

Sex allocation in the sex-changing marine goby, *Coryphopterus personatus*, on atoll-fringing reefs

David J. Allsop* and Stuart A. West

*Institute of Cell, Animal and Population Biology, University of Edinburgh,
King's Buildings, West Mains Road, Edinburgh EH9 3JT, UK*

ABSTRACT

Sex allocation theory applied to sex-changing animals predicts that the amount of sex change and the proportion of individuals that mature early as the second sex depend upon the mating system of the species or population in question. In turn, theory suggests that the mating system is governed by the size and distribution of resources critical to reproduction, and by population density. Here we investigate the social and ecological factors that govern the amount of selection for sex change and the production of alternative male strategies in a protogynous (female first) goby, *Coryphopterus personatus*, on atoll-fringing reefs in Belize. We found that: (1) increasing population density leads to an increase in the proportion of early maturing males on leeward-facing reefs, as predicted, but not on windward reefs; (2) contrary to predictions, the proportion of early maturing males was higher on continuously distributed coral gardens than on isolated patches of reef in windward locations, with no difference in leeward locations; and (3) the proportion of early maturing males can be used as a predictor of the population sex ratio, with less biased sex ratios occurring with a higher proportion of early maturing males, as predicted by theory. We discuss these conflicting results in terms of the differences between windward and leeward reefs that might lead to differing selective regimes acting in these locations.

Keywords: sequential hermaphrodite, sex allocation, sex change, sex ratio, teleost fish.

INTRODUCTION

Many animals and plants have evolved the ability to change sex at some point during their lives (Warner, 1975; Charnov, 1982a; Policansky, 1982; Allsop and West, 2003a,b, 2004). Sex change is favoured when males and females differ in their capacity to produce offspring over the course of a lifetime (Warner *et al.*, 1975; Leigh *et al.*, 1976; Charnov, 1982a; Warner, 1988b). Specifically, selection favours individuals that mature as the sex whose reproductive value increases more slowly with age (first sex), and then change to the other sex (second sex) when older (Ghiselin, 1969; Charnov, 1982a; Warner, 1988a,b).

* Address all correspondence to David J. Allsop, School of Biological Sciences, A08, University of Sydney, Sydney, NSW 2006, Australia. e-mail: david.allsop@bio.usyd.edu.au

Consult the copyright statement on the inside front cover for non-commercial copying policies.

In some sex-changing species there are a proportion of individuals who mature early as the second sex, here termed early maturers. Early maturers can arise either directly from the juvenile stage, having never passed through the 'first sex' (Fennessy and Sadovy, 2002), or they can arise by *pre-maturational* sex change (de Girolamo *et al.*, 1999). Here we treat both developmental routes as being functionally equivalent for the purposes of our investigation and lump both under the umbrella term early maturers. These early maturers often employ alternative mating strategies, such as sneaking or group spawning (Robertson and Choat, 1974; Robertson and Warner, 1978; Warner and Robertson, 1978; Warner and Hoffman, 1980a,b; Charnov, 1982a,b). Their production depends upon the magnitude of the difference between the male and female reproductive value curves, and the abundance of early maturers in a population can be used as a measure of the amount of sex change that is taking place. Sex change is at a maximum when early maturers are absent and at a minimum when early maturers form 50% of the population (Warner, 1984).

The adaptive benefit of sex change and the production of early maturers depends to a large extent on the structure of the mating system (Warner, 1984), which is largely determined by the distribution of ecological resources required by a species (Emlen and Oring, 1977). Emlen and Oring (1977) argued that the distribution of resources (patchy or continuous) determines the ability of one sex to monopolize access to potential mates. Such mate monopolization will act to set the level of variance in mating success in a population, which dictates the intensity of inter- and intra-sexual selection, and thus the form of mating system (Clutton-Brock and Vincent, 1991).

In protogyny (sex change from female to male), the differences between male and female reproductive value curves are invariably associated with polygynous dominance hierarchies (Warner, 1984; Ross, 1990). For example, in the cleaner wrasse *Labroides dimidiatus*, males have total harem control, as females feed at predictable and limited 'cleaning stations' that large males can readily monopolize (Robertson, 1972; Robertson and Hoffman, 1977). Small males are unable to gain any matings, so all fish are born female. Towards the other end of the selective spectrum, in the blue-head wrasse *Thalassoma bifasciatum*, large males are often unable to completely control the preferred spawning sites that females are attracted to. Small males are therefore able to gain some reproduction in this case (by adopting alternative mating strategies), so selection favours the production of early maturing males (Warner and Hoffman, 1980a).

Interacting with the effects of resource distribution (patchy or continuous), population density has been also shown to influence the potential for mate monopolization in sex-changing reef fish (Warner, 1984). Early work on Caribbean labrids demonstrated that the proportion of early maturers increased with increasing population density across several species (Warner and Robertson, 1978). More detailed field studies using the bluehead wrasse, *Thalassoma bifasciatum*, showed that males are capable of defending females in small but not in large populations. Population size and density increased with increasing reef size, and so selection for sex change was highest on small reefs with low population densities (Warner and Hoffman, 1980a,b). In contrast, the pacific rainbow wrasse, *T. lucasamum*, has dramatically higher population densities than the bluehead wrasse and, accordingly, very little sex change takes place in this species, to the extent that it appears gonochoristic, with a sex ratio of 0.5 (Warner, 1982).

