Protogynous hermaphroditism and gonochorism in four Caribbean reef gobies

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Synopsis

The sexual structures of the populations of four Caribbean gobies were examined. *Gobiosoma multifasciatum* and *Coryphopterus personatus* are protogynous hermaphrodites, while *G. illecebrosum* and *G. saucrum* are gonochoristic. Sex changes were induced in females of the first two species in the laboratory, but not in females of the latter two species. The two hermaphroditic species live in large populations while the two gonochorists live in small groups. The significance of these findings to models of the evolution of protogyny are discussed.

Introduction

Sequential hermaphroditism is common among marine fishes. The best-known cases are among the labroid, serranid and sparid fishes (Reinboth 1961, Atz 1964, Smith 1975). Protandry and protogyny have recently been discovered among the damselfishes and angelfishes (Fricke & Holzberg 1974, Fricke & Fricke 1977, Moyer & Nakazono 1978a,b, Bruce 1980), and Lassig (1977) has described protogyny in four species of western Pacific gobies (genus *Paragobiodon*). The gobies that Lassig examined are coral symbionts that live in small groups in small clumps of shrub-like live corals. Typically, a group consists of a heterosexual pair, but may also include some juveniles. Removal of a male leads to a sex change by the largest female in a group. Lassig (1977) suggested that protogyny had evolved in

these fishes because, when group sizes are very small and high predation risks severely limit mobility, sex change would reduce the need for fishes to leave their corals and move about in search of mates.

The research that we describe here had two aims: (1) to determine if marine gobies of genera other than *Paragobiodon* are hermaphroditic, and (2) to determine if the presence or absence of any such hermaphroditism is correlated with social group size in the manner that Lassig (1977) found. We collected data on the distribution, abundance, and sexual structures of the populations of four Carribean gobies, *Gobiosoma multifasciatum* Steindachner, *G. illecebrosum* Böhlke & Robins, *G. saucrum* (Robins) and *Coryphopterus personatus* (Jordan & Thompson). We also attempted to induce sex change in females of each species in the laboratory.

Materials and methods

All data and specimens were collected on reefs off San Blas Point, on the Caribbean coast of Panama.

The study species

Specimens of each species were identified by J.E. Böhlke of the Philadelphia Academy of Natural Sciences and are deposited in that institution's collection (*G. multifasciatum* ANSP 143032, *G. illecebrosum* ANSP 143030, *G. saucrum* ANSP 143031, and *C. personatus* ANSP 143029).

In San Blas, *G. multifasciatum* lives under the sea urchins *Echinometra lucunter* and *Diadema antillarum*. It is commonest in shallow fore-reef areas of reefs that often are subject to heavy wave action. *Gobiosoma illecebrosum*, which cleans parasites from the body surfaces of other fishes (Böhlke & McCosker 1973), is mostly commonly found living on the tops of coral heads of the genera *Montastrea*, *Diploria* and *Colpophyllia*. It also occurs around the entrances of small caves. We only found *G. saucrum* on heads of live corals, principally *Montastrea annularis*. We observed members of this species biting at coral polyps and found coral tissue and nematocysts, and nothing else, in the stomachs of three individuals. *Coryphopterus personatus* is most commonly found at depths over 5 m, in areas where corals are scattered about on a sandy substrate. It hovers a little above the bottom near coral growths and feeds on zooplankton.

Population dispersion

We counted the numbers of *G. multifasciatum* under sea urchins in 1×1 m segments of a 49-m-long transect that was placed in the habitat in which the species typically occurred. We also counted the numbers of *G. illecebrosum* and *G. saucrum* on individual coral heads, and the numbers (to the nearest 10 fish) of *C. personatus* in a series of aggregations in the area from which specimens were collected for histological examination. Individual *C. personatus* were considered to be members of the same aggregation if they were not more than 0.5 m apart; in practice, members of an aggregation typically were only 2–5 cm apart.

