

Sexual selection explains sex-specific growth plasticity and positive allometry for sexual size dimorphism in a reef fish

Stefan P. W. Walker* and Mark I. McCormick

*School of Marine and Tropical Biology, and the ARC Centre of Excellence for Coral Reef Studies,
James Cook University, Townsville, Queensland 4811, Australia*

In 1950, Rensch noted that in clades where males are the larger sex, sexual size dimorphism (SSD) tends to be more pronounced in larger species. This fundamental allometric relationship is now known as ‘Rensch’s rule’. While most researchers attribute Rensch’s rule to sexual selection for male size, experimental evidence is lacking. Here, we suggest that ultimate hypotheses for Rensch’s rule should also apply to groups of individuals and that individual trait plasticity can be used to test those hypotheses experimentally. Specifically, we show that in the sex-changing fish *Parapercis cylindrica*, larger males have larger harems with larger females, and that SSD increases with harem size. Thus, sexual selection for male body size is the ultimate cause of sexual size allometry. In addition, we experimentally illustrate a positive relationship between polygyny potential and individual growth rate during sex change from female to male. Thus, sexual selection is the ultimate cause of variation in growth rate, and variation in growth rate is the proximate cause of sexual size allometry. Taken together, our results provide compelling evidence in support of the sexual selection hypothesis for Rensch’s rule and highlight the potential importance of individual growth modification in the shaping of morphological patterns in Nature.

Keywords: Sexual selection; sexual size dimorphism; Rensch’s rule; growth plasticity; sex change; reef fish

1. INTRODUCTION

When species are compared within a clade, sexual size dimorphism (SSD) is often found to vary with body size, a pattern initially observed by Rensch (1950). This allometry is detected as $\beta \neq 1$, where β is the slope of a model II regression of log(male size) on log (female size) (Fairbairn 1997, 2005). Most frequently, β exceeds 1 (i.e. positive size allometry), representing an increase in SSD with size when males are the larger sex and a decrease in SSD with size when females are the larger sex, a trend formalized as ‘Rensch’s rule’ (*sensu* Fairbairn 1997) (primates, Clutton-Brock *et al.* 1977; turtles, Berry & Shine 1980; water striders, Anderson 1997; Fairbairn 2005; mites, Colwell 2000; salmonid fishes, Young 2005; birds, Payne 1984; Colwell 2000; Székely *et al.* 2004; Raihani *et al.* 2006; Dale *et al.* 2007). The conformation of Rensch’s rule in a broad range of taxa highlights the need to examine the evolutionary processes behind it (Fairbairn 1997). This remains an important research focus (Fairbairn 1997; Dale *et al.* 2007).

In comparative studies of SSD, it is generally assumed that adult female and male body size is genetically fixed, such that Rensch’s rule reflects coevolution between absolute female and male body size coupled with greater evolutionary divergence in absolute male body size (Fairbairn 1997; Teder & Tammaru 2005; Dale *et al.* 2007). However, recent studies have documented a pattern of positive size allometry among genetically

similar subpopulations (e.g. Fernández-Montraveta & Moya-laraño 2007; Pyron *et al.* 2007; Lengkeek *et al.* 2008), suggesting that (i) Rensch’s rule can also represent an environmentally induced sex-specific phenotypic response, such that (ii) comparative studies of SSD among populations and species may be confounded by intrapopulation processes (Fairbairn 2005; Teder & Tammaru 2005; Young 2005), but that (iii) we can use body-size plasticity to test evolutionary theories pertaining to broader morphological patterns (e.g. Rensch’s rule) (Warner 1991; Buston & Cant 2006; Kohda *et al.* 2008).

Absolute interspecific patterns in trait expression represent the genetic response of different species to selection through evolutionary time. Similarly, trait plasticity represents a functional adaptive response to local environmental conditions (Bradshaw 1965; Warner 1991). Hence, irrespective of the taxonomic scale of inference or the details of proximate causality, ultimate hypotheses (i.e. those pertaining to adaptive significance) for positive size allometry are general (Mayr 1961; Tinbergen 1964; Sherman 1988; Warner 1991), and can be grouped into three broad categories (*sensu* Dale *et al.* 2007): (i) sex-specific constraints, (ii) natural selection, and (iii) sexual selection.

- (i) The sex-specific constraints hypothesis argues that positive allometry is the product of each sex responding differently to a similar selection pressure (Clutton-Brock *et al.* 1977; Webster 1992; Fairbairn 1997). At the population and species level, positive allometry can be proximately manifest, for example, if there are different

* Author for correspondence (stefan.walker@jcu.edu.au).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.0767> or via <http://rspb.royalsocietypublishing.org>.

amounts of genetic variation in males and females and the sex with more additive genetic variation for body size has a stronger evolutionary response to selection (Leutenegger & Cheverud 1982). Similarly, a natural selection gradient (e.g. temperature) among subpopulations may trigger a correlated, but divergent phenotypic response in females and males (Fairbairn 2005; Teder & Tammaru 2005). A pattern of positive size allometry is ultimately expected when optimal female body size varies less than optimal male body size in relation to the selection gradient (Fairbairn 2005; Teder & Tammaru 2005).

- (ii) Natural selection, such as intersexual resource competition (Clutton-Brock *et al.* 1977; Payne 1984; Webster 1992; Fairbairn 1997). For example, if increased body size is associated with a reduction in the amount of interspecific competition, then larger species may become more size dimorphic as the sexes genetically diverge into different ecological niches (MacArthur 1972; Shine 1989). Similarly, reduced interspecific competition with greater subpopulation mean body size may trigger a plastic response in sex-specific growth and body size, so the sexes may use different niches (Kohda *et al.* 2008).
- (iii) The sexual selection hypotheses states that size allometry is ultimately due to greater size-dependent reproductive success in one sex compared with the other (Smith 1977; Payne 1984; Webster 1992; Fairbairn 1997), where the strength of sexual selection acting on the targeted sex drives the overall magnitude of SSD (Shuster & Wade 2003). Among populations and species, a pattern of size allometry is expected as the non-targeted sex displays a correlated, but weaker evolutionary response to selection on the targeted sex. A pattern of positive allometry consistent with Rensch's rule is expected in taxa where sexual selection is stronger for males (the typical scenario; Shuster & Wade 2003), irrespective of whether large or small male size is sexually selected (Székely *et al.* 2004; Dale *et al.* 2007). In contrast, in taxa where sexual selection is stronger for female size, negative allometry is expected. Similarly, if mean body size increases with group size and the level of polygyny among subpopulations, we may ultimately expect a pattern of positive size allometry as males allocate more energy to rapid somatic growth in response to the increasing benefit of large body size in securing and maintaining reproductive dominance (Grosenick *et al.* 2007).

