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Mating Behavior and Hermaphroditism in Coral Reef Fishes

Robert R. Warner

The diverse forms of sexuality found among tropical marine fishes can be viewed as adaptations to their equally diverse mating systems

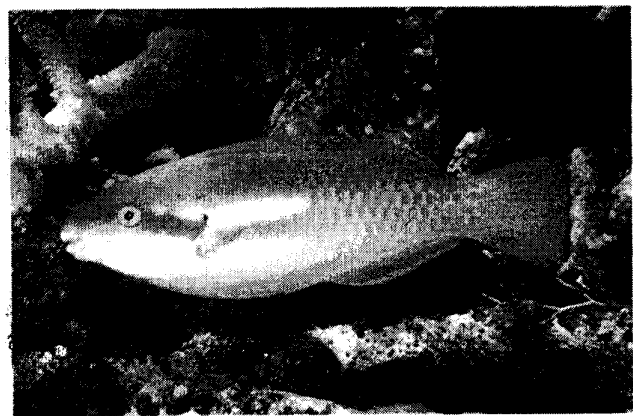
The colorful diversity of coral-reef fishes has long been a source of fascination for both scientists and amateurs. We now know that this diversity of form and color is matched by an immense variety of social behaviors and sexual life histories, including several kinds of functional hermaphroditism. Recent observations and experimental work suggest that the sexual patterns found in fishes may best be viewed as evolutionary responses to the species' mating systems, and much of the evidence I review here bears out this idea. Since most theory in behavioral ecology has been derived from studies of terrestrial vertebrates and insects, which have strictly separate sexes, the relationships between sexual expression and mating behavior in fishes offer new insights into the role of sexuality in social evolution.

Like other vertebrates, most fish species have separate sexes, a condition known as gonochorism. However, fishes are by no means restricted to this pattern: in many species individuals are capable of changing sex, a phenomenon sometimes called sequential hermaphroditism, and in others fishes can be both sexes at the same time, displaying simultaneous hermaphroditism.

This sexual flexibility is quite widespread. At least fourteen fish families contain species that exhibit sex change from female to male, termed protogyny, as a normal part of their life histories (see Policansky 1982 for a recent review). Eleven of these families are common in coral-reef areas; and in the wrasses (Labridae), parrotfishes (Scaridae), and larger groupers (Serranidae) protogyny occurs in the great majority of the species studied (Fig. 1). Changes from female to male are also known to occur in damselfishes (Pomacentridae; Fricke and Holzberg 1974), angelfishes (Pomacanthidae), gobies (Gobiidae), porgies (Sparidae), emperors (Lethrinidae; Young and Martin 1982), soapfishes (Grammistidae), and dottybacks (Pseudochromidae; Springer et al. 1977). However, we have no indication of how common sex change might be in these families, since few species have been carefully investigated. New reports

of protogynous species are constantly cropping up, and the phenomenon may be much more frequent than previously imagined.

Change of sex from male to female—protandry—appears to be less common. It is known in eight families of fishes, three of which—porgies (Sparidae), damselfishes (Pomacentridae), and moray eels (Muraenidae; Shen et al. 1979)—are found on coral reefs. The damselfish and porgy families also include species that are protogynous. Such variability within a family offers an important opportunity to test sex-change theory, and deserves further study.



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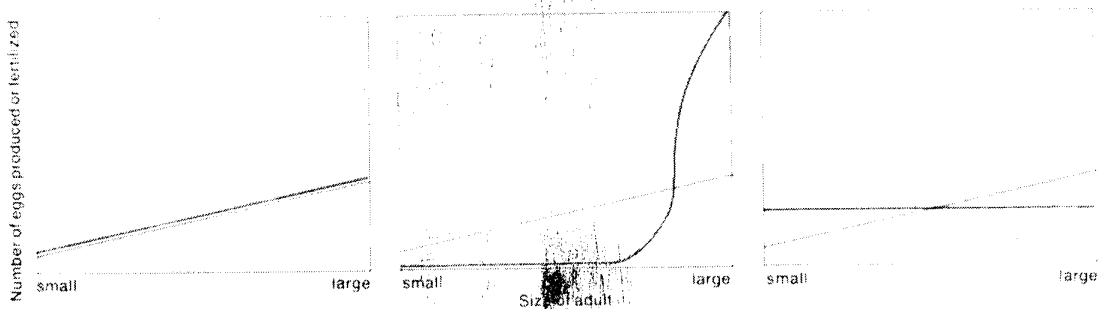


Figure 2. The expected fertility of a female fish (gray line), measured as the number of eggs produced, usually depends directly on size and thus shows a steady increase with growth. By contrast, a male's expected fertility (colored line), measured as the number of eggs fertilized, is affected by the mating system. When males and females form monogamous pairs matched by size or when males compete with each other to fertilize eggs and thus to produce the most sperm, both sexes show a similar increase of fertility with size (left), and no selection for sex change exists.

