

Male mating opportunities affect sex allocation in a protandric-simultaneous hermaphroditic shrimp

J. Antonio Baeza

Received: 24 March 2006 / Revised: 17 July 2006 / Accepted: 22 July 2006 / Published online: 13 September 2006
© Springer-Verlag 2006

Abstract Sex allocation theory predicts phenotypic adjustments by individuals in their investments into the male and female reproductive function in response to environmental conditions. I tested for phenotypically plastic shifts in sex allocation in a protandric simultaneous hermaphrodite, in which individuals mature and reproduce as males first, and later in life, as simultaneous hermaphrodites. I predicted that initially maturing males should adjust the timing of maturation as hermaphrodites according to male mating opportunities mediated by population size of hermaphrodites. In a first experiment, males maintained with only one hermaphrodite reduced the time they spent as males in comparison to males maintained with no conspecifics, presumably because total reproductive output is maximized by two individuals being simultaneous hermaphrodites when the mating system is a pair. Conversely, males maintained in groups with two or more hermaphrodites increased the time they spent as males in comparison to single males. This delay in maturation was not an effect of resource depletion with increasing shrimp density because the growth rate of males did not differ among most of the experimental treatments. One hypothesis to explain this social mediation of sex allocation is that the smaller males are more successful in mating as males than are the larger hermaphrodites: it will pay reproductively for males to delay maturation as hermaphrodites in large but not in small groups. In agreement with this notion, a second experiment demonstrated that smaller males were four times more successful than were larger hermaphrodites in inseminating shrimps

reproducing as females. The informative cue that males may use to perceive different group sizes deserves further attention.

Keywords Sex allocation · Phenotypic plasticity · Social mediation · Hermaphrodite

Introduction

Sex allocation theory predicts phenotypic adjustments by individuals in their investments to the male and female reproductive function in response to environmental conditions (Charnov 1982). This plastic sex allocation is expected in species featuring a wide range of breeding systems. In species with separate sexes (gonochorists), mothers should bias their offspring sex ratio toward daughters with decreases in the number of reproductive females in the local group (local mate competition model—Hamilton 1967). Sequential hermaphrodites are expected to defer sex change with increases in the proportion of members of the opposite sex in the population (sex-ratio induction of sex change—Charnov 1982). Lastly, simultaneous hermaphrodites should increase the proportion of resources devoted to sperm production with increasing local population size of conspecifics (Charnov 1982; Petersen 1991). In support of these predictions, experimental studies have confirmed short term sex allocation shifts in species with separate sexes (Werren 1980; Herre 1985; Shuker and West 2004) in sequential hermaphrodites (Warner et al. 1996; Collin 1995) and in simultaneous hermaphrodites (Trouvé et al. 1999; Locher and Baur 2000; Schärer and Ladurner 2003; Tan et al. 2004). Phenotypically plastic

Communicated by P. Backwell

J. A. Baeza (✉)
Department of Biology, The University of Louisiana at Lafayette,
Lafayette, LA 70504-2451, USA
e-mail: jab9444@louisiana.edu

adjustments in sex allocation should also occur in species with “mixed” breeding systems, featuring sex allocation patterns that do not conform to the three classical animal breeding systems above (see Munday et al. 2006).

Recently, studies reporting species with mixed sex allocation patterns have increased substantially (e.g. males coexisting with simultaneous hermaphrodites in androdioecious clam shrimps—Zucker et al. 1997; bi-directional sex change in goby fishes—St. Mary 1994; Munday et al. 1998). One of the most enigmatic mixed sex allocation patterns is protandric simultaneous hermaphroditism, in which individuals consistently mature and reproduce initially as males, and later in life, become functional simultaneous hermaphrodites. Protandric simultaneous hermaphroditism has been confirmed in a polychaete worm (*Ophryotrocha diadema*—Premoli and Sella 1995), in a land snail (*Achatina fulica*—Tomiya 1996), and in various marine shrimp species from the genus *Lysmata* (Bauer 2000). In these protandric simultaneous hermaphrodites, initially maturing male individuals should adjust their timing of maturation as hermaphrodites, and terminal phase simultaneous hermaphrodites should vary the proportion of resources allocated to male vs female gametes, to optimize their lifetime reproductive success.