Knowledge on the details of trait plasticity is key to evolutionary theories of phenotypic variation and origins of diversity (Scheiner 1993; Gross 1996; Badyaev 2002; Tomkins 2005; Bonduriansky 2007), while the identification of selection gradients that trigger a plastic response provides insight into why patterns of diversity evolve in the first place, and how they are maintained (Gause 1942; Bradshaw 1965; Fricke 1980; Warner & Hoffman 1980; Warner 1991; Scheiner 1993; Gross 1996). It is therefore of general interest to determine whether the hypothesized ultimate drivers (such as sexual selection)

of broad macroevolutionary patterns (such as Rensch's rule) drive similar morphological patterns among groups of flexible individuals.

For several reasons, tropical reef fishes are an important and ideal model system for investigating individual trait plasticity and subpopulation patterns of SSD. First, most reef fish life histories include a dispersive pelagic larval phase, making local genetic adaptation of populations a potentially slow process (Warner 1991; Leis & McCormick 2002). Second, individuals frequently settle in an environment that is very different from the natal state. Habitat patch size, temperature and water-chemistry regime, substrate type, vertical relief and depth, food availability, predator and competitor assemblage, and the number and density of conspecifics can all vary within the dispersive range of larvae (Leis & McCormick 2002). In addition, many reef fishes are restricted to the local population or reproductive group into which they settle; migration at a later stage to a more appropriate environment is often limited to those habitats available in the immediate area. Hence, reef fish cohorts will be frequently distributed across a number of physical, ecological and social gradients post-settlement. These attributes should place strong selective pressure on the evolution of flexible morphological, physiological and behavioural traits (Warner 1991; Scheiner 1993; Blanckenhorn 2000; Badyaev 2002), including growth and body size (Ross 1987; Buston 2003). Finally, individuals from a broad range of fish taxa start life as one sex and later change sex to function as the other (sequential hermaphroditism; Warner 1975, 1988; Shapiro 1988; Munday *et al.* 2006; see electronic supplementary material, table S1). This means that females and males carry the same genes, providing a unique opportunity to examine the role that shared developmental modifiers play in SSD patterns and processes; an important and frequently neglected aspect of SSD evolution (Badyaev 2002).

In this study, we conduct an intrapopulation test on the ultimate sexual selection hypothesis for positive size allometry, and the proximate differential plasticity hypothesis for positive size allometry, using the sex-changing polygynous reef fish *Parapercis cylindrica* (family Pinguipedidae). Like many harem sex-changing fishes (electronic supplementary material, table S1), individuals form hierarchical social groups (Walker & McCormick 2004, 2009). Dominance rank is based on relative body size and the male represents the top breeding status. The dominant female within the harem will change sex to function as male following the death of the dominant male, or following a female recruitment pulse (Frisch *et al.* 2007; see also Warner 1975, 1988; Shapiro 1988; Munday *et al.* 2006). In a previous study, we found evidence to suggest that *P. cylindrica* individuals accelerate somatic growth during sex change to facilitate reproductive dominance (Walker & McCormick 2004). Here, we use a null model approach to test for positive allometry among social groups in the wild (monogamous pairs and harems), and examine whether the magnitude of SSD increases with the level of polygyny. In addition, using manipulative experiments in the wild and in laboratory microcosms, we test the hypothesis that polygyny potential (the number of resident females) determines the magnitude of growth acceleration during sex change.

2. METHODS

(a) *Model species*

P. cylindrica is a short-lived fish that occupies macro-algae and coral-rubble habitat within sheltered tropical waters (Randall *et al.* 1997). Each female defends a permanent all-purpose territory in which it feeds, spawns and seeks shelter, and males form harems by defending up to 10 neighbouring females (Stroud 1982). Mating and social-system type ranges from isolated monogamous groups in low-density areas to contiguous harems of up to 10 females per male in high-density areas (S. P. W. Walker *et al.* 2005, unpublished data). A strict, size-based dominance hierarchy exists within each harem, and the male is always the largest individual within the group. Males are derived exclusively from females (sequential monandric protogyny) and can be distinguished from females by the presence of black pigmentation on the jaws and branchiostegal rays (Stroud 1982). The largest, dominant female of a polygynous group will change sex within 14–33 days following male removal (Walker & McCormick 2004; Frisch *et al.* 2007).

Reproduction entails the male and female simultaneously releasing gametes into the water column (Stroud 1982; Thresher 1984). Spawning occurs within the hour prior to sunset, and a harem male can sequentially pair-spawn with up to 10 females during that time (S. P. W. Walker *et al.* 2005, unpublished data; Stroud 1982). Reproduction occurs throughout the year, with peaks in gamete production and spawning activity occurring around the new and full moon (S. P. W. Walker *et al.* 2005, unpublished data).

Harem size can be used as an accurate proxy for male reproductive success; Stroud (1982) illustrated that females spawn with the male in whose territory they reside 98 per cent of the time (spawn observation $n = 465$, male $n = 20$), and while infrequently a neighbouring harem male may steal or join in on a spawning bout, roaming bachelor males are absent from populations. Data on individual spawning frequencies, size-based egg production rates and fertilization rates illustrate that male reproductive output is primarily driven by harem-group size, but starts to asymptote at larger group sizes (S. P. W. Walker *et al.* 2005, unpublished data).

(b) *The ultimate sexual selection hypothesis for Rensch's rule*

The ultimate sexual selection hypothesis for Rensch's rule was tested among 55 reproductive social groups (monogamous pairs and harems) within the lagoon of Lizard Island, Great Barrier Reef, Australia (14°40.9' S, 145°26.8' E). Social group composition was first determined by observing the coloration and behaviour of individual fish (232) and by the mapping of their territories. One 15 min observation was made on each individual. Females ($n = 177$) were assigned to the male ($n = 55$) whose territory encompassed the particular female. Pilot studies revealed that a 15 min observation time gives an accurate estimate of individual territory location (see electronic supplementary material, figure S1). Following the determination of social group composition, all individuals were collected with clove oil anaesthetic and a hand net, and measured with callipers (mm total length; TL). The largest female within each group was assigned as the dominant female, and SSD was defined as the difference between log(male body size mm TL) and log(dominant female body size mm TL).