When large males monopolize mating to the detriment of small males, however, male fertility rises dramatically at a certain point in growth (center), and an individual that remains a female when small and changes to a male at a large size will be selectively favored. When mating consists of random pairing (right), an individual would do best to function as a male while small (with a chance of fertilizing a larger female) and as a female when large (capitalizing on a high capacity for egg production). (After Warner 1975.)

Species in which individuals are simultaneous hermaphrodites, producing eggs and sperm at the same time, are common among deep-sea fishes (Mead et al. 1964) but quite rare elsewhere. However, several species of small sea basses (Serranidae) found in shallow water in tropical areas are known to be simultaneous hermaphrodites (Smith 1975). The existence of this sexual pattern in an abundant species such as the sea basses poses special evolutionary problems that are discussed below.

Because the warm, clear waters of coral reefs create conditions that are nearly ideal for observing animal behavior, the social and mating systems of tropical marine fishes have been particularly well studied. It is my intention here first to outline a central hypothesis which relates sexual patterns to social behavior, and then to test this hypothesis at several levels, using information available in the literature.

Sex change

Why should natural selection favor sexual patterns different from pure gonochorism? In other words, under what circumstances might we expect hermaphroditism to be adaptive? This question was first dealt with in a comprehensive fashion by Ghiselin (1969; 1974), who suggested the general conditions under which hermaphroditism would be expected to evolve. More recent work has related these generalities to the specific social systems of hermaphroditic species (Warner 1975; Fischer 1980; Charnov 1982). It is best to view sequential her-

maphroditism, or sex change, separately from simultaneous hermaphroditism, because they are distinct phenomena under the influence of very different selective regimes.

Ghiselin proposed the "size-advantage model" to account for many cases of sex change. The concept is simple: if the expected number of offspring (measured, say, as the number of eggs produced or fertilized) differs between the sexes with size, then an individual that changes sex at the right size or age will have more offspring than one that remains exclusively male or female.

What might cause such sexual differences in the distribution of expected fertility? Two factors are important here: the relative number of male and female gametes produced and the characteristic mating behavior of the species. In many cases, a female's fertility is limited by the number of eggs she can hold or manufacture, which in turn is controlled by her size, her store of energy, or both. Thus it makes little difference whether she mates with one male or with many. Male fertility, on the other hand, is often limited not by the number of sperm an individual can produce but rather by the number of females with whom he mates and their fertility. Because of this, the fertility of males is potentially much more variable than that of females, and can reach very high levels in certain circumstances (Williams 1966; Trivers 1972).

While size of gamete production sets the stage for potential differences in the reproductive success of males and females of various sizes, it is often the mating system that determines the actual values (Fig. 2). For example, in monogamous species where both members of a pair are normally about the same size, the fertility of males and females is approximately the same over their entire size range, and changing sex conveys no advantage.

By contrast, many coral-reef fishes have mating systems in which larger males monopolize the spawning of females. In this situation smaller males may not spawn at all, while females of equivalent size have little trouble finding a mate. The spawning rate of small males is thus lower than that of small females, but large males expe-

Figure 1. The parrotfish family Scaridae is one of several common families of coral-reef fishes in which the majority of species include individuals that change from female to male, a phenomenon known as protogyny. In the striped parrotfish, *Scarus iserti*, small females are boldly striped (top); as females grow larger, they change sex and adopt the brilliant blue and yellow coloration found in older males (bottom). Groups of young females defend territories along the edges of reefs; males and sex-changed females have larger territories which usually encompass several of these harems. (Photos by D. R. Robertson.)

rience relatively high mating success. Since the distribution of fertility differs between the sexes with size, we would expect sex change to be adaptive: an individual that functioned as a female when small and as a male after attaining a large size would have more offspring over its lifetime than one that remained either male or female, and thus protogyny should be favored by natural selection (Warner 1975).

