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Sex-dependent energetic cost of a protandric simultaneous hermaphroditic shrimp *Lysmata wurdemanni* under different social conditions

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ABSTRACT

We tested a hypothesis (sex-dependent energetic cost) in a protandric simultaneous hermaphroditic (PSH) shrimp *Lysmata wurdemanni* under different social conditions to explain the adaptive value of PSH. Two components (sex-dependent energetic cost and resource holding power) of the hypothesis were tested. Growth reduction was used to represent the energetic cost in reproduction. This study demonstrated that energetic cost of reproduction of the shrimp is generally sex-dependent, but they are strongly affected by the social environment. When male phase (MP) or euhermaphridite phase (EP) shrimp were housed individually (i.e. without social and reproductive behavior), reproductive cost (energy for gametic production only) of MP shrimp was significantly lower than that of EP shrimp (with both male and female functions). However, growth of MP shrimp did not differ from that of EP individuals when they were housed with EP shrimp, i.e. when costs of both social and mating behavior were considered. When a MP shrimp copulated with EP shrimp more than once within a molt cycle, growth was significantly reduced. Result also indicated that resource holding power of *L. wurdemanni* was not associated with energy burden of female function. Our results do not support the hypothesis of size-dependent energetic cost in *L. wurdemanni*.

1. Introduction

Protandric simultaneous hermaphroditism (PSH) is a rare reproductive system that exists in some animals, such as flatworms (Vizoso and Schärer, 2007), polychaetes (Premoli and Sella, 1995), snails (Tomiyama, 1996), and shrimp species in the genera *Lysmata* (e.g. Bauer and Holt, 1998; Fiedler, 1998; Bauer and Newman, 2004) and *Exhippolysmata* (Kagwade, 1982; Laubenheimer and Rhyne, 2008). In PSH, individuals mature as male first (male phase—MP), i.e. they only function sexually as males. Female function may develop later, so that male and female functions coexist in the later phase (euhermaphrodite phase—EP) of the organism. Although sex allocation theory has well explained pure hermaphroditism (i.e. sequential hermaphroditism and simultaneous hermaphroditism) (Ghiselin, 1969; Charnov, 1982; Stella, 1990; Schärer and Ladurner, 2003), limited studies exist to explain intermediate or mixed sexual system (such as PSH) (Leonard, 2005; Bauer, 2006). Sexual selection is considered to be important in the evolution of PSH (Leonard, 2005). However, sexual selection may not be adequate to explain the evolution of PSH in *Lysmata* species, because mating success of male role shrimp is weakly correlated with their size (Zhang and Lin, 2005a).

PSH system in decapod crustaceans is only found in two genera, *Lysmata* Risso, 1816 (e.g., Bauer and Holt, 1998; Fiedler, 1998; Bauer and Newman, 2004) and *Exhippolysmata* Stebbing, 1915 (Kagwade, 1982; Laubenheimer and Rhyne, 2008). A few empirical studies have dealt with the adaptive significance of PSH in *Lysmata* species (Bauer, 2002; Zhang and Lin, 2005a), and a hypothesis (sex-dependent energetic cost) that was proposed originally to explain size-dependent allocation in pure simultaneous hermaphrodites (Klinkhamer et al., 1997; St. Mary, 1997; Angeloni et al., 2002; Cadet et al., 2004) was tested on *Lysmata wurdemanni* (Gibbes, 1850) (Baeza, 2006). Sex-dependent energetic cost model predicts that if growth rate differs between the sexes, the sex with a higher growth rate is favored first. The model indicates that the female function needs higher energetic cost of reproduction than the male function so that male grows faster than female; larger individuals have greater resource holding power than smaller ones (Lloyd and Bawa, 1984; de Jong and Klinkhamer, 1994; Angeloni et al., 2002). If protandric simultaneous hermaphroditism is considered as a form of size-dependent sex allocation, larger euhermaphroditic individuals should grow slower and have greater resource holding power which is referred to as ability to hold onto food than males do because they allocate more energy to both male and female functions (Baeza, 2006). Although this model was supported