Shifts in sex allocation have recently been demonstrated in the polychaete worm, *O. diadema* (Lorenzi et al. 2005; Schleicherová et al. 2006), and in the shrimp, *Lysmata wurdemanni* (Baeza and Bauer 2004). In *L. wurdemanni*, males reared in groups with a greater proportion of hermaphrodites than males delayed maturation as hermaphrodites compared to those reared in groups in which the proportion of hermaphrodites and males was the same. This behavioral plasticity might be considered adaptive if pure males are more successful in the male role than hermaphrodites. It will pay (in term of fitness) for males to defer maturation as hermaphrodites in hermaphrodite-biased but not male-biased groups (Bauer and Holt 1998). Recent experiments have shown that males gain female mating partners more frequently than hermaphrodites mating in the male role in a competitive environment (Zhang and Lin 2005). Other observations suggest that male mating ability does not differ between males and hermaphrodites (Bauer 2002a). The male mating ability of the different sexual phases of *L. wurdemanni* in a competitive environment deserves further attention.

Notwithstanding the breeding system of the species in which adjustments on sex allocation have been experimentally examined, most studies have not controlled for resource availability (for exceptions see Schärer and Ladurner 2003; Tan et al. 2004; Lorenzi et al. 2005). Resource depletion may increase with group size or relative abundance of one sex because of density- or size-dependent resource competition. For instance, in strict simultaneous

hermaphrodites, resource depletion may lead to increases in allocation to the male function, regardless of group size, as individuals are expected to allocate more resources to the cheapest of the sex functions (sperm production) when energy becomes limited (Charnov 1982). The question, thus, remains whether sex allocation shifts detected for several gonochoric and hermaphroditic species does actually represent an adaptive phenotypic adjustment of individuals responding to local conditions or simply is a consequence of nonadaptive constraints dictated by limited food supply.

In this study, two experiments were conducted to test if variation in the sex allocation of *L. wurdemanni* is an adaptive response to individual mating opportunities. First, small male shrimp were reared with a variable number of hermaphrodites, while controlling for resource availability, to test whether sex allocation adjustments conform to predictions of sex allocation theory. The mating success of males vs hermaphrodite breeding in the male role was then compared to determine if males might benefit from delaying maturation into hermaphrodites when there are large numbers of hermaphrodites in the population.

Materials and methods

Biology of the model species

In the marine shrimp, *L. wurdemanni*, juveniles invariably mature as male individuals (hereafter pure males to distinguish them from hermaphrodites breeding in the male role, see below). These pure males bear typical caridean male sexual characters (appendix masculina) and are only capable of reproducing as males (Bauer and Holt 1998). Pure males later attain the female sexual function, developing into functional simultaneous hermaphrodite individuals (hereafter hermaphrodites). Externally, these hermaphrodites resemble females of caridean gonochoric species, brooding embryos in an abdominal chamber (Bauer 2000). However, hermaphrodites retain testicular tissue, male ducts and gonopores, and thus, have the ability to reproduce as both male and female (Bauer and Holt 1998). Hermaphrodites can mate as males frequently, but copulation with another hermaphrodite is not reciprocal. A newly molted pre-spawning hermaphrodite copulates as a female, with a pure male or another hermaphrodite that acts only as male at that time. Sperm from a mating is used to fertilize only the eggs released during the spawning event that occurs 2–3 h later because there is no long-term sperm storage in this shrimp. Hermaphrodites do not revert to their initial pure male sexual condition (Bauer 2002a).

Collection and maintenance of shrimps

Individuals of *L. wurdemanni* were collected with a long-handled dip net from the rock jetty at Mustang Island, Port Aransas, Texas (27°50' N, 97°03' W) between July 2003 and September 2004. Collected specimens were placed in large plastic bags containing aerated seawater and transported to the laboratory at The University of Louisiana at Lafayette (ULL). In the laboratory, individuals were maintained before the experiments in a 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 (1/2 food pellet per shrimp, Wardley® Shrimp Pellets).