Studies of non-labrid fish have highlighted similar effects of resource size or distribution shaping the mating system and subsequent selection for sex change. For example, numerous species within the damselfish genus *Dascyllus* have been investigated from the perspective of

the potential for mate monopolization (Fricke, 1980; Shpigel and Fishelson, 1986; Godwin, 1995). The general pattern is that small patchily distributed habitats are more easily defended and hence lead to high reproductive skew and polygynous mating systems, favouring more sex change. In contrast, larger or more continuously distributed habitats, with more potential for the formation of large groups or for migration between groups, result in more promiscuous mating systems with little or no skew, less sex change and more equal sex ratios.

Here we test these ideas in a field study of the masked goby, *Coryphopterus personatus*, on atoll-fringing reefs in the Caribbean. Before conducting our field observations, we performed a laboratory experiment to demonstrate that Belizean populations are capable of changing sex, and to test the effects of the social environment on the sex change decision. We then carried out field observations to test the following predictions:

1. Increasing local population density makes it more difficult to defend females or resources critical to females, leading to a reduction in the amount of sex change and an increase in the proportion of early maturing males.
2. Females on isolated patches of reef are easier to defend than females on continuous coral garden habitats, leading to more sex change and fewer early maturing males on isolated patches of reef.
3. The difference in energetic environment between windward and leeward reef locations (Stoddart, 1962) leads to differences in the selection pressures for sex change. Specifically, the higher turbulence on windward reefs restricts inter-group movement, leading to easier mate monopolization, higher selection for sex change and fewer early maturing males than on more protected leeward reefs.

Furthermore, we take the opportunity to test a final prediction that the population sex ratio should show less extreme biases in partially sex-changing populations, where some individuals mature directly into the second sex (Charnov, 1989; Allsop and West, 2004). Previous empirical work attempting to test this prediction has found quantitative support for the theory at a cross-species level when using the presence or absence of early maturing males as a discreet binomial predictor, but has failed to find any relationship between sex ratio and the proportion of early maturing males when using the proportion of these males as a continuous predictor across species (Allsop and West, 2004).

MATERIALS AND METHODS

Study sites

The eastern coast of Belize, Central America, is home to the second longest barrier reef system in the world, extending from the Mexican border to the Gulf of Honduras. To the east of the barrier reef system, formed from the fault-controlled Yucatan continental block, lie three of the Caribbean's coral atolls, Turneffe, Glovers and Lighthouse (Fig. 1). The present study focuses on Turneffe and Glovers Atolls. Both atolls are orientated roughly north-south, and are surrounded on both the windward and leeward sides by fringing reef. The windward sides generally receive high wave energy and, as a consequence, have developed segmented reefs of spectacular high relief, often consisting of spur and groove

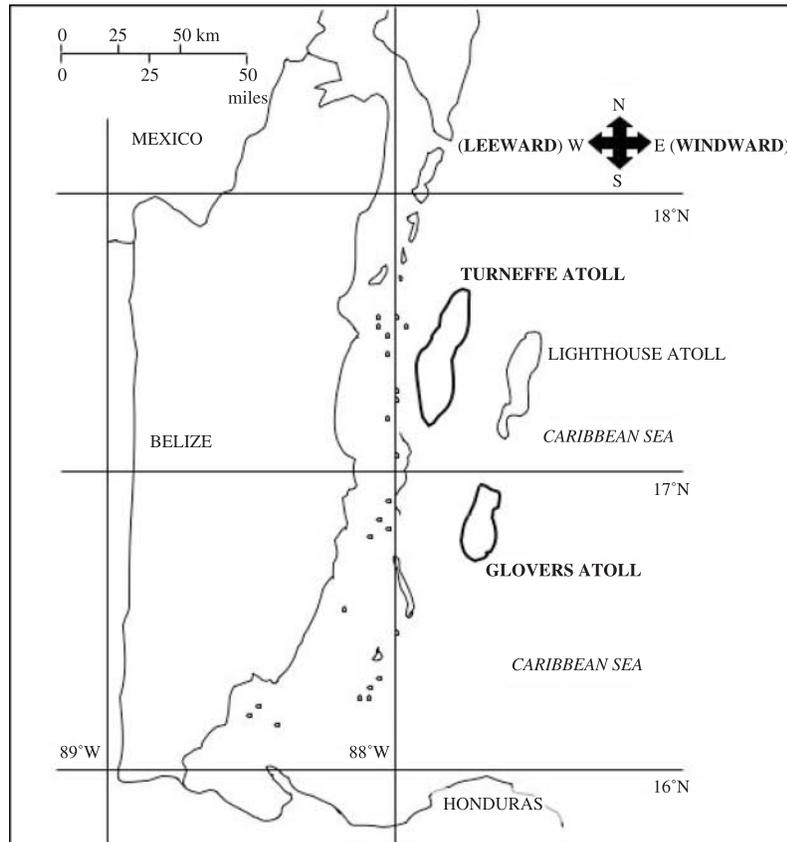


Fig. 1. Map of study area. The Belize Barrier Reef is demarked by the string of small islands (running north-south) to the west of the atolls. Study atolls are outlined in bold.

topography (Stoddart, 1962). The leeward sides, on the other hand, are generally more protected, receiving considerably less wave energy. As a consequence, the leeward reefs tend to be of lower relief, forming a more continuous distribution of 'coral gardens'.