To test for positive allometry among social groups (Rensch's rule), and to explore the relationship between polygyny (social group size) and SSD (the sexual selection hypothesis for Rensch's rule) a random distribution of body sizes expected under a null model was constructed using a Monte Carlo procedure (Manly 1997). This procedure was necessary because at least some level of SSD is expected when males are derived from females. In addition, when there is only one male per group, and the male is ubiquitously the largest individual within each group, both group size and the shape of the body-size distribution intrinsically affect the expected overall magnitude of SSD and the expected linear regression slope between log(dominant female body size) and log(male body size) when groups of individuals are formed randomly (see electronic supplementary material, figures S2 and S3). The Monte Carlo procedure involved the random selection of individuals from the pool of 232 individuals and combining them into groups based on the exact distribution of group sizes found in our sample. The randomly selected individuals allocated to each group were then ranked according to relative body size, where rank 1 = male and rank 2 = dominant female. We then calculated the expected intercept and slope between log(dominant female body size mm TL) and log(male body size mm TL) (i.e. the expected pattern of sexual size allometry) using reduced major axis (RMA) regression (Fairbairn 1997) and the expected intercept and slope between social group size and SSD (i.e. the expected pattern between polygyny and SSD) using ordinary least-squares (OLS) regression. This whole procedure was iterated 10 000 times, generating two final expected intercept and expected slope-probability distributions. (electronic supplementary material, figures S2–S4). The best-fit RMA regression slope for observed log(dominant female body size mm TL) versus observed log(male body size mm TL) and the best-fit OLS regression slope for observed harem size versus observed SSD were then assigned statistical significance based on their probability of occurrence, according to their corresponding null model slope distribution. This null model design was appropriate since it excludes the factors of interest (the relationships between polygyny and dominant female and male body size) while retaining the protogyny sex change rule and all other factors of the sampling design (i.e. group- and body-size distributions) (Manly 1997; Buston & Cant 2006).

(c) *The proximate growth plasticity hypothesis for Rensch's rule: field experiment*

The growth plasticity hypothesis for Rensch's rule was tested both in the wild and in laboratory microcosms by removing the male from social groups to induce sex change in the dominant female. It was predicted that growth during sex change would be positively related to the potential for polygyny (the number of females the sex changer encounters during sex change).

In the wild, a population displaying natural variation in social group size was found, and a reference grid at 5 × 5 m resolution was laid over the substrate. All individuals ($n = 53$) were captured and measured (as above), visually sexed (based on coloration) and tagged with a subcutaneous elastomer tattoo for individual recognition using a 27-gauge hypodermic needle (Northwest Marine Inc.). Individuals were held until full recovery from anaesthetization and then returned to the site of capture, and all individuals were

observed to remain within their original location. Pilot studies in aquaria revealed a 0 per cent mortality rate over 30 days associated with tattooing ($n = 30$). Three 15 min observations were made on all individuals to determine territory location and harem membership (as above). Once individuals and social groups were mapped (in relation to the reference grid) the male was removed from each reproductive social group ($n = 11$) to induce sex change. Immediately following male removal (at approx. 1, 2 and 3 h) and then each day for 30 days, 15 min observations were made on remaining females to track changes in coloration and behaviour. After 30 days, all individuals were euthanized to determine growth and the gonads fixed in formalin–acetic acid–calcium chloride solution. The final sex of each individual was initially determined by colour patterns and behaviour (Stroud 1982; Frisch *et al.* 2007), and was later confirmed by gonad histology, based on the presence of characteristic sex cells (Patiño & Takashima 1995; Frisch *et al.* 2007). Analysis of variance was used to test for a statistically different standardized growth ($\log(\text{final size mm TL}) - \log(\text{initial size mm TL})$) between sex-changers ($n = 12$) and non-sex-changing females of adjacent dominance rank (i.e. the next largest female within each group), with $\log(\text{initial size})$ and polygyny potential entered as covariates. Multiple regression and residual analysis were then used to examine the independent effects of $\log(\text{initial size mm TL})$ and polygyny potential on standardized growth among sex changers and non-sex-changing dominant females.

(d) The proximate growth plasticity hypothesis for Rensch's rule: laboratory experiment

Laboratory experiments were carried out at Lizard Island Research Station to isolate the effect of polygyny potential (number of females) on growth during sex change. Experimental fish within each aquarium were collected from a different social group and site within the Lizard Island lagoon, such that they had never interacted before the experiment. A total of 20 social groups were created in individual 100–150 l microcosms containing equal quantities of rubble and algae habitat per individual; 10 containing one male and four females (at 85, 80, 75 and 70 ± 0.2 mm TL); the 'polygyny' treatment, and 10 containing one male and two females (at 85 and 80 ± 0.2 mm TL); the 'monogamy' treatment (following male removal). The male was always the largest individual. After 5 days of acclimation, the male was removed from 5 of the 10 social groups at random from the polygyny and monogamy treatments to induce sex change. The other five social groups in each treatment served as controls for male removal. At 0900 h and 1500 h each day, individuals were fed to satiation with brine shrimp and commercial fish food. Observations were carried out to ensure that all individuals were feeding (which was found to be the case). Thirty days following male removal, all individuals were euthanized to determine growth and the gonads fixed for histological processing. The final sex of individuals was determined by colour patterns and gonad histology (as above).

Two-way ANOVA was used to test for statistically different standardized growth ($\log(\text{final size}) - \log(\text{initial size})$) as a function of treatment (monogamy versus polygyny), reproductive state (sex changer versus control non-sex-changing female (the largest female from social groups where the male was not removed)) and the interaction between treatment and reproductive state.

3. RESULTS

(a) The ultimate sexual selection hypothesis for Rensch's rule

Paraperis cylindrica was found to display a pattern of positive allometry for SSD concordant with Rensch's rule. The observed best-fit slope from the $\log(\text{dominant female size})$ versus $\log(\text{male body size})$ RMA regression was statistically greater than that predicted by the protogynous sex change rule and sampling regime alone (i.e. the null model for positive allometry; $\beta_{(\text{RMA null})} = 1.10$, $y_{0(\text{RMA null})} = -0.15$; electronic supplementary material, figure S2 and S4) (observed best-fit RMA model; $\log(\text{male body size mm TL}) = 1.31 \times \log(\text{dominant female body size mm TL}) - 0.53$, $r^2 = 0.71$, Tukey's t -test; $t_{(\beta_{\text{RMA observed}})} = 2.15$, d.f. = 53, $p = 0.018$; figure 1a), representing greater-than-expected variability in male size and an increase in SSD with dominant-female size. In addition, the observed relationship between the level of polygyny and SSD was found to support the ultimate sexual selection hypothesis for Rensch's rule. The magnitude of SSD was frequently less than that predicted by the null regression model among monogamous pairs, and increasingly greater than that predicted by the null model with an increase in harem-group size (null model for SSD; $\beta_{(\text{OLS null})} = -0.003$, $y_{0(\text{OLS null})} = 0.06$; electronic supplementary material, figure S3) (residual SSD = $0.008(\text{harem size}) - 0.02$, $r^2 = 0.4$, $F = 35.32$, d.f. = 1, 53, $p < 0.01$; figure 1b).