Experimental design

The effect of male mating opportunities on sex allocation

In replicates of this experiment ($n=15$ per treatment), a single small pure male ($5.0 < \text{carapace length, CL [mm]} < 7.0$) capable of maturing as a hermaphrodite within a short period of time was maintained in a 38-l aquarium either with no conspecific, or with one, two, five, or ten hermaphrodites. Hermaphrodites were distinguished from pure males in each aquarium by a colored elastomer tag injected into their abdomen as in Baeza and Bauer (2004). The time (in days) that each pure male took from the start of the experiment up until maturation as a hermaphrodite was recorded. The null hypothesis of no difference in time required by pure males to mature as hermaphrodites among treatments was tested with the Wald Chi-square method, part of Cox's maximum partial likelihood regression (Allison 1995), an event-time (survival) analysis technique (SAS Institute 2001). The rationale for this experiment, in which pure males were reared alone or with a varying number of hermaphroditic individuals, was twofold. The treatment in which pure males were reared alone provided information on how quickly these pure males change to the terminal hermaphroditic phase in the absence of social stimuli. In the remaining treatments, opportunities for mating as males were increased by increasing group size (i.e., number of hermaphroditic shrimps).

Food availability and group size

In the experiment above, food was provided ad libitum (more than 1/2 food pellet per shrimp per day, Wardley® Shrimp Pellets) to avoid increasing food depletion with group size, thus, controlling for any potential confounding effect (suboptimal food conditions) on sex allocation in

pure male shrimps other than male mating opportunities mediated by the population size of hermaphrodites. I examined whether food availability varied among treatments by calculating the growth rate of pure males from the start of the experiment until they matured as hermaphrodites. The CL of each pure male shrimp was measured under the stereomicroscope just before the start of the experiment and immediately after they matured as hermaphrodites. The null hypothesis of no differences in growth rate among pure males from the different treatments was tested with an ANOVA and subsequent Tukeys' HSD multiple comparison tests (SAS Institute 2001). No significant differences in mean CL of pure males just before the start of the experiment were found among the different treatments (ANOVA, $F_{4,69}=0.05$, $P=0.996$).

Mating ability of pure males and hermaphrodites

To test for differences in male mating ability between pure males and hermaphrodites, I compared the behavior of pairs of shrimps competing to inseminate a 'parturial' hermaphrodite in the laboratory. Parturial hermaphrodites are pre-spawning hermaphrodites close to molting and reproducing as females (Bauer 2002a). Two shrimps, one pure male and one hermaphrodite (both shrimps >6.0 mm CL, size at which both pure males and hermaphrodites are behaviorally mature to copulate as males), were placed into an aquarium (20 l, $40 \times 20 \times 25$ cm). After an initial acclimatization period of at least 8 h, one 'parturial' hermaphrodite was introduced into the same aquarium. The identity of the shrimp inseminating this 'parturial' hermaphrodite was recorded with time-lapse video (GYRR model TLC1400). A Cohu CCD surveillance video camera equipped with a 6-mm lens sensitive to both low-intensity white and infrared light was used. Fluorescent and infrared (880 nm) lamps provided day and night illumination, respectively. The experiment was repeated 20 times. To determine differences in male mating ability between pure males and hermaphrodites, I compared the observed distribution of inseminations by shrimps of the different sexual phases with the binomial random distribution using a Chi-square exact test of goodness of fit (SAS Institute 2001).

In this experiment, it was not possible to control for body size of the experimental shrimps because pure males never attain body sizes as large as those exhibited by hermaphrodites in natural populations (Baldwin and Bauer 2003). Consequently, the body size of pure males (range, 6.63–7.93; mean \pm SD, 7.45 \pm 0.44) was significantly smaller than that of hermaphrodites (range, 10.01–11.96; mean \pm SD, 10.61 \pm 0.64) (t -test, $t_{38}=18.26$, $P=0.001$). Nonetheless, this experimental setup emulates potential competitive interactions between pure males and hermaphrodites during mating in the field.