Sample collections and basic reef ecology

We sub-sampled assemblages of the marine goby, *Coryphopterus personatus*, from fore-reef habitats on the fringing reefs around Glovers Atoll (16°42'00"N to 16°55'00"N; 87°53'00"W to 87°41'00"W) and Turneffe Atoll (17°09'00"N to 17°38'00"N; 87°44'30"W to 87°57'30"W). We sampled locations randomly from around the leeward and windward sides of both atolls at a depth of 15–30 m using scuba and the anaesthetic quinaldine sulphate, administered in aqueous solution from a squeeze bottle. We were able to capture a large sub-sample of the individual populations using a single cloud of the anaesthetic, due to the small size of the animals (maximum body size 34 mm).

We collected basic ecological data for each individual population to assess the influence of ecology on the sex-change decisions of *C. personatus*. We made measurements of

the surface dimensions of the section of reef from which the population was taken and converted these measurements to surface area. We then used these surface area scores to calculate the population density for each group, as number of fish per square metre. In addition, we classified each capture site as isolated or continuous by subjective interpretation, depending on whether the section of reef on which the fish lived was a single, prominent topographic entity (such as a bluff, bolder or turret), or an area of reef with little or no topography (such as low-lying coral gardens).

Following capture, we transported fish to the shore whereupon populations were processed for sex/size distribution data. We sexed fish using the external appearance of the genital papillae, which is short and rounded for females and long and pointed for males (Cole and Robertson, 1988), and maximum length was recorded as the distance in millimetres from the tip of the snout to the distal tip of the caudal fin, using callipers accurate to 0.1 mm.

Social control of sex-change experiment

We performed the sex-change experiment at the University of Belize marine field station, on Calabash Caye, Turneffe Atoll. We made separate collections of fish from the nearby fringing reefs in front of the field station using the same methodology as above. Following capture, we sexed and measured fish before placing them into experimental groups of known sex and size distribution in aquaria in the flow-through sea-water laboratory. To test for an effect of social environment (sex/size ratio) on sex change, we carried out the following experiment. We established a control ‘inhibition only’ treatment consisting of a single large male and five smaller females, in which we expected the dominant effects of the larger male to inhibit sex change in the smaller females. Our experimental ‘inhibition/stimulation’ treatment consisted of one larger male and ten smaller females, in which we tested for a stimulatory effect of small females above that of the male’s inhibitory effects. We maintained fish for the duration of the experiment (20 days) with a constant supply of fresh, aerated sea water, and fed them *ad libitum* on a diet of ground fish flakes.

Estimating life-history variables for natural populations

As there is no difference between the gonads of sex-changed males and males that mature directly from the juvenile phase in this species (Cole and Robertson, 1988), we were unable to estimate directly the proportion of early maturing males using gonadal histology. Instead, we estimated the proportion of early maturing males for each population separately using a logistic regression procedure, with sex ratio (proportion male) as the response variable and body size as the predictor variable. This procedure outputs a roughly S-shaped curve, with a higher proportion of females in the smallest size categories and a higher proportion of males in the largest size categories. We then used the logistic regression parameters to calculate the sex ratio (proportion male) at the 5th percentile of the population body size distribution using the following equation:

$$\text{sex ratio (proportion male)} = \frac{e^{(a+bx)}}{1 + e^{(a+bx)}}$$

where a is the intercept of the logistic regression, b is the slope and x is the body size at the 5th percentile. We chose to use the sex ratio at the 5th percentile because this is sufficiently close to the lower end of the population size distribution to ensure that the males present were early maturing males and not the product of sex change, and yet sufficiently far in from the smallest animal so as to minimize the noise inherent in measuring and sexing these smallest size groupings.

Statistical analysis

Proportion data, such as the proportion of early maturers, are bound between 0 and 1, and usually characterized by non-normal error variances and unequal sample sizes. The most powerful way to allow for this is to assume a binomial error structure and a logit link function in a generalized linear model (GLM) (Crawley, 1993; Wilson and Hardy, 2002). The results of the sex-change experiment are analysed using this procedure, and the analysis of the prediction of less extreme sex ratio bias in partial sex changers is performed using a combination of angular transformation and GLM with binomial error structure. However, we were unable to use the GLM approach for our analysis of the effects of socio-ecology on the proportion of early maturing males because we estimated our proportion of these males using the logistic regression (see above). Thus, we did not have access to the population size information required for this approach. Consequently, we used the next best method of arcsine square root transforming our proportion early maturer data, and performing standard analysis assuming normal errors. To investigate the factors affecting habitat preferences and the proportion of early maturing males, we constructed general linear models including all main effects and higher-level interactions. We then carried out model simplification with standard methodology, using stepwise deletion (Crawley, 1993).

