



# Molecular phylogeny of broken-back shrimps (genus *Lysmata* and allies): A test of the ‘Tomlinson–Ghiselin’ hypothesis explaining the evolution of hermaphroditism



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## ABSTRACT

The ‘Tomlinson–Ghiselin’ hypothesis (TGh) predicts that outcrossing simultaneous hermaphroditism (SH) is advantageous when population density is low because the probability of finding sexual partners is negligible. In shrimps from the family Lysmatidae, Bauer’s historical contingency hypothesis (HCh) suggests that SH evolved in an ancestral tropical species that adopted a symbiotic lifestyle with, e.g., sea anemones and became a specialized fish-cleaner. Restricted mobility of shrimps due to their association with a host, and hence, reduced probability of encountering mating partners, would have favored SH. The HCh is a special case of the TGh. Herein, I examined within a phylogenetic framework whether the TGh/HCh explains the origin of SH in shrimps. A phylogeny of caridean broken-back shrimps in the families Lysmatidae, Barbouriidae, Merguiidae was first developed using nuclear and mitochondrial markers. Complete evidence phylogenetic analyses using maximum likelihood (ML) and Bayesian inference (BI) demonstrated that Lysmatidae + Barbouriidae are monophyletic. In turn, Merguiidae is sister to the Lysmatidae + Barbouriidae. ML and BI ancestral character-state reconstruction in the resulting phylogenetic trees indicated that the ancestral Lysmatidae was either gregarious or lived in small groups and was not symbiotic. Four different evolutionary transitions from a free-living to a symbiotic lifestyle occurred in shrimps. Therefore, the evolution of SH in shrimps cannot be explained by the TGh/HCh; reduced probability of encountering mating partners in an ancestral species due to its association with a sessile host did not favor SH in the Lysmatidae. It is proposed that two conditions acting together in the past; low male mating opportunities and brooding constraints, might have favored SH in the ancestral Lysmatidae + Barbouriidae. Additional studies on the life history and phylogenetics of broken-back shrimps are needed to understand the evolution of SH in the ecologically diverse Caridea.

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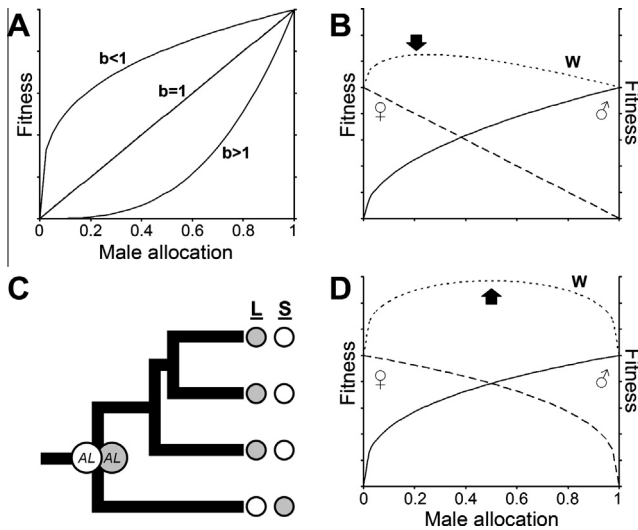
## 1. Introduction

Simultaneous hermaphroditism (SH) occurs in species in which individuals allocate resources to both male and female function and simultaneously reproduce as both sexes (Charnov, 1982). Sex allocation theory aims to understand those conditions favoring different sexual systems and predicts the evolution and stability of SH given three primary conditions. First, at least one of the two curves depicting the relationship between sex-specific investment and fitness gains (i.e., fitness gain curves) should follow the law of diminishing returns; fitness increases at a decreasing rate with a unit increase in investment (Charnov, 1982; Klinkhamer et al., 1997; Baeza, 2007a,b) (Fig. 1A). Second, the male fitness gain curve is the one that most commonly follows the law of diminishing returns (Fig. 1A and B). Third, saturation of the male fitness curve

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is driven by low population abundance which implies infrequent sexual encounter rates and low intensity of sperm competition (Charnov, 1982; Michiels et al., 2009). Under these circumstances, individuals investing resources only to the male function will be wasting energy compared to individuals investing resources to both male and female functions. Thus, a ‘low-density’ population is exposed to the invasion by individuals harboring genes that command the production of sperm and ova at the same time. The rationale above was early proposed as a model by Tomlinson (1966) and Ghiselin (1969) and is here named the ‘Tomlinson–Ghiselin’ hypothesis (see also Ghiselin, 1974).