Results

The effect of male mating opportunities on sex allocation

The time that shrimps spent as males before maturing as hermaphrodites varied significantly among treatments (Wald Chi-square test, $\chi_1^2=39.7$, $P<0.001$, $N=75$). There were two main patterns in the relative time that individuals spent as males. First, in comparison to pure males maintained with no conspecific, pure males in groups with two or more hermaphrodites increased the time they spent as male. The larger the number of hermaphrodites in the aquarium, the longer these pure males took to mature as hermaphrodites. Second, pure males maintained with only one hermaphrodite reduced the time they spent as males in comparison to single pure males (Fig. 1).

Food availability and group size

The growth rate (mm CL/day) of pure males varied significantly among treatments (one-way ANOVA on log transformed data, $F_{4,69}=5.9$, $P=0.0004$) (Fig. 2). The growth rate of pure males maintained with ten hermaphrodites was significantly slower than that recorded for pure males maintained with one hermaphrodite (a posteriori Tukey's HSD test adjusted for multiple comparisons $P<0.05$). However, no other significant differences in growth rate of pure males among treatments were found ($P>0.05$ in the remaining of the comparisons).

Mating ability of pure males and hermaphrodites

Pure males were four times more successful in inseminating shrimps reproducing as females than were hermaphrodites

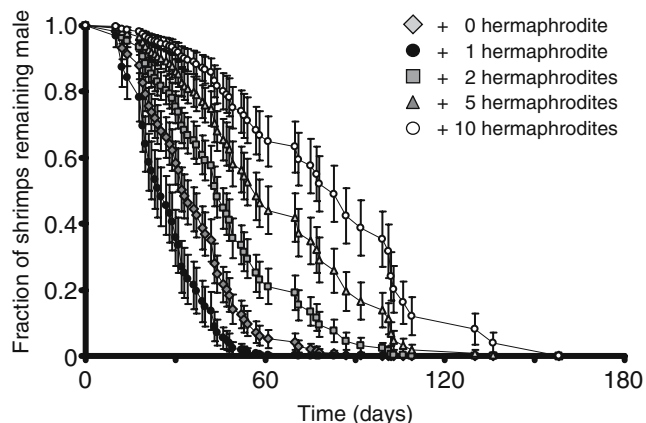


Fig. 1 Social mediation of sex allocation in *Lysmata wurdemanni*. Curves denoting the proportion of shrimps remaining male over time (days) when reared with different numbers of hermaphrodites. Error bars are binomial standard errors of the estimates (for details see Materials and methods section)

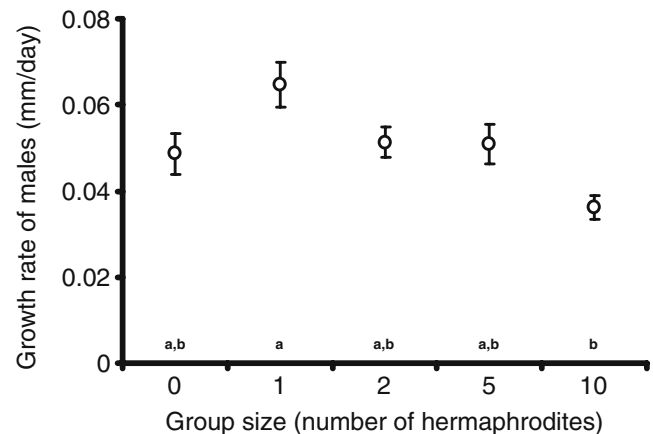


Fig. 2 Growth rate (average±standard error) of males reared with different number of hermaphrodites in *Lysmata wurdemanni*. Treatments labelled with different letters are significantly different ($P<0.05$) (for details see Materials and methods section)

acting as males (16 out of 20 vs four out of 20, $\chi_1^2=7.2$, $P_{\text{exact}}=0.012$).