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in Baeza's (2006) study of *L. wurdemanni*, the results are problematic because the cost of non-mating social encounter and mating process was not considered in the group-living species (Bauer and Holt, 1998). Social environment is a very important factor in the study of evolution and many biological processes. Many studies have shown that density plays a significant role in the evolution of characteristics within populations (reviewed by MacArthur and Wilson, 1967) and affects a number of processes, such as competition (e.g., reviewed by Brown, 1964), population regulation (e.g., Hopper and Crowley, 1996), territoriality (e.g., Elliott, 1994), growth (e.g., Karplus, 2005), and reproductive behavior (e.g., Woolbright et al., 1990; Jirotkul, 1999; Moksnes, 2004) on either genetic or phenotypic level. To test resource allocation, the population structure and relationships among individuals in a population need to be taken into account (Charnov, 1985).

According to Baeza's (2006) results, male phase (MP) shrimp grow faster than euhermaphrodite phase (EP, termed female phase by Bauer and colleagues, or simultaneous hermaphrodite by Calado) shrimp, so MP shrimp in a cohort should be larger in size than EP shrimp. However, EP shrimp are normally larger in a cohort/population due to the fact that the shrimp mature as male first and many of them change to simultaneous hermaphrodite later (Bauer and Holt, 1998; Lin and Zhang, 2001; Baldwin and Bauer, 2003). Obviously the energetic cost of the male function for producing spermatophores alone is not enough to explain the adaptive significance of PSH. Therefore, energetic costs in mating, including locating mates, courtship, competing with rival suitors, and copulation (Daly, 1978) should also be considered because they are a substantial part of male costs (Given, 1988; Sparkes et al., 1996). For example, male frogs with low calling effort during breeding seasons grow faster than the ones with high calling efforts (Given, 1988). In the PSH polychaete worm *Ophryotrocha diadema*, male behaviors have been shown to be expensive (Lorenzi et al., 2006). Male role *L. wurdemanni* may spend up to 8 h on pre-copulatory behavior before EP shrimp molt (Zhang and Lin, 2004, 2005b, 2006) which might be a energetic cost process.

Baeza (2006) compared the resource holding power of an larger EP with a smaller MP shrimp. However, in natural populations, some MP shrimp are larger than EP shrimp due to the delay in sex change (Bauer and Holt, 1998; Baldwin and Bauer, 2003). If the resource holding power in *L. wurdemanni* is size-dependent as Baeza (2006) suggested, then larger MP shrimp should be more powerful in holding food than smaller EP shrimp as well. Then the resource holding power difference between EP and MP shrimp may not be related to higher female energy cost as Baeza (2006) suggested, i.e. the resource holding power may not be an adaptive value of PSH.

Resource allocation between reproduction and somatic growth has long been a focus in ecological studies (Roff, 1992; Sterns, 1992), and is assumed to be compensatory, i.e. an increase in reproductive expenditure results in decreased growth (Reekie and Bazzaz, 1992; Sterns, 1992), so the reduction in growth is usually used as a measurement of reproductive cost (e.g., Berglund and Rosenqvist, 1986).

In this study, we re-tested the two predictions that the MP shrimp should grow faster than EP shrimp, and EP shrimp should have higher food holding power than MP shrimp under different social environments.