Population sampling

We sampled individuals throughout the size range of adults and subadults of each species to determine the sex ratio in different size classes. Particular attention was paid to small fish, because, in a species suspected to be composed entirely of protogynous individuals, one would be likely to find that most or all of the small fish were females. Specimens were collected with Quinaldine anesthetic and fixed in Bouin's solution within one hour after collection. Transverse sections were cut through the entire body in the region of the gonads, and stained with Delafield's Haematoxylin/Putt's Eosin. Histological preparations were made of the gonads of 104 *G. multifasciatum*, 67 *G. illecebrosum*, 86 *G. saucrum* and 102 *C. personatus*.

Experiments

In several species of sequentially hermaphroditic fishes, it has been found that in the absence of individuals of the 'terminal' sex (i.e., males in protogynists and females in protandists), there are sex changes by fish of the 'initial' sex (Fishelson 1970, Robertson 1972, Fricke & Fricke 1977, Lassig 1977, Moyer & Nakazono 1978a). Therefore we placed groups of mature females of each species in aquaria to see if any changed sex. The sexes could be distinguished in each species by the shapes of their genital papillae, which are conical and pointed in males and ovate with a blunt, labiate end in females. Specimens were collected in the field and transported to STRI's marine facility on the Pacific coast of Panama within 24 hours of capture. There they were placed in aquaria supplied with running seawater and fed daily on brineshrimp larvae. All four species fed actively and readily on these nauplii. At intervals of 10 days to 6 weeks afterwards, these groups of fish were removed and histological preparations made of their gonads.

Results

Population dispersion

The mean density ($\pm$ 95% C.I.) of *G. multifasciatum* on the transect was 0.55 ± 0.709 fish m^{-2}

(n = 49). Three percent of the 100 *Diadema antillarum* and 3.4% of the 715 *Echinometra lucunter* that were on the transect had *G. multifasciatum* living with them. The usual pattern of dispersion was one fish per urchin; we found 112 fish living singly under urchins and only two instances of two fish under the same urchin. *Gobiosoma illecebrosum* was found in groups of 1–12 fish and the mean number (± 95% C.I.) of fish on a coral head was 3.3. ± 0.58 (n = 73). *Gobiosoma saucrum* was also found in small groups on coral heads. These groups ranged in size from 2–17 fish, with a mean of 5.5 ± 1.55 fish per coral head (n = 26). *Coryphopterus personatus* was very abundant and very dense. It formed sheet-like aggregations of hundreds or even thousands of fish spread across the substrate. The number of fish in 30 such aggregations ranged from 10 to 500 with a mean of 100 individuals.

Sexual structure of populations

Small *G. multifasciatum* were invariably females, whereas most large fish were males. Males reached a larger size than females did (Fig. 1). We found six 'females' whose ovaries contained a few isolated spermatogenic crypts. One of the 33 males that we examined had oogenic remnants in its testes.

Males and females were distributed throughout the size range of *G. illecebrosum* and there was no indication of differences in the sex-ratio in different size classes (Fig. 2). There was no tendency for either solitary fish or the largest fish in groups of
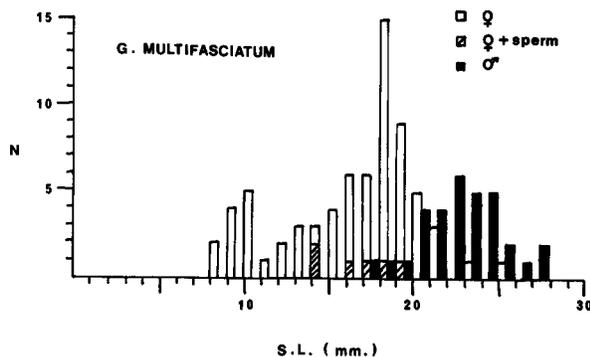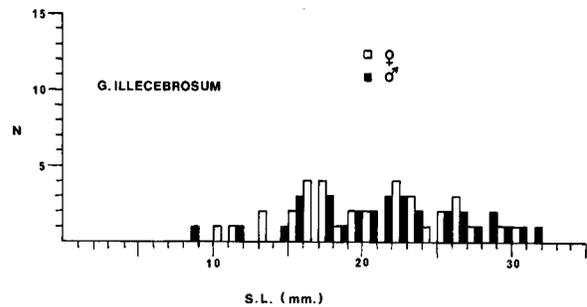

Fig. 2. Number of individuals of different sexual identities that were found in each size class.

two or more fish to be of a particular sex; we collected three single males and three single females, and a male was the largest fish in 7 of 13 groups that contained 2–12 fish. Large groups contained many individuals of both sexes; seven groups of 4 or more fish had a total of 22 males and 22 females.