Discussion

Pure males of *Lysmata wurdemanni* adjust the timing of maturation as hermaphrodites according to male mating opportunities mediated by group size. In comparison to single males (in which change to the terminal hermaphroditic phase occurred in the absence of social stimuli), pure males kept together with just one hermaphrodite, reduced the time they spent as males. Most probably, total reproductive output is maximized by two individuals being simultaneous hermaphrodites when the mating system is a pair. Conversely, pure males in groups with two or more hermaphrodites increased the time they spent as males in comparison to single pure males. Is this increase in investment to male reproductive function simply a consequence of increasing resource depletion with group size? The only treatment in which it was not possible to rule out food depletion in this study was that in which pure males were reared with ten hermaphrodites. In this treatment, pure males experienced a reduction in growth rate, but only when compared to pure males reared with a single other hermaphrodite. Most probably, delayed maturation of pure males as hermaphrodites, when maintained with ten other hermaphrodites, was due to the combined effect of both male mating opportunities and suboptimal food conditions. However, reduced growth rate in pure males at such large densities may also be explained simply by increased 'social stress,' regardless of resource depletion.

Additionally, with increasing male mating opportunities, pure male shrimps should increase male related activities (i.e., mate searching, sperm production) that may compete for resources available for growth, hence, reducing it.

Because of the recognized trade-off between growth and reproduction (Stearns 1992), the larger the amounts of resources individuals invest in reproduction in the protandric phase, the smaller the amount they should be able to allocate later in life to growth, maintenance, maturation, and reproduction as female. The cost of allocation to the male function during the early protandric phase of this shrimp should have long-term consequences on future sex allocation and reproductive success that remain to be addressed. In the remaining treatments, growth rate of shrimps did not differ significantly, and thus, resource depletion does not appear to play a role in eliciting pure males to delay maturation as hermaphrodites with increasing group size (male mating opportunities) in these treatments. These results suggest that the observed increase in investment to male reproductive function in *L. wurdemanni* is mostly an adaptive response of shrimps to male mating opportunities mediated by the population size of hermaphroditic shrimps. The actual informative cue that pure male shrimps may use to perceive different mating group sizes deserves further attention.

A reason to explain this plastic shift in sex allocation is that pure males are more successful in mating as males than are hermaphrodites. It will pay, reproductively, for pure males to delay maturation as hermaphrodites in large but not in small groups. In agreement with this hypothesis, pure males were experimentally confirmed to be four times more successful in reproducing as males than hermaphrodites, which may be a consequence of morphological differences among these sexual morphotypes. In *L. wurdemanni*, hermaphrodites are bulkier than males because they develop wider abdominal sterna and pleural plates to brood their embryos (Bauer and Holt 1998). This bulkiness may ultimately decrease maneuvering ability of hermaphrodites compared to males, and thus, reduce their mobility to chase and grasp swimming shrimps reproducing as females. In addition, the small body size of pure males may increase their mate searching efficiency compared to hermaphrodites (Andersson 1994). Overall, socially mediated shifts in sex allocation rely upon precopulatory male–male competition in this protandric simultaneous hermaphrodite.

The present study helps explain some of the natural variation in the relative abundance of sexual phases reported for *L. wurdemanni*. Large pure males (shrimps delaying maturation as hermaphrodites) are more frequently found later during the reproductive season (i.e., autumn and winter) than they are earlier (i.e., spring and summer) (Baldwin and Bauer 2003; Bauer 2002b). Even though there is an increase in the proportion of large pure males, there is also an increase in the overall abundance of shrimps, including hermaphrodites, throughout the reproductive season (Baldwin and Bauer 2003; Bauer 2002b). A

greater abundance of fertile hermaphrodites late during the breeding season may signify larger average mating group sizes and male mating opportunities for pure males recruiting late as compared to those recruiting early during the same season. Therefore, it will pay (in fitness) for pure males to delay maturation as hermaphrodites late, but not early, during the reproductive season. Overall, variability in size/age at which pure males mature as hermaphrodites in the field appears to be influenced by both abiotic (i.e., water temperature and photoperiod—Bauer 2002a) and social conditions in *L. wurdemanni* (Baeza and Bauer 2004; present study).