Sex allocation is a thriving research field that has achieved considerable theoretical sophistication since its formal proposal (Charnov, 1982; Strathmann et al., 1984; Petersen, 1990, 1991; Petraitis, 1990; Greeff and Michiels, 1999; Cadet et al., 2004; Michiels et al., 2009). Yet, the conditions driving SH have rarely been formally explored within a phylogenetic framework (e.g., Eppley and Jesson,



**Fig. 1.** (A) Fitness gain curves that relate investments in a particular reproductive function (e.g., male allocation) to fitness gains derived from these investments. Curves are represented as power functions ( $y = ax^b$ ) where the exponent ( $b$ ) determines their shape and whether the reproductive success is a linear ( $b = 1$ ), accelerating ( $b > 1$ ), or diminishing ( $b < 1$ ) function of investment. (B) Simultaneous hermaphroditism is favored when the male curve saturates with increasing investment to the male function. In this graph, the female fitness gain curve does not saturate. Under these conditions, simultaneous hermaphroditism represents the optimal resource allocation strategy that maximizes (arrow) the sum or product of the fitness derived from the male and female investment, denoted by the curve  $W$  in the figure. (C) A possible phylogeny in the Lysmatidae and allies supporting Bauer's (2000) historical contingency hypothesis on the evolution of simultaneous hermaphroditism in broken-back caridean shrimps. In the tree, the ancestral Lysmatidae exhibits a symbiotic (white circle) and pair-living (grey circle) lifestyle. The conditions above are expected to favor simultaneous hermaphroditism in agreement with that predicted by the 'Tomlinson–Ghiselin' hypothesis. See Introduction for further details. Column of circles to the right of the tree terminals represent the lifestyle (L, free-living [grey circles], symbiotic [white circles]) and socioecology (S, pair living [grey circles], gregarious and/or group living [white circles]) exhibited by extant species in the Lysmatidae. (D) Simultaneous hermaphroditism is also favored when both the male and female curves saturates with increasing allocation to each function. In all panels, the x-axis, a value of zero indicates that an individual is allocating 0% of its resources to the male function, and subsequently, 100% to the female function.

2008). Attempts to answer this question provide an opportunity to test predictions fundamental to sex allocation theory from a historical perspective. In this study, I examined whether or not the 'Tomlinson–Ghiselin' hypothesis explains the origin of SH in caridean 'broken-back' shrimps from the family Lysmatidae (*sensu* Christoffersen, 1987) and allies.

Among caridean shrimps, one of the most species-rich crustacean clades (De Grave et al., 2009), the genera *Exhippolydium*, *Lysmata*, and *Lysmatella* pertaining to the family Lysmatidae are recognized for their ecological diversity (Fig. 2) and unusual sexual system; SH with an adolescent male phase (Bauer and Holt, 1998; Fiedler, 1998; Braga et al., 2009; Onaga et al., 2012). In these species, juveniles invariably mature first as males bearing typical caridean male characteristics (i.e., appendix masculina on the second pair of pleopods). Later, they become functional simultaneous hermaphrodites (Bauer, 2000). After maturation, hermaphrodites resemble females of caridean gonochoric species brooding embryos under the abdomen. However, hermaphrodites retain testicular tissue, male ducts, and gonopores and can and do reproduce as both male and female (Bauer, 2000; Baeza, 2009). After becoming hermaphrodites, individuals do not revert to males and no self-fertilization has been observed (Bauer, 2000; Baeza, 2009). This sex allocation pattern is also called 'adolescent protandry' (*sensu* Ghiselin, 1974) and 'protandric simultaneous hermaphroditism' (*sensu* Bauer and Holt, 1998).

