimps to produce and inseminate female-role hermaphrodites with large amounts of sperm as full paternity is assured with no multi-male mating (Parker, 1998). Instead, hermaphrodites might be investing in behaviours that should increase the frequency of finding and inseminating female-role shrimps. For instance, roaming, considered a male behaviour because it increases the chances of finding receptive females (Andersson, 1994), might have increased with group size during the experiment. Components of sex allocation other than gonad tissue (i.e. physiological, anatomical and behavioural investments) should be included in future studies measuring sex allocation shifts with social conditions in simultaneous hermaphrodites (Lorenzi et al., 2006).

In addition to the absence of sperm competition, two other reasons might explain the absence of shifts in sex allocation with group size in *L. wurdemanni*. First, increased male allocation with increasing group size might have occurred as an increased rate of sperm production. When with a single female-role partner, shrimps take 3 d on average to refill

their ejaculatory ducts (Baeza, 2006). The rate of 'sperm recovery' from after an ejaculation in shrimps experiencing larger group sizes was not measured here and should be examined in future experiments. Second, because several focal shrimps lost their first batch of eggs after maturing as hermaphrodites, the number of replicates for measuring sex allocation was reduced by 40%. The available replicates for the ANCOVA were not randomly distributed among treatments but were clumped together into two of them (1 and 2 hermaphrodites). This small sample size and unbalanced distribution of replicates determined the low power of the ANCOVA tests. Thus, the absence of shifts in sex allocation might simply be due to the failure of the tests to detect real significant differences among treatments. The behaviour of shrimps (loosing eggs when maintained in large groups) should be taken into account in future studies examining shifts in sex allocation with group size in *L. wurdemanni*.

This research was funded by a Sigma Xi Grant in Aid of Research, the Lerner-Gray Fund for Marine Science (NMNH), the 'Graduate Student Fellowship' of The Crustacean Society, and a National Science Foundation Doctoral Dissertation Improvement Grant IBN 0506908 to J.A. Baeza. I acknowledge a 'President of the Republic' fellowship (Chile). Support from the Smithsonian Tropical Research Institute (STRI, Panama) Marine Fellowship and Smithsonian Marine Station (Fort Pierce, Florida) Fellowship during the data analysis and writing of this manuscript is appreciated. The comments by two anonymous referees substantially improved this manuscript. The help of Scott Jones in improving the English of the manuscript is deeply appreciated.

REFERENCES

- Andersson, M., 1994. *Sexual selection*. Princeton: Princeton University Press.
- Angeloni, L., Bradbury, J.W. & Burton, R.S., 2003. Multiple mating, paternity, and body size in a simultaneous hermaphrodite, *Aphysia californica*. *Behavioral Ecology*, **14**, 554–560.
- Baeza, J.A., 2006. Testing three models on the adaptive significance of protandric simultaneous hermaphroditism in a marine shrimp. *Evolution*, **60**, 1840–1850.
- Baeza, J.A., 2007. Male mating opportunities affect sex allocation in a protandric simultaneous hermaphroditic marine shrimp. *Behavioral Ecology and Sociobiology*, **61**, 365–370.
- Baeza, J.A. & Bauer, R.T., 2004. Experimental test of socially mediated sex change in a protandric simultaneous hermaphrodite, the marine shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae). *Behavioral Ecology and Sociobiology*, **55**, 544–550.
- Baldwin, A.P. & Bauer, R.T., 2003. Growth, survivorship, life span, and sex change in the hermaphroditic shrimp *Lysmata wurdemanni* (Decapoda: Caridea: Hippolytidae). *Marine Biology*, **143**, 157–166.
- Bauer, R.T., 2002a. Reproductive ecology of a protandric simultaneous hermaphrodite, the shrimp *Lysmata wurdemanni* (Decapoda: Caridea: Hippolytidae). *Journal of Crustacean Biology*, **22**, 742–749.
- Bauer, R.T., 2002b. Test of hypotheses on the adaptive value of an extended male phase in the hermaphroditic shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae). *Biological Bulletin. Marine Biological Laboratory, Woods Hole*, **203**, 347–357.
- Bauer, R.T. & Holt, G.H., 1998. Simultaneous hermaphroditism in the marine shrimp *Lysmata wurdemanni* (Caridea: Hippolytidae): an undescribed sexual system in the decapod Crustacea. *Marine Biology*, **132**, 223–235.
- Charnov, E.L., 1982. *The theory of sex allocation*. Princeton: Princeton University Press.