Other mating systems lead to selection for protandry. Males usually produce millions of sperm, and small individuals are physically capable of fertilizing females of almost any size. Thus in mating systems where no monopolization occurs and where mating consists of random pairing, it should be advantageous to be a male when small (since it is probable that any mating will be with larger individuals) and a female when large (thereby taking advantage of a high capacity for egg production).

Because the fertilization of eggs occurs outside the body in many fish species, spawning is not limited to simple pairs: numerous individuals can mate simultaneously in large groups. Although mating occurs more or less at random in such spawning groups, protandry is not necessarily adaptive if many males release sperm simultaneously. In this case, competition among sperm from several males to fertilize eggs creates a situation in which male fertility is limited by the number of sperm produced. Such production should increase with size in a fashion similar to egg production by females, and thus no fertility differential between the sexes exists.

The size-advantage model has been refined over the years to allow for sexual differences both in mortality and in the rate at which fertility changes with size (Warner et al. 1975; Leigh et al. 1976; Jones 1980; Char-

nov 1982; Goodman 1982). Individuals should change sex when the other sex has a higher reproductive value—that is, higher future expected reproduction taking into account the probability of death. This means that individuals may (and do) change sex and suffer an initial drop in reproductive success, but by making the change they increase the probability of attaining a high level of success in the future. These are complications we need not consider here, since they do not affect the general idea that the mating system can determine the adaptive value of various forms of sex change.

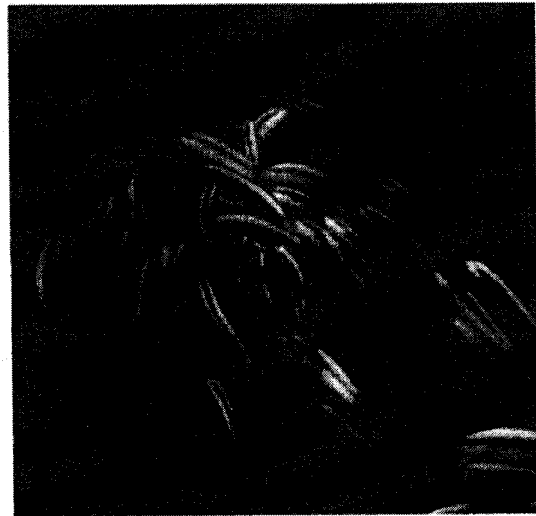
Testing an evolutionary idea such as this is difficult, since experimental manipulations are often impossible or exceedingly time-consuming. Typically, one must rely instead on a search for correlations between the hypothesized cause and effect. As long as sufficient variation exists in the traits in question, the search may take place among unrelated species, within a related group, or even within a single species. The wide diversity of sexual patterns and behaviors among coral-reef fishes allows investigation on all these levels. In addition, the fact that sex changes are often direct responses to external cues makes possible experimental study as well.

Mating in sex-changers

In general, the mating systems of sex-changing species are those in which reproductive success varies with sex and size. Larger males tend to monopolize mating, either by defending spawning sites that females visit or by controlling a harem of females. In most of the species, eggs are simply released into the water, and males are free to devote a large amount of time to courtship, spawning, and defense of mating sites.



Figure 3. The sexual pattern and mating system of the bluehead wrasse, *Thalassoma bifasciatum*, is typical of many wrasses. As in most protogynous species, large males play a dominant role. These older individuals—both primary males and sex-changed females—defend spawning grounds, pair-mating with as many as 150 visiting females daily (left). Young primary males engage in group spawning (right) and in “sneaking,” the practice of



interfering with the mating of older males by rushing in as sperm is released. Young females and young primary males such as those shown group-spawning are characterized by greenish-black lateral markings, whereas both older primary males and sex-changed females display a distinctive white band bordered with black, like the larger individual at the left. (Photos by S. G. Hoffman.)

Figure 4. The study of three closely related species of the wrasse genus *Bodianus* seems to support the idea that sex change is less common in species in which large males have less opportunity to monopolize mating. Both *Bodianus rufus* (top), a species in which large males defend harems of females, and *B. diplotaenia* (center), one in which large males defend temporary spawning sites, are protogynous, as might be expected in mating systems where large males dominate. By contrast, *B. eclancheri* (bottom), which spawns in groups with no pattern of domination by large males, is functionally gonochoric, with the sexes existing in equal ratios. (Photos by S. G. Hoffman.)