RESULTS

We sampled a total of 49 populations of *Coryphopterus personatus* from depths ranging from 10 to 25 m, with a mean capture depth of 17.8 m ($\pm 95\%$ confidence interval, CI = 16.7–18.9 m). Populations ranged in size from 28 individuals up to 302, with a mean population size of 93.2 ($\pm 95\%$ CI = 77.2–109.4). Collections were split equally between the two atolls, with 24 populations collected from Glovers Atoll and 25 from Turneffe Atoll. Sex ratios (proportion male) ranged from 0.11 to 0.50, with an average of 0.33 ($\pm 95\%$ CI = 0.3–0.36).

Our estimate of the proportion of early maturing males ranged from 0.11 to 0.79, with an average of 0.44 ($\pm 95\%$ CI = 0.38–0.49). There was a high incidence of overlap between male and female size distributions in all populations studied (mean proportion overlap = 0.78; $\pm 95\%$ CI = 0.72–0.84, range = 0.33–1; Fig. 2), and the proportion of females in the upper 5th of the population size distributions was generally high (mean proportion female in upper 5th of size distribution = 0.5; $\pm 95\%$ CI = 0.4–0.6, range = 0–1).

Social control of sex-change experiment

We observed sex change taking place in six out of ten of our ‘inhibition/stimulation’ experimental replicates and no instances of sex change in our ‘inhibition only’ control populations. This difference between experimental and control treatments was highly

significant using a GLM with binomial error structure and a logit link function ($F_{1,17} = 9.00$, $P = 0.008$). Our experiment demonstrates that *C. personatus* on atoll-fringing reefs in Belize does have the ability to change sex, and indicates that the proximal mechanism controlling sex change includes a stimulatory effect of the presence of smaller females, and/or an inhibitory effect of larger males.

Four of the populations in which sex change occurred fitted the predictions of the size-advantage hypothesis (Warner, 1988b), with the largest female changing sex. One of those populations had multiple sex changes occurring, with the second largest female changing sex also. In the remaining two sex-changing populations, it was the second largest female which changed sex. Overall, there was a significant tendency for the females that changed sex to be larger than the average sized non-sex-changing female in the group (mean difference = 3.3, $t_5 = 2.7$, $P = 0.05$).

Basic ecology and population density

Considering both atolls together, reef areas from which captures took place ranged in size from 2 to 70 m², with a mean reef size of 21 m² ($\pm 95\%$ CI = 17–25 m², $n = 49$). Of the 49 populations sampled, 25 were taken from continuous coral cover habitats and 24 from topographically isolated patches of reef. On the windward sides of the atolls, where wave energy is highest, 61% of the habitats sampled were topographically isolated patches of reef, and on the leeward sides of the atolls 88% of habitats sampled were continuous coral cover with low-lying, indistinct topography.

Population size increases with increasing reef area (OLS regression: population size = $53.18 + 1.93 \times \text{reef area}$; significance of slope: $t = 3.68$, $P < 0.01$, $r^2 = 0.22$, $n = 49$), but population density decreases with increasing reef size in a quadratic fashion [significance of quadratic term: $F_{1,46} = 23.99$, $P < 0.01$; best fit predictor of population density is given by: $\log(\text{population density}) = 1.28 - 0.004 \times \text{reef area} + 0.0005 \times \text{reef area}^2$ ($\pm 95\%$ CI of the linear (α) and quadratic (β) terms: $\alpha \pm 0.001$, $\beta \pm 0.0002$)]. There was no significant difference between population density on isolated and continuously distributed reefs [isolated: mean = 8.12 fish per m² ($\pm 95\%$ CI = 2.18), $n = 24$; continuous: mean = 4.08 fish per m² ($\pm 95\%$ CI = 1.01), $n = 25$; $F_{1,47} = 2.10$, $P > 0.1$]. There was, however, a significant difference in population density between windward and leeward reefs, with higher

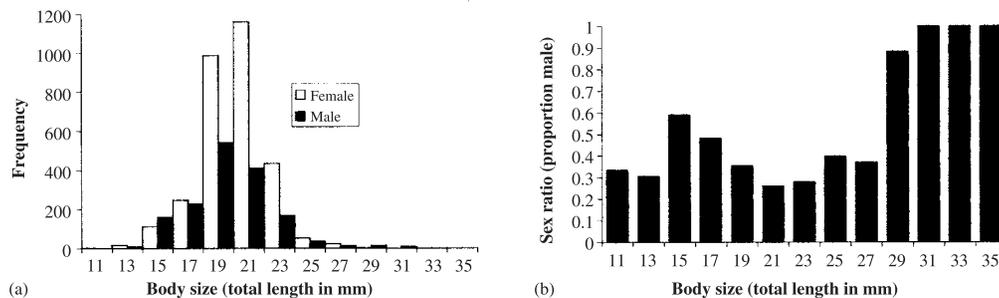


Fig. 2. Sex/size distribution for whole study population of *C. personatus* collected on atoll-fringing reefs in Belize. (a) Frequency distribution, (b) proportion male. Note the large overlap in size distribution between the two sexes.

population densities on windward sides of the study site [windward mean population density = 7.7 fish per m^2 ($\pm 95\%$ CI = 1.7), $n = 33$; leeward mean population density = 2.8 fish per m^2 ($\pm 95\%$ CI = 0.4), $n = 16$; $F_{1,47} = 19.09$, $P < 0.0001$].