Most studies on shrimps from the family Lysmatidae (containing the genera *Calliasmata*, *Lysmata*, *Lysmatella* and *Exhippolydium*) have focused on explaining the adaptive value of the adolescent male phase (Bauer, 2002, 2004, 2005; Baeza, 2006, 2007a,b), the benefits and mechanisms enforcing social monogamy (Baeza, 2010a,b; Wong and Michiels, 2011) and have examined phenotypic plasticity of the size at first maturity (Bauer, 2002; Baeza and Bauer, 2004; Baeza, 2006; Zhang et al., 2007). In spite of the increasing knowledge regarding the behavior and ecology of the family Lysmatidae, the evolutionary origins of simultaneous hermaphroditism in the genus remains uncertain. Although recent studies have shown that the variety of lifestyles in the Lysmatidae is greater than originally recognized (Baeza et al., 2008; Baeza and Anker, 2008; Baeza, 2009; Wirtz et al., 2009), an emerging dichotomy in social organization and ecology was noticed by initial studies. One group of species (named "crowd" species by Bauer (2000)) was described as inhabiting warm subtropical environments, occurring as dense aggregations in their refuges and exhibiting no specialized fish-cleaning behavior (i.e., *Lysmata californica* – Bauer and Newman, 2004; *L. wurdemanni* – Baeza, 2006) (Fig. 2). A second group (named 'pair' species by Bauer (2000)) was described as mostly tropical, occurring at low densities in the subtidal, and dwelling as socially monogamous pairs on sea anemones used as spots for fish cleaning activities (i.e., *L. grabhami* – Wirtz, 1997; *L. bovinensis* – Fiedler, 1998) (Fig. 2). Based on this initial dichotomy, Bauer (2000) proposed that SH (with an adolescent male phase) evolved in the tropics from an ancestral protandric species of *Lysmata* that adopted a symbiotic lifestyle (symbiosis here defined *sensu* De Bary (1879) as dissimilar organisms living together) and became a specialized fish cleaner. Restricted mobility of individuals due to their association with sessile hosts, and hence, reduced probability of encountering mating partners, would have favored simultaneous hermaphroditism (also, see Bauer, 2006). Bauer's (2000) hypothesis is a more specific case of the more general model proposed by Tomlinson (1966) and Ghiselin (1969) (Fig. 1A and B). Simultaneous hermaphroditism is advantageous when population density is low because the probability of finding sexual partners is negligible (Tomlinson, 1966; Ghiselin, 1969). Bauer's hypothesis for the evolution of SH in shrimps was explored by Baeza (2009) who recognized that the information available at that time on the reproductive biology of the Lysmatidae and from other closely related genera was too scarce to accurately resolve the character-state of the ancestral species of the Lysmatidae. Nonetheless, the body of literature on the natural history of the Lysmatidae accumulated during the last years and recent advances in ancestral character-state reconstruction using maximum likelihood (Maddison and Maddison, 2010) and Bayesian inference (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2012) makes it possible to test whether the ancestral lysmatid shrimp featured a symbiotic lifestyle and a socially monogamous mating system as proposed by Bauer (2000).

The resolution of the phylogenetic relationships within and between the family Lysmatidae and other closely related families (e.g., Barbouriidae and Merguiliidae *sensu* Christoffersen, 1987) is of paramount importance to deciphering the historical conditions favoring SH in shrimps. Simultaneous hermaphroditism is believed to be a fixed trait in the family Lysmatidae (Baeza, 2009; Braga et al., 2009; Onaga et al., 2012). Thus, SH most probably evolved only once in the ancestral Lysmatidae (Bauer, 2000). However, the recent discovery of SH with an early male phase in *Parhippolyte misticia* (Onaga et al., 2012), pertaining to the closely related family Barbouriidae, raises the issue of this sexual system evolving before the origin of the ancestral Lysmatidae or more than once during the phylogenetic history of the species-rich infraorder Caridea. Recent phylogenetic studies have shown that the families Lysmatidae (containing *Calliasmata*, *Lysmata*, *Lysmatella* and *Exhippolydium*),

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