- Chiba, S., Goshima, S. & Shinomiya, Y., 2003. Male-male competition selects for delayed sex change in the protandrous shrimp *Pandalus latirostris*. *Marine Biology*, **142**, 1153–1157.
- Collin, R., 1995. Sex, size, and position: a test of models predicting size at sex change in the protandrous gastropod *Crepidula fornicata*. *American Naturalist*, **146**, 815–831.
- Collin, R., McLellan, M., Gruber, K. & Bailey-Jourdain, C., 2005. Effects of conspecific associations on size at sex change in three species of calyptraeid gastropods. *Marine Ecology Progress Series*, **293**, 89–97.
- Correa, C., Baeza, J.A., Hinojosa, I.A. & Thiel, M., 2003. Male dominance hierarchy and mating tactics in the rock shrimp *Rhynchocinetes typus* (Decapoda: Caridea). *Journal of Crustacean Biology*, **23**, 33–45.
- Fiedler, G.C., 1998. Functional, simultaneous hermaphroditism in female-phase *Lysmata amboinensis* (Decapoda: Caridea: Hippolytidae). *Pacific Science*, **52**, 161–169.
- Fischer, E.A., 1984. Local mate competition and sex allocation in simultaneous hermaphrodites. *American Naturalist*, **124**, 590–596.
- Leonard, J.L. & Lukowiak, K., 1991. Sex and the simultaneous hermaphrodite: testing models of male-female conflict in a sea slug, *Navanax inermis* (Opisthobranchia). *Animal Behaviour*, **41**, 255–266.
- Leonard, J.L., 2006. Sexual selection: lessons from hermaphroditic mating systems. *Integrative and Comparative Biology*, **46**, 349–367.
- Locher, R. & Baur, B., 2000. Mating frequency and resource allocation to male and female function in the simultaneous hermaphrodite land snail *Arianta arbustorum*. *Journal of Evolutionary Biology*, **13**, 607–614.
- Lorenzi, M.C., Sella, G., Schleicherová, D. & Ramella, L., 2005. Outcrossing hermaphroditic polychaete worms adjust their sex allocation to social conditions. *Journal of Evolutionary Biology*, **18**, 1341–1347.
- Lorenzi, M.C., Schleicherová, D. & Sella, G., 2006. Life history and sex allocation in the simultaneously hermaphroditic polychaete worm *Ophryotrocha diadema*: the role of sperm competition. *Integrative and Comparative Biology*, **46**, 381–389.
- Manríquez, P.H. & Castilla, J.C., 2005. Self-fertilization as an alternative mode of reproduction in the solitary tunicate *Pyura chilensis*. *Marine Ecology Progress Series*, **305**, 113–125.
- Michiels, N.K., 1998. Mating conflicts and sperm competition in simultaneous hermaphrodites. In *Sperm competition and sexual selection* (ed. T.R. Birkhead and A.P. Møller), pp. 219–254. San Diego: Academic Press.
- Munday, P.L., Caley, M.J. & Jones, G.P., 1998. Bi-directional sex change in a coral-dwelling goby. *Behavioral Ecology and Sociobiology*, **43**, 371–377.
- Munday, P.L., Buston, P.M. & Wagner, R.R., 2006. Diversity and flexibility of sex-change strategies in animals. *Trends in Ecology and Evolution*, **21**, 89–95.
- Parker, G.A., 1998. Sperm competition and the evolution of ejaculates. In *Sperm competition and sexual selection* (ed. T.R. Birkhead and A.P. Møller), pp. 3–54. San Diego: Academic Press.
- Petersen, C.W., 1991. Sex allocation in hermaphroditic sea basses. *American Naturalist*, **138**, 650–667.
- Petersen, C.W., 2006. Sexual selection and reproductive success in hermaphroditic seabasses. *Integrative and Comparative Biology*, **46**, 439–448.
- Petersen, C.W. & Fischer, E.A., 1996. Intraspecific variation in sex allocation in a simultaneous hermaphrodite: the effect of individual size. *Evolution*, **50**, 636–645.
- Premoli, M.C. & Sella, G., 1995. Sex economy in benthic polychaetes. *Ethology, Ecology and Evolution*, **7**, 27–48.
- Schärer, L., Karlsson, L.M., Christen, M. & Wedekind, C., 2001. Size-dependent sex allocation in a simultaneous hermaphrodite parasite. *Journal of Evolutionary Biology*, **14**, 55–67.
- Schärer, L. & Wedekind, C., 2001. Social situation, sperm competition and sex allocation in a simultaneous hermaphrodite parasite, the cestode *Schistocephalus solidus*. *Journal of Evolutionary Biology*, **14**, 942–953.
- Schärer, L. & Ladurner, P., 2003. Phenotypically plastic adjustment of sex allocation in a simultaneous hermaphrodite. *Proceedings of the Royal Society of London, Series B*, **270**, 935–941.
- Schärer, L., Sandner, P. & Michiels, N.K., 2005. Trade-off between male and female allocation in the simultaneously hermaphroditic flatworm *Macrostomum* sp. *Journal of Evolutionary Biology*, **18**, 396–404.
- Schleicherová, D., Lorenzi, M.C. & Sella, G., 2006. How outcrossing hermaphrodites sense the presence of conspecifics and suppress female allocation. *Behavioral Ecology*, **17**, 1–5.
- Shuker, D.M. & West, S.A., 2004. Information constraints and the precision of adaptation: sex ratio manipulation in wasps. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 10363–10367.
- St Mary, C.M., 1994. Sex allocation in a simultaneous hermaphrodite, the blue-banded goby (*Lythrypnus dalli*): the effects of body size and behavioral gender and the consequences for reproduction. *Behavioral Ecology*, **5**, 304–311.
- Tan, G.N., Govedich, F.R. & Burd, M., 2004. Social group size, potential sperm competition and reproductive investment in a hermaphroditic leech, *Helobdella papillomata* (Euhirudinea: Glossiphoniidae). *Journal of Evolutionary Biology*, **17**, 574–580.
- Tomiyama, K., 1996. Mate-choice criteria in a protandrous simultaneously hermaphroditic land snail *Achatina fulica* (Férussac) (Stylommatophora: Achatinidae). *Journal of Molluscan Studies*, **62**, 101–111.
- Trouvé, S., Jourdane, J., Renaud, F., Durand, P. & Morand, S., 1999. Adaptive sex allocation in a simultaneous hermaphrodite. *Evolution*, **53**, 1599–1604.
- Warner, R.R., Fitch, D.L. & Standish, J.D., 1996. Social control of sex change in the shelf limpet, *Crepidula norrisiarum*: size-specific responses to local group composition. *Journal of Experimental Marine Biology and Ecology*, **204**, 155–167.
- Zhang, D. & Lin, J., 2005. Comparative mating success of smaller male-phase and larger male-role euhermaphrodite-phase shrimp, *Lysmata wurdemanni* (Caridea: Hippolytidae). *Marine Biology*, **147**, 1387–1392.

Submitted 14 March 2007. Accepted 27 July 2007.