Individuals of the protandric simultaneous hermaphrodite shrimp, *L. wurdemanni*, delayed maturation as hermaphrodites, and thus, increased lifetime allocation to the male function, with increasing male mating opportunities mediated by the number of hermaphroditic shrimps in the surroundings (group size). This situation may be considered analogous to the effect of sperm competition that also increases allocation to the male function (sperm production) in strict simultaneous hermaphrodites (Trouvé et al. 1999; Locher and Baur 2000; Schärer and Ladurner 2003; Tan et al. 2004). Pure males of *L. wurdemanni* additionally delay maturation as hermaphrodites with increases in the proportion of hermaphrodites in the population. This latter situation is similar to sex-ratio induction of sex allocation, as predicted for strict sequential hermaphrodites (Baeza and Bauer 2004). That a species featuring mixed hermaphroditism shifts sex allocation in agreement with predictions raised for strict sequential and strict simultaneous hermaphrodites supports new ideas that consider different sexual systems as part of an evolutionary continuum (see Cadet et al. 2004).

This study represents an example of flexible adjustment of the phenotype to environmental (i.e., social) conditions. This social mediation of sex allocation in a protandric simultaneous hermaphrodite supports the fundamental prediction of sex allocation theory (plastic adjustments in resource allocation—Charnov 1982) adding up to other studies that have demonstrated offspring sex-ratio shifts in gonochoric wasps (Shuker and West 2004), shifts in the size at female maturity in strict protandric marine snails (Collin 1995), and adjustments in male reproductive investment in strict simultaneous hermaphrodites both at the interspecific (Petersen and Fischer 1996) and intraspecific level (Schärer and Ladurner 2003).

Acknowledgements The author thanks C.W. Petersen, R. Jaeger, M. Thiel, S. Martin, and S. Fuentes, for their insightful comments on the drafts of the manuscript. The helpful comments and suggestions of two anonymous reviewers are gratefully acknowledged. Thanks to J. Caskey and J. Noel for improving the language of the manuscript. This research was funded by a Sigma Xi Grant in Aid of Research,

Lerner-Gray Fund for Marine Science (NMNH), and NSF Doctoral Dissertation Improvement Grant IBN No. 0506908 to J. A. Baeza, and NSF Grant No. 9982466 to R.T. Bauer. The author acknowledges a 'President of the Republic' fellowship (Chile). The experiments comply with the current laws of the United States of America.