(b) The proximate growth plasticity hypothesis for Rensch's rule

Results from both the wild and laboratory experiments were found to support the proximate growth plasticity hypothesis for Rensch's rule. In the wild, a total of 12 females from 11 male-removed social groups were observed to take on the male-behavioural mode and subsequently change sex. At the end of the experimental period (30 days), these 12 individuals all had gonads containing proliferating testicular tissue, either developing or fully developed peripheral sperm sinuses, and only remnant degenerating ovarian tissue. By contrast, all individuals that maintained female coloration and behaviour had gonads containing both mature and developing oocytes, indicating active oogenesis. The largest dominant female was the one to change sex and take over the social group from which they originated in all but one case. In the exception, the two largest females changed sex and the harem was split between them.

Standardized growth ($\log(\text{final size}) - \log(\text{initial size})$) during the 30-day experimental period was found to be statistically greater for sex-changing individuals compared with non-sex-changing females (the next largest female within each harem) for any given $\log(\text{initial size mm TL})$ or level of polygyny potential (ANOVA; $F = 16.56$, d.f. = 2, 19, $p < 0.001$; figure 2), confirming that individuals accelerate growth during sex change to become the largest members of the population. Moreover, while $\log(\text{initial size mm TL})$ was a strong predictor of growth among non-sex-changed females (standardized growth = $-3.43 \times \log(\text{initial size mm TL}) + 0.67$, $r^2 = 0.54$, $F = 10.67$, d.f. = 1, 9, $p = 0.009$; figure 2a), this was not the case among sex-changed individuals ($F = 4.57$, d.f. = 1, 10, $p = 0.06$; figure 2a). Incorporating polygyny potential

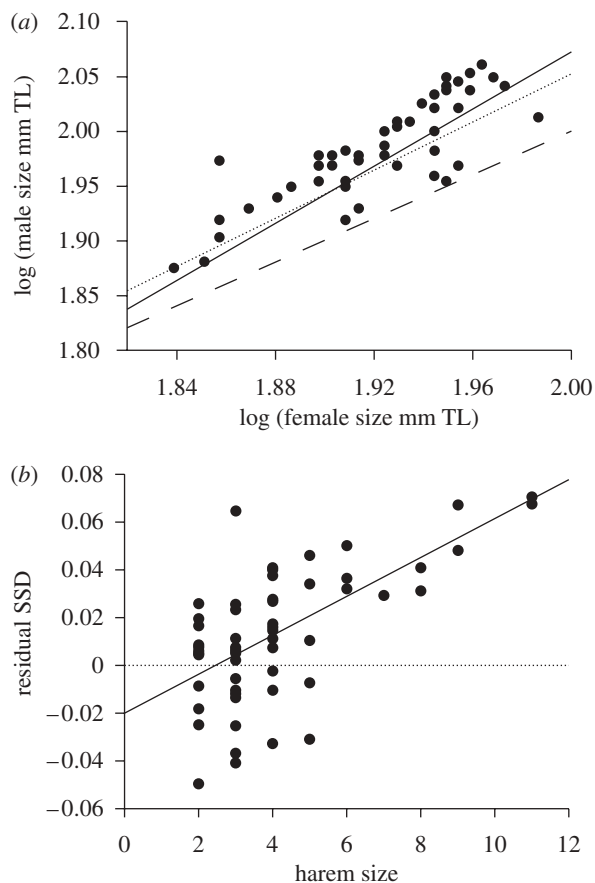


Figure 1. (a) Relationship between standardized dominant female and male body size among social groups illustrating positive sexual size allometry. Solid line, best-fit RMA linear regression model; dotted line, Monte Carlo null regression model (i.e. that predicted by the protogynous sex change rule and sampling regime; see §2); dashed line; isometric line ($x = y$). (b) Relationship between the level of polygyny (harem size including one male) and residual SSD from the reduced null model (observed SSD – expected SSD from the Monte Carlo null regression model; dotted line).

into the regression model increased the amount of variance explained (adjusted $r^2 = 0.66$, $F = 12.06$, d.f. = 2,9, $p = 0.003$), and illustrated female density to have a greater effect on standardized growth during sex change (partial correlation coefficient = 0.8, $p = 0.004$) compared with log(initial size) (partial correlation coefficient = -0.7, $p = 0.03$) (figure 2b). Polygyny potential did not help to explain residual standardized growth in non-sex-changing females (figure 2b). Laboratory results support field results; only the dominant female from each male-removed social group changed sex, and these sex-changed individuals displayed greater standardized growth than control non-sex-changed females of equal initial size (i.e. dominant females from social groups where the male was not removed; figure 2c). In addition, there was a significant interaction between sex changer versus non-sex-changer and treatment ($F = 7.1$, d.f. = 1,16, $p = 0.016$); monogamous sex changers displayed only slightly greater growth compared with monogamous control non-sex-changing females, while polygynous sex changers displayed more than twice the growth of polygynous control non-sex-changing females (figure 2c).