Large individuals of *G. saucrum* were all males. Both sexes were represented among the smaller size classes, although females predominated (Fig. 3).

All of the small *C. personatus* were females, while medium-sized fish were of both sexes and almost all of the large fish were males (Fig. 4). None of the 33 sectioned males had oogenic remnants in its testes.

Experiments

Gobiosoma multifasciatum

Two groups of five females and another of 15 females were placed in aquaria for 3, 4, and 5 weeks, respectively. At the end of the experiment, all fish in the two small groups had intersexual gonads. The gonads of the largest individual in each group had greater amounts of spermatogenesis than did the
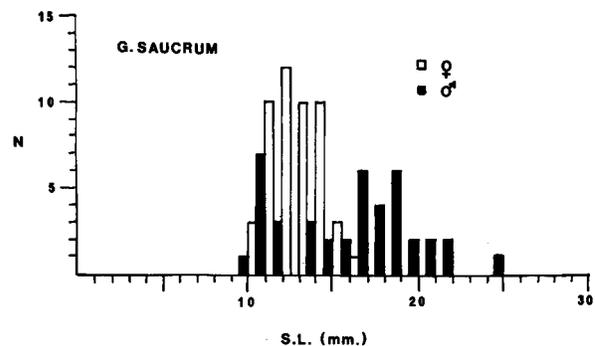

Fig. 1. Number of individuals of different sexual identities that were found in each size class. Female + sperm = intersexual gonad in which oogonesis predominates and only small amounts of spermatogenesis are evident.

Fig. 3. Number of individuals of different sexual identities that were found in each size class.
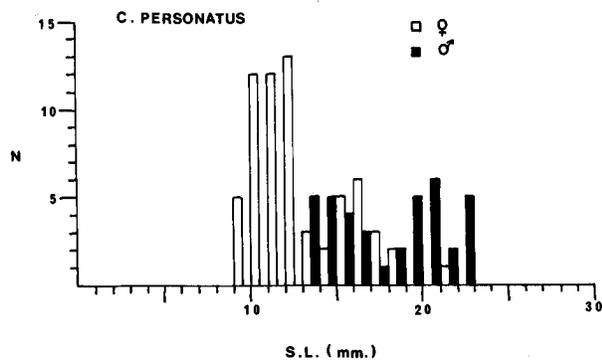
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Fig. 4. Number of individuals of different sexual identities that were found in each size class.

gonads of any of the other fish. The largest three fish in the group of 15 had testes with a few oocytic remnants. They also had genital papillae that were intermediate in shape between normal male and female papillae. The remaining 12 fish had 'female' genital papillae. The three largest individuals of these 12 had intersexual gonads, while none of the remaining 9 exhibited any spermatogenesis in the sectioned parts of their ovaries.

Gobiosoma illecebrosum

Four groups, each of 4–6 fish, were kept in aquaria for 3–5 weeks. One individual in a group that was kept for three weeks proved to be a male. As there were no signs of oogenesis in its testes, we assume we had made a mistake in identifying its sex before placing it in the aquarium. All of the remaining fish were females, with no spermatogenesis in the sectioned parts of their ovaries.

Gobiosoma saucrum

Four groups of 4–7 females were maintained in tanks for 15–30 days. There were no signs of spermatogenesis in the ovaries of any of those 24 fish.

Coryphopterus personatus

Four groups of 8–11 females remained in aquaria for 10–30 days. The largest 5–6 fish in each group were then sectioned. The remaining fish in each group had female-shaped genital papillae. In all four cases, there were 2–4 fish among those that we sectioned that had intersexual gonads. Most of the material in their gonads was testicular. They also

had male-shaped genital papillae, and an elongate spine that is normally found in the first dorsal fin of males but not females.