Ecological factors and sex change

We investigated the effects of population density, habitat distribution (isolated or continuous) and windward or leeward reef location on the amount of sex change and the production of early maturing males using a generalized linear model with stepwise deletion of non-significant terms. Our minimal model included significant interactions between: (1) population density and windward or leeward location ($F_{1,44} = 5.17$, $P < 0.05$; Fig. 3), and (2) habitat distribution (isolated or continuous reefs) and windward or leeward reef location ($F_{1,44} = 6.3$, $P < 0.05$; Fig. 4).

The significant interaction between population density and windward or leeward reef location (Fig. 3) arises because the proportion of early maturing males increases with increasing population density on low-energy leeward reefs (slope = 0.98; $\pm 95\%$ CI = 0.07, $t = 14.00$, $P = 0.01$, $r^2 = 0.35$), but there is no such relationship on higher-energy windward reefs (slope = -0.16 ; $\pm 95\%$ CI = 0.22, $t = 0.73$, $P > 0.1$, $r^2 = 0.06$). The significant interaction between windward or leeward locations and habitat distribution arises because there are more early maturing males on isolated reefs than on continuous reefs in windward locations ($F_{1,32} = 5.06$, $P < 0.05$; Fig. 4), but no significant difference on leeward locations ($F_{1,15} = 0.43$, $P > 0.1$), with the trend actually being in the opposite direction.

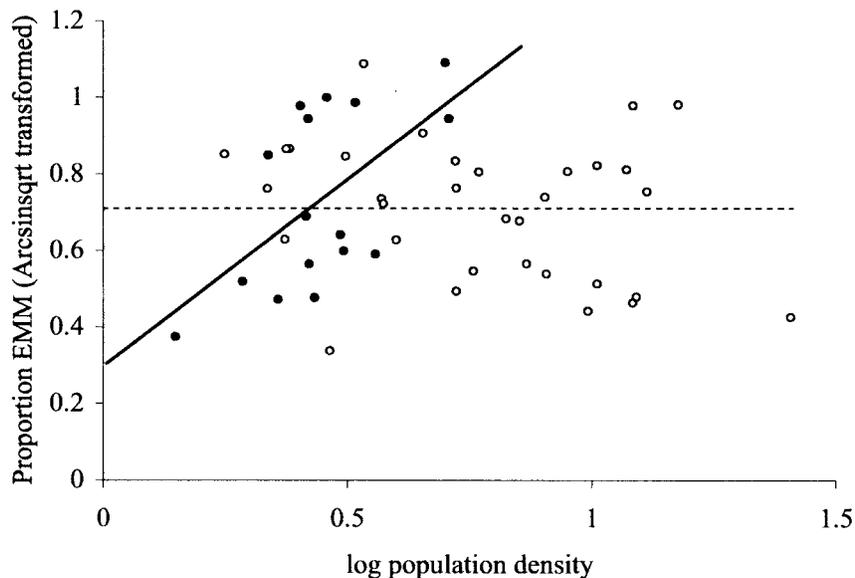


Fig. 3. The correlation between population density and the proportion of early maturing males (EMMs), on windward (○) and leeward (●) reefs. There is a positive correlation between population density and the proportion of early maturing males in leeward but not windward populations.

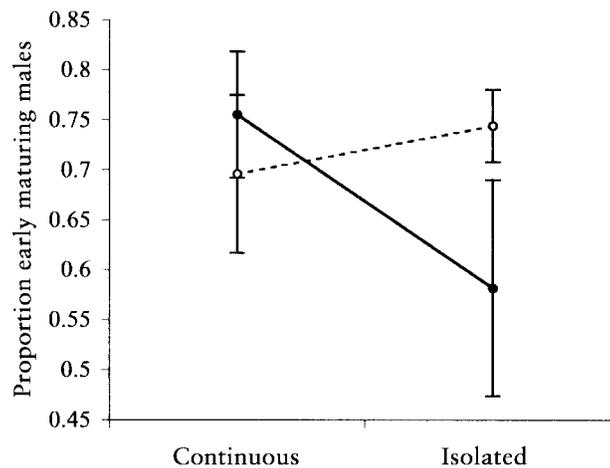


Fig. 4. Isolated reefs have fewer early maturing males than continuous coral gardens on leeward (●) but not windward (○) locations.

Sex ratio bias and the proportion of early maturing males

We tested whether the sex ratio bias was less for populations with a greater proportion of early maturing males by angular transformation of the proportion early maturing males (see ‘statistical analysis’ in the Methods section), and using that transformed data as a predictor of the population sex ratio as defined using a GLM with a binomial error structure and a logit link function. Our analysis demonstrates that indeed there is a trend for a less biased sex ratio as the proportion of early maturing males increases across populations (intercept = -1.5 ; $\pm 95\%$ CI = 0.4 ; slope = 1.3 ; $\pm 95\%$ CI = 0.5 ; $r^2 = 0.29$, $F_{1,47} = 18.8$, $P < 0.0001$).