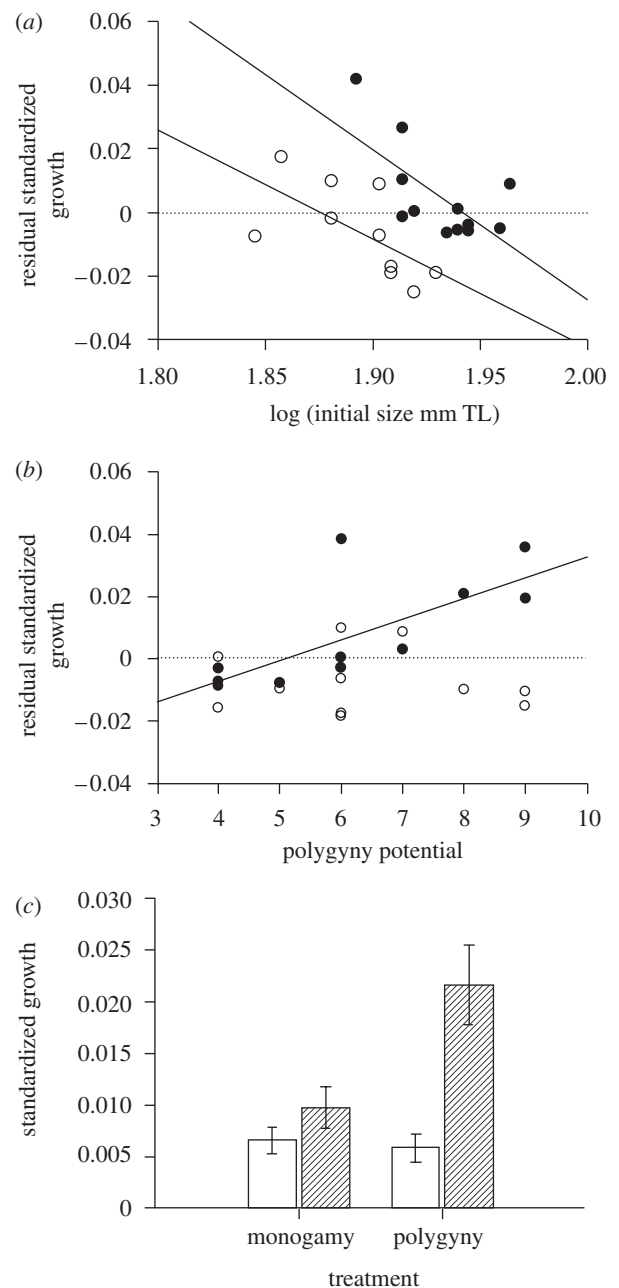


Figure 2. (a) Relationship between log(initial size) and residual standardized growth (from the reduced polygyny-potential model) in non-sex-changing females (white dots) and sex-changed individuals (black dots) during the 30-day experiment in the wild. (b) Relationship between polygyny potential and residual standardized growth (from the reduced log(initial size) model) among non-sex-changing females (white dots) and sex-changed individuals (black dots) in the wild. (c) Differences in standardized growth (\pm s.e.) between control non-sex-changing females (white) and sex-changed individuals (shaded) with respect to treatment during the 30-day laboratory experiment. All initial sizes = 85 ± 0.2 mm TL.

4. DISCUSSION

In the wild, *P. cylindrica* displayed a pattern of positive allometry for SSD concordant with Rensch's rule, illustrating greater phenotypic variation in male size compared with dominant female size. In addition, SSD was found to predictably increase with the level of polygyny, consistent with the ultimate sexual selection hypothesis

for positive size allometry. Manipulative experiments illustrated that polygyny potential (the number of resident females) affects the magnitude of growth acceleration during sex change from female to male, and it is this sex-specific differential growth plasticity that proximately drives variation in SSD among social groups. Since the number of resident females reflects the potential advantage of changing sex, the number of competitors for the harem-male role and the cost of maintaining dominance, there is more incentive for a highly polygynous sex changer to invest in relatively larger body size, both to aid in combat and as an honest signal of dominance, thereby reducing the probability of contest (Grosenick *et al.* 2007).

Dominant female body size positively covaried with polygyny and SSD. Ultimately, female *P. cylindrica* also benefit from relatively larger body size owing to an increase in egg production capacity (i.e. fecundity selection; Head 1995; S. P. W. Walker *et al.* 2005, unpublished data). The fact that dominant female body size varies less than male body size suggests the presence of sex- and/or rank-specific growth and body-size strategies. First, females experience a stronger energetic trade-off between growth and gamete production compared with males (Walker & McCormick 2004). Second, there is potential for conflict over dominance rank via sex change; if a dominant female was to approach a size equal to that of the male (or a new dominant sex-changing individual), then the male/sex-changing individual may be forced to attack and evict that female from the social group so as to maintain the top breeding status (Johnstone 2000; Buston 2003; Wong *et al.* 2007). By remaining smaller than the harem-male, the dominant female avoids the prospect of punishment, and may inherit a productive harem in the future (i.e. via sex change, as illustrated in the present study).

Studies to date on SSD patterns and processes have largely focused on adult sex-specific morphology at the population and species level, where it is generally assumed that adult female and male body size is genetically fixed, such that Rensch's rule reflect coevolution between absolute adult female and male body size coupled with greater evolutionary divergence in absolute adult male body size (Fairbairn 1997; Dale *et al.* 2007). Our study illustrates, however, that Rensch's rule may also be manifest through the evolution of sex-specific developmental modifiers (Badyaev 2002), and the phenotypic expression of relative body size in response to an ultimate sex-specific selection gradient. Clearly, the potential for adaptive sex-specific differential growth plasticity to explain patterns of SSD will diminish when inference is made at higher taxonomic levels. Nonetheless, our results illustrate that such inferences may not simply reflect sex-specific genetic divergence, or patterns of absolute body size. Yet, irrespective of the taxonomic level of inference, or the details of proximate causation, Rensch's rule remains general with respect to ultimate causal factors. Using birds as the focal taxa, Dale *et al.* (2007) recently provided the strongest evidence to date that Rensch's rule, among species, is the product of sexual selection processes. Here, we complement Dale and coworkers' findings by providing the first experimental evidence that a sexual selection gradient among social groups drives growth and body-size plasticity, and a pattern of positive allometry for SSD. Our study highlights

both the usefulness of phenotypic plasticity for testing evolutionary theories (Warner 1991), and the role that individual growth modification can play in the shaping of morphological patterns in nature (see also Buston 2003; Fairbairn 2005; Pyron *et al.* 2007; Kohda *et al.* 2008; Lengkeek *et al.* 2008).

Theory suggests that traits targeted by sexual selection (such as male body size) should evolve heightened condition dependence; a form of developmental plasticity that links the degree of trait expression to the quantity of metabolic resources available to the individual, optimizing the trade-off between viability and reproduction (*sensu* Bonduriansky 2007) (McAlpine 1979; Andersson 1982; Nur & Hasson 1984; Rowe & Houle 1996). Indeed, several studies on polygynous species illustrate that males display more pronounced changes in growth rate and body size in response to food supply compared with females, subsequently driving a pattern of positive allometry for SSD (e.g. Badyaev 2002; Bonduriansky 2007; Fernández-Montraveta & Moya-laraño 2007). In the present study, however, we illustrate that males (i.e. sex-changing individuals) regulate growth rate and body size in response to the strength of sexual selection itself, even when food is unlimited. Essentially, we illustrate that growth and body size is conservative, but finely tuned to ultimate selection pressures. These results suggest that there are costs associated with either rapid growth rate or large body size independent of metabolic viability. For example, it is possible that rapid growth during sex change reduces longevity, but that reduced longevity is traded-off with the higher reproductive success associated with attaining larger body size in more polygynous societies. We suggest that the modification of sexually selected traits (e.g. growth and body size) in response to social conditions, rather than—or in addition to—current food availability, may be common when individuals are able to perceive their social setting and status accurately and continuously, when there are potential costs associated with the expression of the targeted trait (independent of metabolic viability), and when individuals must act quickly to secure dominance should the opportunity arise (e.g. when a dominant male dies in a polygynous size hierarchy) (see also Buston 2003; Wong *et al.* 2008).