2. Materials and methods

2.1. Study organism and maintenance

L. wurdemanni naturally occurs along the Atlantic coast of North and South America from New Jersey to Brazil (Williams, 1984). They usually live under rock jetties in high density (Bauer and Holt 1998; Baldwin and Bauer, 2003). An individual first matures as a functional male having male external characteristics: (1) cincinnulli on the endopods of pleopods 1, and (2) appendices masculinae on the endopods of pleopods 2 (Bauer and Holt, 1998). MP shrimp have ovotestes with an undeveloped ovarian portion (Bauer and Holt, 1998). Most MP shrimp pass through four transitional phases (i.e. four transitional molts) to become EP with both male and female functions, in which the external male characteristics gradually disappear (Zhang and Lin, 2005c). EP shrimp are able to function as males during intermolt and females during postmolt, but they are not able to self fertilize (Bauer and Holt, 1998). Male shrimp (MP shrimp or EP shrimp serving male role) displays pre-copulatory behavior (approach, follow, and chase) toward the EP shrimp that is about to molt for up to 8 h prior to molting and then proceed to copulate with the newly molted EP shrimp (Zhang and Lin, 2004, 2005b, 2006). In the wild, the maximum recorded size of EP shrimp is 1.4 cm carapace length (Baldwin and Bauer, 2003) which is about 5.3 cm in total length (TL) (Lin and Zhang, 2001). Male function matures when organisms reach about 1.2 cm TL (Zhang and Lin, 2005c). The size at the time of the sex change varies, with the minimum around 2.4 cm TL (Lin and Zhang, 2001; Baldwin and Bauer, 2003; Zhang and Lin, 2007). This variation in the timing of sex change is mainly controlled by the social environment (Lin and Zhang, 2001; Baeza and Bauer, 2004; Zhang and Lin, 2007). Presence of EP shrimp in a population inhibits MP shrimp from changing sex to EP (Baeza and Bauer, 2004; Zhang and Lin, 2007). Some MP shrimp may never change sex to EP (Bauer, 2002).

The parent shrimp were collected from the rock jetty at Sebastian inlet, Sebastian, Florida. They were maintained prior to the experiments in 75-L flow through tanks at a temperature of 27–28 °C, 34–35 ppt salinity, and a14 h (fluorescent) light:10 h dark cycle, and were fed with frozen *Artemia* sp. twice daily. The same conditions were applied to all the experiments as will be described later.

F_2 shrimp were raised in the laboratory. The postlarvae were cultured for about 50 days in a density of 10 per 20 L bucket, then those shrimp were used for the experiments. The growth rate of *L. wurdemanni* is both size and age dependent, older individuals might grow slower than younger ones even if they are similar in size (personal observation). Hence, sibling MP (2.6 to 2.75 cm TL) and EP shrimp (2.7 to 3.0 cm) were used for investigating reproductive cost to eliminate the confounding effects of age and size on growth. Prior to formal experiment we ran a pre-test with 10 MP (2.6 to 2.75 cm TL) and EP shrimp (2.7 to 3.0 cm TL), and similar sizes of EP shrimp (2.71 ± 0.02 cm TL) and MP shrimp (2.71 ± 0.01 cm TL) to confirm the growth of the sibling MP and EP shrimp is sex-dependent, and the shrimp size used in this study did not affect growth of MP and EP shrimp. Results indicated that growth rates of non-mating EP and MP shrimp were not size correlated (for MP $r^2 = 0.155$, $P > 0.05$; for EP, $r^2 = 0.200$, $P > 0.05$), and the growth rates of non-mating EP shrimp and MP shrimp with similar sizes over 11 days (one molt cycle) were significantly different (Student's *t*-test, $t = 5.993$, $df = 18$, $P < 0.001$).

2.2. Energetic cost of reproduction

This experiment is to determine the difference between the sexes in overall energetic cost of reproduction, i.e. cost spending for non-mating social interaction (encounters during the intermolt period of EP shrimp before MP shrimp start displaying pre-mating behavior), sperm, eggs, pre-copulatory behavior, and copulation because Baeza's (2006) study only considered energetic cost of gamete production. This experiment included two tests: 1) overall energetic cost of reproduction; and 2) comparison of energetic cost with different mating times.

EP shrimp is able to serve as male role (Em) during intermolt, hence effect of male function on growth of both MP and EP shrimp was examined during mating and no-mating periods. This experiment was conducted in 20 L buckets. Initial sizes of MP shrimp for mating