DISCUSSION

We performed a laboratory experiment and observational field collections using 49 populations of the masked goby, *Coryphopterus personatus*, from atoll-fringing reefs in Belize. Our results show that: (1) *Coryphopterus personatus* from this population is capable of facultative sex change, and that this sex-change process is consistent with a proximal control mechanism involving an inhibitory effect of larger males and/or a stimulatory effect of smaller females. (2) The proportion of early maturing males is positively correlated with population density in leeward environments, as predicted, but this relationship does not hold in windward locations (Fig. 3). (3) The proportion of early maturing males is higher on isolated patches of reef than on continuous coral gardens in windward environments, contrary to predictions (Fig. 4). (4) The proportion of early maturing males is positively correlated with the population sex ratio, with higher proportions of early maturing males being associated with less extreme sex ratio biases, as predicted by theory (Charnov, 1989; Allsop and West, 2004).

Overall, our results provide mixed support to the predictions we set out to test. Although we found support for the idea that increasing population density leads to an increase in the proportion of early maturing males, possibly because higher population densities

destabilize the potential for mate monopolization and thus selection for sex change (Warner, 1982, 1984), this was only the case on the leeward sides of the atolls (Fig. 3). Why might the effects of population density break down in windward environments? One possibility is that animals find it more difficult to migrate between groups in high-energy turbulent environments such as those found on windward reefs, especially small-bodied animals such as *C. personatus*. Restricting inter-group movement in this way would encourage mate monopolization and select for higher levels of sex change and fewer early maturing males, in an analogous way to the restriction of movement in patchily distributed habitats (Fricke and Fricke, 1977; Godwin, 1995). However, our data also highlight the fact that population densities on windward sides of the atolls are at least double those in the leeward environments. If increasing population density in any way destabilizes group structure leading to difficulty in harem control, then our observations of higher population densities on windward sides would predict less sex change to occur here and more early maturing males to be produced. Population density may therefore always be so high on windward sides that variation in population density has a negligible effect on selection for early maturing males (and sex change).

Our finding of a higher proportion of early maturing males on isolated patches of reef than on continuous coral gardens is contrary to our original prediction. Aside from the possible effects of the energetic environment in windward locations, it may be that windward and leeward reefs differ in other characteristics that might influence the timing of life-history events. For instance, it is possible that food supply varies between these sites, which would have an effect on the growth rates and thus the timing of life-history decisions for the animals living in the respective environments (Kerrigan, 1994). Alternatively, there may be variability in population recruitment rates between leeward and windward reefs caused by physical differences in the local ocean currents (Sammarco and Andrews, 1988; Wolanski and Hamner, 1988; Swearer *et al.*, 1999), which would alter the population demographics and potentially lead to differences in selective pressures in the two environments. While we do find support for the prediction that sex change should be more frequent on isolated reefs than on continuous reefs, when we look at the leeward side of the study site, the low sample size for isolated reefs in this area means that we can make no inference about these results. More data on isolated, leeward reefs would be required to determine if this trend is real.

Our finding of less extreme sex ratio bias in populations with a larger proportion of early maturing males supports the idea that the presence of these males lowers the average reproductive value of males in the population (early maturing males plus sex-changed males), leading to a lower ratio of females to males being needed to equalize the genetic contribution of males and females to the next generation (Allsop and West, 2004).

As a general observation, our data reveal that there is a high proportion of early maturing males present in all populations captured (average = 0.44; \pm 95% CI = 0.06), a large overlap in the male–female size distributions (mean proportion overlap = 0.78; \pm 95% CI = 0.06; Fig. 2) and a relatively high proportion of females in the upper 5th of the population size distributions (mean proportion of females in upper 5th of size distribution = 0.5; \pm 95% CI = 0.1). When taken together, these findings could indicate that there is very little sex change taking place in these natural populations of *C. personatus*. Yet, our experiment demonstrates that these animals are indeed capable of changing sex. Why, then, do we see such low levels of sex change taking place? One potentially important factor is that *C. personatus* exhibits male parental care, where males guard the eggs in their nest until

hatching (Cole and Robertson, 1988). This could reduce the males' potential reproductive rate (Clutton-Brock, 1991; Clutton-Brock and Vincent, 1991; Kokko and Jennions, 2003), and hence reduce selection for sex change (Warner and Lejeune, 1985).

Another possible explanation for these patterns that we find in our data may be that there is a high risk of sperm competition for these fish in the atoll-fringing reef environments of the present study. Certainly, the very presence of the high numbers of small males in the lower size categories would indicate the opportunity for high levels of sperm competition to take place, through sneak, streak or group spawning tactics (Gross, 1982, 1991). Such high risks of sperm competition can act to reduce the reproductive value of following the classical size advantage route, and changing sex when old and/or large (Munoz and Warner, 2003). Thus, it is also possible that the large overlaps in sex/size distributions observed across populations are the product of small females changing sex rather than the largest females. Such a strategy could be selected for if there are opportunities for engaging in sperm competition and using 'small male interference reproductive strategies' (Munoz and Warner, 2003). However, it should also be mentioned that our method for estimating the proportion of early maturing males (using the logistic regression) and our measures of sexual size dimorphism (proportion overlap in size distribution of the sexes) may be sensitive to other factors that can affect the degree of sexual size dimorphism, such as the effects that variation in the population density can have on intra-sexual competition (and thus male size) and on levels of food competition between the sexes, leading to sex-specific selection on body size to reduce dietary overlap (Stamps *et al.*, 1997).