References

- Allison PD (1995) Survival analysis using the SAS system: practical guide. SAS Institute, Cary, North Carolina, USA
- Andersson M (1994) Sexual Selection. Princeton Univ. Press, Princeton, New Jersey
- Baeza JA, Bauer RT (2004) Experimental test of socially mediated sex change in a protandric simultaneous hermaphrodite, the marine shrimp *Lyasmata wurdemanni* (Caridea: Hippolytidae). Behav Ecol Sociobiol 55:544–550
- Baldwin AP, Bauer RT (2003) Growth, survivorship, life span, and sex change in the hermaphroditic shrimp *Lyasmata wurdemanni* (Decapoda: Caridea: Hippolytidae). Mar Biol 143:157–166
- Bauer RT (2000) Simultaneous hermaphroditism in caridean shrimps: a unique and puzzling sexual system in the Decapoda. J Crustac Biol 20 (Spec. No. 2):116–128
- Bauer RT (2002a) Test of hypotheses on the adaptive value of an extended male phase in the hermaphroditic shrimp *Lyasmata wurdemanni* (Caridea: Hippolytidae). Biol Bull 203:347–357
- Bauer RT (2002b) Reproductive ecology of a protandric simultaneous hermaphrodite, the shrimp *Lyasmata wurdemanni* (Decapoda: Caridea: Hippolytidae). J Crustac Biol 22:742–749
- Bauer RT, Holt GJ (1998) Simultaneous hermaphroditism in the marine shrimp *Lyasmata wurdemanni* (Caridea: Hippolytidae): an undescribed sexual system in the decapod Crustacea. Mar Biol 132:223–235
- Cadet C, Metz JAJ, Klinkhamer PGL (2004) Size and the not-no-single sex: disentangling the effects of size and budget on sex allocation in hermaphrodites. Am Nat 164:779–792
- Charnov EL (1982) The Theory of Sex Allocation. Princeton Univ. Press, Princeton, New Jersey
- Collin R (1995) Sex, size, and position: a test of models predicting size at sex change in the protandrous gastropod *Crepidula fornicata*. Am Nat 146:815–831
- Hamilton WD (1967) Extraordinary sex ratios. Science 156:477–488
- Herre EA (1985) Sex ratio adjustment in fig wasps. Science 228:896–898
- Locher R, Baur B (2000) Mating frequency and resource allocation to male and female function in the simultaneous hermaphrodite land snail *Arianta arbustorum*. J Evol Biol 13:607–614
- Lorenzi MC, Sella G, Schleicherova D, Ramella L (2005) Outcrossing hermaphroditic polychaete worms adjust their sex allocation to social conditions. J Evol Biol 18:1341–1347
- Munday PL, Caley MJ, Jones GP (1998) Bi-directional sex change in a coral-dwelling goby. Behav Ecol Sociobiol 43:371–377
- Munday PL, Buston PM, Wagner RR (2006) Diversity and flexibility of sex-change strategies in animals. Trends Ecol Evol 21:89–95
- Petersen CW (1991) Sex allocation in hermaphroditic sea basses. Am Nat 138:650–667
- Petersen CW, Fischer EA (1996) Intraspecific variation in sex allocation in a simultaneous hermaphrodite: the effect of individual size. Evolution 50:636–645
- Premoli MC, Sella G (1995) Sex economy in benthic polychaetes. Ethol Ecol Evol 7:27–48
- SAS Institute (2001) SAS/STAT software; version 8.2. SAS Institute, Cary, North Carolina, USA
- Schärer L, Ladurner P (2003) Phenotypically plastic adjustment of sex allocation in a simultaneous hermaphrodite. Proc R Soc Lond B 270:935–941
- Schleicherová D, Lorenzi MC, Sella G (2006) How outcrossing hermaphrodites sense the presence of conspecifics and suppress female allocation. Behav Ecol 17:1–5
- Shuker DM, West SA (2004) Information constraints and the precision of adaptation: sex ratio manipulation in wasps. Proc Natl Acad Sci USA 101:10363–10367
- St. Mary CM (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. Behav Ecol 5:304–311
- Stearns SC (1992) The evolution of life histories. Oxford University Press, New York, USA
- Tan GN, Govedich FR, Burd M (2004) Social group size, potential sperm competition and reproductive investment in a hermaphroditic leech, *Helobdella papillornata* (Euhirudinea: Glossiphoniidae). J Evol Biol 17:574–580
- Tomiyama K (1996) Mate-choice criteria in a protandrous simultaneously hermaphroditic land snail *Achatina fulica* (Férussac) (Stylommatophora: Achatinidae). J Molluscan Stud 62:101–111
- Trouvé S, Jourdan J, Renaud F, Durand P, Morand S (1999) Adaptive sex allocation in a simultaneous hermaphrodite. Evolution 53:1599–1604
- Warner RR, Fitch DL, Standish JD (1996) Social control of sex change in the shelf limpet, *Crepidula norrisiarum*: size-specific responses to local group composition. J Exp Mar Biol Ecol 204:155–167
- Werren JH (1980) Sex ratio adaptations to local mate competition in a parasitic wasp. Science 208:1157–1159
- Zhang D, Lin J (2005) Comparative mating success of smaller male-phase and larger male-role euhemaphrodite-phase shrimp, *Lyasmata wurdemanni* (Caridea: Hippolytidae). Mar Biol 147:1387–1392
- Zucker N, Cunningham M, Adams HP (1997) Anatomical evidence for androdioecy in the clam shrimp *Eulimnadia texana*. Hydrobiologia 359:171–175