Discussion

Our field data and experiments strongly indicate that *G. multifasciatum* and *C. personatus* are protogynous hermaphrodites. The absence of males among the small fish indicates that there are no males that are born as males in either species. The detection of *G. multifasciatum* with intersexual gonads among individuals that were preserved immediately after they had been collected in the field indicates that the sex changes in laboratory specimens of this species are not laboratory artifacts.

Gobiosoma illecebrosum and *G. saucrum*, on the other hand, are gonochorists, as far as we can tell. Males were present throughout the sampled size range in each species and there were no signs of sex change in females that we maintained in the laboratory under conditions that induced sex change in females of *G. multifasciatum* and *C. personatus*. However, in one respect *G. saucrum* resembles the two protogynous species more closely than it does *G. illecebrosum*: large individuals of *G. multifasciatum*, *C. personatus* and *G. saucrum* were mostly males, while males and females of *G. illecebrosum* characteristically achieved the same size.

Our data also show that the development of protogyny among gobies is not limited to species that live in small social groups. Indeed, the reverse was true among the four species we studied. It could be argued that because *G. illecebrosum* is a parasite-cleaner it has some immunity to predation and would not be so restricted in its movements as the *Paragobiodon* spp., that Lassig (1977) studied, i.e., groups of *G. illecebrosum* are not as small as they seem. This argument, however, is difficult to sustain with *G. saucrum* which has no such protection from predators.

Ghiselin (1969) considered three models that account for the development of hermaphroditism: the low-density model, the size advantage model and the gene dispersal model (see also Warner 1975). It seems to us that the model that is most applicable to the protogynous Panamanian gobies is the size advantage model-sequential hermaphro-

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ditism is favoured when a fish reproduces most efficiently as a member of one sex when small and as a member of the other sex when large. Because of the sizes of the populations of these fishes and their mobility, the low-density and gene-dispersal models are less applicable. However, we cannot say why only two of the four species are protogynous. Indeed, the predominance of males among large individuals of *G. saucrum* indicates that large size is advantageous to males; if so, we might expect that protogyny would be favoured in that species. Information on the breeding biology and mating system structure of all four species could resolve this question.

Böhlke & Robins (1968) recognized five subgenera among the Caribbean species of *Gobiosoma*. They placed *G. multifasciatum* and *G. saucrum* in one subgenus and *G. illecebrosum* in another. Although two basically different patterns of sexuality are evident among those three species, those patterns do not segregate along subgeneric lines. Nevertheless, such differences in the sexual makeup of populations may eventually prove useful in determining phytogenetic relations among the different species of *Gobiosoma* when more species have been examined. Any such approach to phylogenetic studies must be a cautious one because it has recently become evident that the expression of different patterns of sexuality among closely related fishes can be very flexible (Warner & Robertson 1978, Robertson & Warner 1978).

There are two curious features of hermaphroditism in *Paragobiodon*, the significance of which remains obscure. First, males of *Paragobiodon* spp., but not those of *G. multifasciatum* or *C. personatus*, normally have partly developed oocytes in their testes. This finding led Lassig (1977) to suggest that *Paragobiodon* males might be able to revert to a female identity. As this seems highly unlikely with males of *G. multifasciatum* and *C. personatus*, there may be fundamental differences in the nature of sex change in *Paragobiodon* and in the species that we studied. However, oocyte-like structures are occasionally found in the testes of fishes that do not appear to change sex (Atz 1964) and such structures in *Paragobiodon* testes may have little functional significance to a sex-change capability. Second, according to Lassig, the *Paragobiodon* species form

only monogamous pairs. Even when a social group contains more than one female that is large enough to be mature, only the male and the largest female are reproductively active. The sequentially hermaphroditic anemonefishes also form such monogamous pairs, and, in groups of more than two fish, all but the largest two are immature. However, the anemonefishes are protandrous (Fricke 1979, Fricke & Fricke 1977, Moyer & Nakazono 1978, Ross 1978). It is not obvious how a size advantage that favors one type of sex change in one of these groups of fishes might work in the opposite direction in another when the two groups are so similar ecologically and socially. Thus, the question of which of Ghiselin's (1969) models is most appropriate to *Paragobiodon* hermaphroditism remains open.

Acknowledgments

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