When we consider all potential factors that might disrupt a large male's reproductive value, it begs the question: 'Why bother changing sex at all?' One explanation may be that large males are able to care for many egg clutches at the same time, as is observed in many demersal spawning fish species (Williams, 1975; Blumer, 1979; Clutton-Brock and Vincent, 1991; Reynolds and Jones, 1999; Kokko and Jennions, 2003). Thus, if a female's reproductive potential is limited by her rate of egg production, but parental males can care for many females' eggs, the detrimental impact of paternal care on the male's reproductive value may be ameliorated considerably. Alternatively, sex change can be selected for in smaller females in order to exploit any opportunity to become involved in sperm competition, as discussed above, and not selected for in larger females because of the risk of sperm competition reducing the value of being a large male. It may be that the variation that we observe in the proportion of early maturing males, in the level of sexual size dimorphism and in the proportion of large females in the populations in this study represent points along a continuum of the various forces selecting for sex change.

ACKNOWLEDGEMENTS

This paper is dedicated to the memory of Chris Wysiekierski. We thank Eden Garcia, James Humphreys, Helena Swann, Clare Muller, Camilo Mora and the Sale Group for assistance and useful discussion in the field; Kathleen Cole for advice on the correct use of fish anaesthetic in a field environment; the staff at the University of Belize Marine field station on Turneffe Atoll and the Wildlife Conservation Society field station on Glovers Atoll; Nic Colegrave and David Shuker for useful discussion and comments on the manuscript; BBSRC, NERC, The Royal Society, The Royal Commission for the Exhibition of 1851 and the Davis Expedition Fund of Edinburgh University for funding.

REFERENCES

- Allsop, D.J. and West, S.A. 2003a. Changing sex at the same relative body size. *Nature*, **425**: 783–784.
- Allsop, D.J. and West, S.A. 2003b. Constant relative age and size at sex change in sequentially hermaphroditic fish. *J. Evol. Biol.*, **16**: 921–929.
- Allsop, D.J. and West, S.A. 2004. Sex ratio evolution in sex changing animals. *Evolution*, **58**: 1019–1027.
- Blumer, L.S. 1979. Male parental care in bony fishes. *Q. Rev. Biol.*, **54**: 149–161.
- Charnov, E.L. 1982a. *The Theory of Sex Allocation*. Princeton, NJ: Princeton University Press.
- Charnov, E.L. 1982b. Alternative life-histories in protogynous fishes: a general evolutionary theory. *Mar. Ecol.-Prog. Ser.*, **9**: 305–307.
- Charnov, E.L. 1989. Evolution of the breeding sex-ratio under partial sex change. *Evolution*, **43**: 1559–1561.
- Clutton-Brock, T.H. 1991. *The Evolution of Parental Care*. Princeton, NJ: Princeton University Press.
- Clutton-Brock, T.H. and Vincent, A.C.J. 1991. Sexual selection and the potential reproductive rates of males and females. *Nature*, **351**: 58–60.
- Cole, K. and Robertson, D.R.R. 1988. Protogyny in the Caribbean reef goby, *Coryphopterus personatus*: gonad ontogeny and social influences on sex change. *Bull. Mar. Sci.*, **42**: 317–333.
- Crawley, M. 1993. *GLIM for Ecologists*. Oxford: Blackwell Scientific.
- de Girolamo, M., Scaggiante, M. and Rasotto, M.B. 1999. Social organization and sexual pattern in the Mediterranean parrotfish *Sparisoma cretense* (Teleostei: Scaridae). *Mar. Biol.*, **135**: 353–360.
- Emlen, S.T. and Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**: 215–223.
- Fennessy, S.T. and Sadovy, Y. 2002. Reproductive biology of a diandric protogynous hermaphrodite, the serranid *Epinephelus andersoni*. *Mar. Freshw. Res.*, **53**: 147–158.
- Fricke, H.W. 1980. Control of different mating systems in a coral reef fish by one environmental factor. *Anim. Behav.*, **28**: 561–569.
- Fricke, H. and Fricke, S. 1977. Monogamy and sex change by aggressive dominance in coral reef fish. *Nature*, **266**: 830–832.
- Ghiselin, M.T. 1969. The evolution of hermaphroditism amongst animals. *Quart. Rev. Biol.*, **44**: 189–208.
- Godwin, J. 1995. Phylogenetic and habitat influences on mating system structure in the humbug damselfishes (Dascyllus, Pomacentridae). *Bull. Mar. Sci.*, **57**: 637–652.
- Gross, M.R. 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Z. Tierpsychol.*, **60**: 1–26.
- Gross, M.R. 1991. Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Phil. Trans. R. Soc. Lond. B*, **332**: 59–66.
- Kerrigan, B.A. 1994. Postsettlement growth and body-composition in relation to food availability in a juvenile tropical reef fish. *Mar. Ecol.-Prog. Ser.*, **111**: 7–15.
- Kokko, H. and Jennions, M. 2003. It takes two to tango. *TREE*, **18**: 103–104.
- Leigh, E.G., Charnov, E.L. and Warner, R.R. 1976. Sex ratio, sex change and natural selection. *Proc. Natl. Acad. Sci. USA*, **73**: 3655–3660.
- Munoz, R.C. and Warner, R.R. 2003. A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size-fecundity skew. *Am. Nat.*, **161**: 749–761.
- Policansky, D. 1982. Sex change in plants and animals. *Annu. Rev. Ecol. Syst.*, **13**: 471–495.
- Reynolds, J.D. and Jones, J.C. 1999. Female preference for preferred males is reversed under low oxygen conditions in the common goby (*Pomatoschistus microps*). *Behav. Ecol.*, **10**: 149–154.
- Robertson, D.R. 1972. Social control of sex reversal in a coral reef fish. *Science*, **177**: 1007–1009.
- Robertson, D.R. and Choat, J.H. 1974. Protogynous hermaphroditism and social systems in labrid fish. *Proc. Second Intl. Coral Reef Symp.*, **1**: 217–225.