Our study experimentally illustrated SSD to be the product of accelerated growth during sex change in a protogynous fish that forms permanent, size-based dominance hierarchies (see also Ross 1987; Walker *et al.* 2007; Munday *et al.* in press). By contrast, female and male growth has been found to diverge well before the mean age at sex change in protogynous polygynous fishes that form loosely organized harems (e.g. parrot fishes *Scarus frenatus* and *Chlorurus sordidus*; Munday *et al.* 2004), or species whose social interactions are largely confined to brief spawning periods (e.g. coral trout *Plectropomas maculatus*; Adams & Williams 2001). It appears that the absence of social constraints on subordinate growth permits high variability in growth to be expressed early in life. Those individuals that achieve relatively larger body size during the juvenile and female phase go on to become large polygynous males via sex change, while those individuals who experience relatively poor growth during the juvenile and female phase tend to remain female, presumably to avoid reproductive

exclusion by larger males (Warner 1975, 1988). Nonetheless, it appears that these sex changers still employ accelerated growth during sex change to achieve SSD, albeit to a lesser degree compared with hierarchical sex changers (Ryen 2008). The shift from sex-change-associated growth divergence to pre-sex-change growth divergence has even been illustrated between populations of the same species (i.e. the wrasse *Halecoeres miniatus*; Ryen 2008). Alternation between these two pathways for SSD was found to be related to the strength of the dominance hierarchy operating within each population. With an increase in the strength of the dominance hierarchy, individuals relied more on sex-change-associated growth acceleration to achieve SSD (Ryen 2008).

Taken together, studies to date on the temporal and ontogenetic relationships between sex change and SSD suggest that while rapid juvenile and female growth may be advantageous within a loosely organized social system (owing to the increased chance of becoming a large dominant male; Adams & Williams 2001), such a strategy may be selected against within a strict, hierarchically organized social group (Buston 2003; Walker & McCormick 2004; Walker *et al.* 2007; Wong *et al.* 2007). Moreover, owing to their larval dispersive phase, and the highly patchy nature of the marine environment, individuals frequently encounter a social environment that is very different from the natal state. Hence, in sequentially hermaphroditic animals (annelids, molluscs, crustaceans, fish), including most polygynous reef fishes (Thresher 1984; Munday *et al.* 2006; electronic supplementary material, table S1), selection for individual growth and body-size plasticity is likely to be stronger than selection for any one particular growth tactic.

Because males are derived from females, sequentially protogynous reef fishes provide a unique opportunity to explore the ways in which sexes achieve divergent phenotypes through the modification of shared developmental programmes; an important and frequently neglected aspect of morphological evolution (Badyaev 2002). In addition, reef fishes display extraordinary flexibility in the expression of behavioural, physiological and morphological traits, and show unprecedented diversity in mating and social-system types (Thresher 1984; Shapiro 1991; Warner 1991; Munday *et al.* 2006). These attributes mean that the proximate and ultimate drivers of SSD are likely to vary considerably among social groups, populations and species, making reef fishes ideal model systems for testing theories pertaining to morphological evolution and diversity (Warner 1991). While the present study highlighted sexual selection to be the driver of positive size allometry among groups of *P. cylindrica*, natural selection for SSD appears to be more important in other species (e.g. Kohda *et al.* 2008). As poikilotherms, moreover, fishes are extremely sensitive to prevailing physical environmental factors, particularly temperature (Atkinson 1994). Fish are therefore likely to experience growth and body-size trade-offs frequently in relation to conflicting environmental selection pressures (Young 2005; Pyron *et al.* 2007; Lengkeek *et al.* 2008). While it is unlikely that physical factors played a significant role in determining the patterns of SSD reported here (owing the extremely small spatial scale of the study), plasticity studies at larger spatial scales should incorporate physical variables in the analysis to get at the true

relationships between ultimate selection pressures and patterns of SSD.

Further research is required on the temporal and ontogenetic relationships between sex change and SSD in fishes, and the mechanisms driving variance in SSD among social groups, populations and species. Such studies will enhance our understanding of morphological evolution and enable predictions of how species with labile sexual differentiation strategies and indeterminate growth respond to natural and anthropogenically induced changes in population density and social organization.

Research was carried out with permission from the Great Barrier Marine Park Authority (permit no. G04/11869) and in accordance with James Cook University ethics guidelines (ethics approval no. A961).

We thank C. Chustz, C. Ryen and the staff of Lizard Island Research Station for their dedicated assistance in the field. We also thank P. Buston, P. Munday, R. Bonduriansky, A. Frisch and two anonymous reviewers for providing valuable comments on the manuscript. Research was funded by a Lizard Island Doctoral Fellowship (Australian Museum), and a JCU merit research grant awarded to S.P.W. and by the ARC center of excellence for coral reef studies, JCU.

REFERENCES

- Adams, S. & Williams, A. J. 2001 A preliminary test of the transitional growth spurt hypothesis using the protogynous coral trout *Plectropomus maculatus*. *J. Fish Biol.* **59**, 183–185. (doi:10.1111/j.1095-8649.2001.tb02350.x)
- Andersen, N. M. 1997 A phylogenetic analysis of the evolution of sexual dimorphism and mating systems in water striders (Hemiptera: Gerridae). *Biol. J. Linnean Soc.* **61**, 345–368. (doi:10.1111/j.1095-8312.1997.tb01796.x)
- Andersson, M. 1982 Sexual selection, natural selection and quality advertisement. *Biol. J. Linnean Soc.* **17**, 375–393. (doi:10.1111/j.1095-8312.1982.tb02028.x)
- Atkinson, D. 1994 Temperature and organism size—a biological law for ectotherms? *Adv. Ecol. Res.* **25**, 1–58. (doi:10.1016/S0065-2504(08)60212-3)
- Badyaev, A. V. 2002 Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends Ecol. Evol.* **17**, 369–378. (doi:10.1016/S0169-5347(02)02569-7)
- Berry, J. F. & Shine, R. 1980 Sexual size dimorphism and sexual selection in turtles (Order Testudines). *Oecologia* **44**, 185–191. (doi:10.1007/BF00572678)
- Blanckenhorn, W. U. 2000 The evolution of body size: what keeps organisms small? *Quar. Rev. Biol.* **75**, 385–407. (doi:10.1086/393620)
- Bonduriansky, R. 2007 The evolution of condition-dependent sexual dimorphism. *Am. Nat.* **169**, 9–19. (doi:10.1086/510214)
- Bradshaw, A. D. 1965 Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.* **13**, 115–155. (doi:10.1016/S0065-2660(08)60048-6)
- Buston, P. 2003 Social hierarchies: size and growth modification in clownfish. *Nature* **424**, 145–146. (doi:10.1038/424145a)
- Buston, P. & Cant, M. A. 2006 A new perspective on size hierarchies in nature. *Oecologia* **149**, 362–372. (doi:10.1007/s00442-006-0442-z)
- Clutton-Brock, T. H., Harvey, P. H. & Rudder, B. 1977 Sexual dimorphism, socioeconomic sex-ratio and bodyweight in primates. *Nature* **269**, 797–800. (doi:10.1038/269797a0)
- Colwell, R. K. 2000 Rensch's rule crosses the line: convergent allometry of sexual size dimorphism in

- hummingbirds and flower mites. *Am. Nat.* **156**, 495–510. (doi:10.1086/303406)
- Dale, J., Dunn, P. O., Figuerola, J., Lislevand, T., Székely, T. & Whittingham, L. A. 2007 Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. *Proc. R. Soc. B* **274**, 2971–2979. (doi:10.1098/rspb.2007.1043)
- Fairbairn, D. J. 1997 Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annu. Rev. Ecol. Syst.* **28**, 659–687. (doi:10.1146/annurev.ecolsys.28.1.659)
- Fairbairn, D. J. 2005 Allometry for sexual size dimorphism: testing two hypotheses for Rensch's rule in the water strider *Aquarius remigis*. *Am. Nat.* **116**(Suppl.), 69–84. (doi:10.1086/444600)
- Fernández-Montraveta, C. & Moya-laraño, J. 2007 Sex-specific plasticity of growth and maturation size in a spider: implications for sexual size dimorphism. *J. Evol. Biol.* **20**, 1689–1699. (doi:10.1111/j.1420-9101.2007.01399.x)
- Fricke, H. W. 1980 Control of different mating systems in a coral reef fish by one environmental factor. *Animal Behav.* **28**, 561–569. (doi:10.1016/S0003-3472(80)80065-0)
- Frisch, A. J., Walker, S. P. W., McCormick, M. I. & Solomon-Lane, T. K. 2007 Regulation of protogynous sex change by competition between corticosteroids and androgens: an experimental test using sandperch, *Parapercis cylindrica*. *Horm. Behav.* **52**, 540–545. (doi:10.1016/j.yhbeh.2007.07.008)
- Gause, G. F. 1942 The relation of adaptability to adaptation. *Q. Rev. Biol.* **17**, 99–114. (doi:10.1086/394649)
- Grosenick, L., Clement, T. S. & Fernald, R. D. 2007 Fish can infer social rank by observation alone. *Nature* **445**, 429–423. (doi:10.1038/nature05511)
- Gross, M. R. 1996 Alternative reproductive strategies and tactics: diversity within sexes. *Trends Ecol. Evol.* **11**, 92–98. (doi:10.1016/0169-5347(96)81050-0)
- Head, G. 1995 Selection on fecundity and variation in the degree of sexual size dimorphism among spider species (class Araneae). *Evolution* **49**, 776–781. (doi:10.2307/2410330)
- Johnstone, R. A. 2000 Models of reproductive skew: a review and synthesis. *Ethology* **106**, 5–26. (doi:10.1046/j.1439-0310.2000.00529.x)
- Kohda, M., Shibata, J., Awata, S., Gomagano, D., Takeyama, T., Hori, M. & Heg, D. 2008 Niche differentiation depends on body size in a cichlid fish: a model system of a community structured according to size regularities. *J. Anim. Ecol.* **77**, 859–868. (doi:10.1111/j.1365-2656.2008.01414.x)
- Leis, M. L. & McCormick, M. I. 2002 The biology, behavior and ecology of the pelagic, larval stage of coral reef fishes. In *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. P. Sale), pp. 171–199. London, UK: Academic Press.
- Lengkeek, W., Dideren, K., Côté, I. M., van der Zee, E. M., Snoek, R. C. & Reynolds, J. D. 2008 Plasticity in sexual size dimorphism and Rensch's rule in Mediterranean blennies (Blenniidae). *Can. J. Zoolog.* **86**, 1173–1178. (doi:10.1139/Z08-103)
- Leutenegger, W. & Cheverud, J. 1982 Correlates of sexual dimorphism in primates: ecological and size variables. *Int. J. Primatol.* **3**, 387–402. (doi:10.1007/BF02693740)
- MacArthur, R. H. 1972 *Geographical ecology*. New York, NY: Harper and Row.
- Manly, B. J. F. 1997 *Randomization, bootstrap and Monte Carlo methods in biology*, 2nd edn. London, UK: Chapman and Hall.
- Maynard Smith, J. 1978 *The evolution of sex*. Cambridge, UK: Cambridge University Press.
- Mayr, E. 1961 Cause and effect in biology. *Science* **134**, 1501–1506. (doi:10.1126/science.134.3489.1501)
- McAlpine, D. K. 1979 Agonistic behavior in *Achias australis* (Diptera, Platystomatidae) and the significance of eye-stalks. In *Sexual selection and reproductive competition in insects* (eds M. S. Blum & N. A. Blum), pp. 221–230. New York, NY: Academic Press.
- Munday, P. L., Hodges, A. L., Choat, J. H. & Gust, N. 2004 Sex-specific growth effects in protogynous hermaphrodites. *Can. J. Fisheries Aquat. Sci.* **61**, 323–327. (doi:10.1139/f04-057)
- Munday, P. L., Buston, P. & Warner, R. 2006 Diversity and flexibility of sex-change strategies in animals. *Trends Ecol. Evol.* **21**, 89–95. (doi:10.1016/j.tree.2005.10.020)
- Munday, P. L., Ryen, C. A., McCormick, M. I. & Walker, S. P. W. 2009 Growth acceleration, behaviour and otolith check marks associated with sex change in the wrasse *Halichoeres miniatus*. *Coral Reefs*. (doi:10.1007/s00338-009-0499-3)
- Nur, N. & Hasson, O. 1984 Phenotypic plasticity and the handicap principle. *J. Theor. Biol.* **110**, 275–297. (doi:10.1016/S0022-5193(84)80059-4)
- Patiño, R. & Takashima, F. 1995 Gonads. In *An Atlas of fish histology: normal and pathological features* (eds F. Takashima & T. Hibiya), pp. 129–150, 2nd edn. Tokyo, Japan: Kondansha Ltd.
- Payne, R. B. 1984 Sexual selection, lek and arena behaviour, and sexual size dimorphism in birds. *Ornithol. Monogr.* **33**, 1–52.
- Pyron, M., Fincel, M. & Dang, M. 2007 Sexual size dimorphism and the ecomorphology of the spotfin shiner (*Ciprinella spiloptera*) from the Wabash River watershed. *J. Freshwat. Ecol.* **22**, 687–696.
- Raihani, G., Székely, T., Serrano-Meneses, M. A., Pitra, C. & Goriup, P. 2006 The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae). *Anim. Behav.* **71**, 833–838. (doi:10.1016/j.anbehav.2005.06.013)
- Randall, J. E., Allen, G. R. & Steene, R. C. 1997 *Fishes of the Great Barrier Reef and Coral Sea*. Honolulu, HI: University of Hawaii.
- Rensch, B. 1950 Die Abhängigkeit der relativen Sexualdifferenz von der Körpergröße. *Bonn. Zool. Beitr.* **1**, 58–69.
- Ross, R. M. 1987 Sex change-linked growth acceleration in a coral reef fish, *Thalassoma duperoy*. *J. Exp. Zoolog.* **244**, 455–461. (doi:10.1002/jez.1402440311)
- Rowe, L. & Houle, D. 1996 The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. Lond. B* **263**, 1415–1421. (doi:10.1098/rspb.1996.0207)
- Ryen, C. A. 2008 Sex-specific growth dynamics in protogynous hermaphrodites. MSc thesis, James Cook University, Townsville, Australia.
- Scheiner, S. M. 1993 Genetics and the evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* **24**, 35–68. (doi:10.1146/annurev.es.24.110193.000343)
- Shapiro, D. Y. 1988 Behavioral influences on gene structure and other new ideas concerning sex change in fishes. *Environ. Biol. Fishes* **23**, 283–297. (doi:10.1007/BF00005240)
- Shapiro, D. Y. 1991 Intraspecific variability in social systems of coral reef fishes. In *The ecology of fishes on coral reefs* (ed. P. Sale), pp. 331–355. London, UK: Academic Press.
- Sherman, P. W. 1988 The levels of analysis. *Anim. Behav.* **36**, 616–619. (doi:10.1016/S0003-3472(88)80039-3)
- Shine, R. 1989 Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Q. Rev. Biol.* **64**, 419–460. (doi:10.1086/416458)