- Robertson, D.R. and Hoffman, S.G. 1977. The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. *Z. Tierpsychol.*, **45**: 298–320.
- Robertson, D.R. and Warner, R.R. 1978. Sexual patterns in the labroid fishes of the western Caribbean. II: The Parrotfishes (Scaridae). *Smithsonian Contrib. Zool.*, **255**: 1–26.
- Ross, R.M. 1990. The evolution of sex-change mechanisms in fishes. *Environ. Biol. Fishes*, **29**: 81–93.
- Sammarco, P.W. and Andrews, J.C. 1988. Localised dispersal and recruitment in Great Barrier Reef corals: the helix experiment. *Science*, **239**: 1422–1424.
- Shpigel, M. and Fishelson, L. 1986. Behavior and physiology of coexistence in two species of *Dascyllus* (Pomacentridae, Teleostei). *Environ. Biol. Fishes*, **17**: 253–265.
- Stamps, J.A., Losos, J.B. and Andrews, R.M. 1997. A comparative study of population density and sexual size dimorphism in Lizards. *Am. Nat.*, **149**: 64–90.
- Stoddart, D.R. 1962. Three Caribbean atolls: Turneffe Islands, Lighthouse Reef, and Glovers Reef, British Honduras. *Atoll Res. Bull.*, **87**: 1–128.
- Swearer, S.E., Caselle, J.E., Lea, D.W. and Warner, R.R. 1999. Larval retention and recruitment in an island population of a coral reef fish. *Nature*, **402**: 799–802.
- Warner, R.R. 1975. The adaptive significance of sequential hermaphroditism in animals. *Am. Nat.*, **109**: 61–82.
- Warner, R.R. 1982. Mating systems, sex change and sexual demography in the rainbow wrasse, *Thalassoma lucasanum*. *Copeia*, **3**: 653–661.
- Warner, R.R. 1984. Mating behavior and hermaphroditism in coral reef fishes. *Am. Sci.*, **72**: 128–136.
- Warner, R.R. 1988a. Sex change in fishes – hypotheses, evidence, and objections. *Environ. Biol. Fishes*, **22**: 81–90.
- Warner, R.R. 1988b. Sex change and the size-advantage model. *Trends Ecol. Evol.*, **3**: 133–136.
- Warner, R.R. and Hoffman, S.G. 1980a. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.). *Evolution*, **34**: 508–518.
- Warner, R.R. and Hoffman, S.G. 1980b. Population density and the economics of territorial defense in a coral reef fish. *Ecology*, **61**: 772–780.
- Warner, R.R. and Lejeune, P. 1985. Sex change limited by paternal care: a test using four Mediterranean labrid fishes, genus *Symphodus*. *Mar. Biol.*, **87**: 89–99.
- Warner, R.R. and Robertson, D.R. 1978. Sexual patterns in the labroid fishes of the western Caribbean. I: The wrasses (Labridae). *Smithsonian Contrib. Zool.*, **254**: 1–27.
- Warner, R.R., Robertson, D.R. and Leigh, E.G. 1975. Sex change and sexual selection: the reproductive biology of a labrid fish is used to illuminate a theory of sex change. *Science*, **190**: 633–638.
- Williams, G.C. 1975. *Sex and Evolution*. Princeton, NJ: Princeton University Press.
- Wilson, K. and Hardy, I.C.W. 2002. Statistical analysis of sex ratios: an introduction. In *Sex Ratios: Concepts and Research Methods* (I.C.W. Hardy, ed.), pp. 48–92. Cambridge: Cambridge University Press.
- Wolanski, E. and Hamner, W. 1988. Topographically controlled fronts in the ocean, and their influence on the distribution of organisms. *Science*, **241**: 177–181.