- Shuster, S. M. & Wade, M. J. 2003 *Mating systems and strategies*. Princeton, NJ: Princeton University Press.
- Smith, J. M. 1977 Parental investment—a prospective analysis. *Animal Behav.* **25**, 1–9.
- Stroud, G. J. 1982 The taxonomy and biology of fishes from the genus. In *Parapercis*. PhD dissertation, James Cook University, Queensland, Australia.
- Székely, T., Freckleton, R. P. & Reynolds, J. D. 2004 Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proc. Natl Acad. Sci.* **101**, 12 224–12 227. (doi:10.1073/pnas.0404503101)
- Teder, T. & Tammara, T. 2005 Sexual size dimorphism within species increases with body size in insects. *Oikos* **108**, 321–334. (doi:10.1111/j.0030-1299.2005.13609.x)
- Thresher, R. E. 1984 *Reproduction in reef fishes*. NSW, Australia: T. F. H. Publications Inc. Ltd.
- Tinbergen, N. 1964 On aims and methods of ethology. *Z. Tierpsychol.* **20**, 410–433.
- Tomkins, J. L., Kotiaho, J. S. & LeBas, N. R. 2005 Matters of scale: positive allometry and the evolution of male dimorphisms. *Am. Nat.* **165**, 389–402. (doi:org/10.1086/427732)
- Walker, S. P. W. & McCormick, M. I. 2004 Otolith-check formation and accelerated growth associated with sex change in a harem reef fish. *Mar. Ecol. Prog. Ser.* **266**, 201–212. (doi:10.3354/meps266201)
- Walker, S. P. W. & McCormick, M. I. 2009 Fish ears are sensitive to sex change. *Biol. Lett.* **5**, 73–76. (doi:10.1098/rsbl.2008.0555)
- Walker, S. P. W., Ryen, C. A. & McCormick, M. I. 2007 The temporal and ontogenetic relationships between sex change and sexual size-dimorphism in a protogynous hermaphrodite, *Parapercis synderi* Jordan & Starks 1905. *J. Fish Biol.* **71**, 1347–1357. (doi:10.1111/j.1095-8649.2007.01595.x)
- Warner, R. R. 1975 The adaptive significance of hermaphroditism in animals. *Am. Nat.* **109**, 61. (doi:org/10.1086/282974)
- Warner, R. R. 1988 Sex change in fishes: hypotheses, evidence, and objections. *Environ. Biol. Fishes* **22**, 81–90. (doi:10.1007/BF00001539)
- Warner, R. R. 1991 The use of phenotypic plasticity in coral reef fishes as tests of theory in evolutionary ecology. In *The ecology of fishes on coral reefs* (ed. P. Sale), pp. 387–396. London, UK: Academic Press.
- Warner, R. R. & Hoffman, S. G. 1980 Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.). *Evolution* **34**, 508–518. (doi:10.2307/2408220)
- Webster, M. S. 1992 Sexual dimorphism, mating system and body size in New-World blackbirds (Icterinae). *Evolution* **46**, 1621–1641. (doi:10.2307/2410020)
- Wong, Y. L., Buston, P. M., Munday, P. L. & Jones, G. P. 2007 The threat of punishment enforces peaceful cooperation and stabilizes queues in a coral-reef fish. *Proc. R. Soc. B* **274**, 1093–1099. (doi:10.1098/rspb.2006.0284)
- Wong, Y. L., Munday, P. L., Buston, P. M. & Jones, G. P. 2008 Fasting or feasting in a social hierarchy. *Curr. Biol.* **18**, R372–R373. (doi:10.1016/j.cub.2008.02.063)
- Young, K. A. 2005 Life-history variation and allometry for sexual size dimorphism in Pacific salmon and trout. *Proc. R. Soc. B* **272**, 167–172. (doi:10.1098/rspb.2004.2931)