A good example of such a mating system is found in the wrasse *Labridae dimidiatus*, which feeds by cleaning the skin, mouth, and gills of other fishes at specific "cleaning stations" on the reef. The cleaner-wrasses at a station live in a group consisting of a single male and a harem of five or six females. The male actively defends these females and mates with each one every day. This appears to be a system in which there is no advantage to being a small male, and indeed the species is totally protogynous (Robertson 1972).

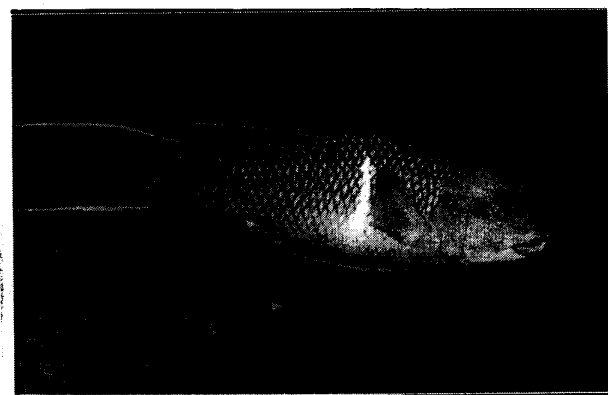
In the last decade, marine biologists have begun to study the mating behavior of a wide variety of protogynous species in their coral-reef habitats. It is striking that virtually all these species exhibit some form of monopolization of mating by large males, even though they are found in a diverse array of families such as wrasses, parrotfishes, damselfishes, angelfishes, basses, and gobies (see, for example, Moyer and Nakazono 1978a; Robertson and Warner 1978; Cole 1982; and Thresher and Moyer 1983). Harem mating systems appear to be most common among these protogynous species. Coral-reef fishes are often quite sedentary, and it is not surprising that large males have come to dominate and defend a local group of females in many cases. It is just this kind of situation that evolutionarily favors sex change from female to male.

There are also some apparent exceptions to the trend toward the dominance of the large male in protogynous species. In a number of species of gobies (Lassig 1977), a small bass (Jones 1980), and a wrasse (Larsson 1976), the social system appears to be monogamous, and thus protogyny would not be adaptive. Lassig (1977) suggests that sex change in the gobies he studied is an adaptation to allow reconstitution of a mated pair in case of death. This explanation probably would not apply to the more active wrasses and basses, however.

For other families in which protogyny occurs, such as the groupers and the emperors, we simply lack sufficient knowledge of the mating behavior to state whether the predictions of the size-advantage model hold.

Our knowledge of the mating habits of protandrous fishes is also incomplete. Many of the species known to be protandrous live in large schools not closely associated with the substrate; however, the details of their mating behavior have not been reported. The size-advantage model suggests that mating might consist of haphazard pairing, but this prediction remains to be tested. The anemonefishes, the one group of protandrous species whose mating system is well known, fit the size-advantage model in a precise but unexpected way, as is discussed below.

While most studies of fishes known to change sex



lend support to the size-advantage model, approaches from the opposite direction are less satisfactory. For example, sex change is not found in every species in which mating is monopolized by large males. Perhaps this is asking too much of evolution, since an adaptive situation does not guarantee the appearance of a trait. It may simply be that the capacity for sexual flexibility has not yet evolved in some species, or that unknown factors reduce the advantage of sex change. Unfortunately, like many evolutionary arguments, this one is virtually untestable.

Comparisons within families

We can avoid some of the uncertainty inherent in broad comparisons among families by examining the sexual patterns and mating behaviors of a group of species within a family in which we know sex change is widespread. Using this approach, the absence of sex change where it is theoretically adaptive is less easily dismissed as evolutionary lag.

The wrasses (Labridae) and the parrotfishes (Scaridae) are large and well-known families of coral-reef fishes that include many species made up of both primary males—that is, fish that remain males for their entire lives—and protogynous individuals. Both primary males and females can become dominant, territorial males if they grow large enough. The proportion of smaller males is a measure of the degree of sex change present in the species: in cases where small males are absent, sex change is at a maximum, and when they form half the population, the species is essentially gonochoristic.

The diversity of sexual types within the wrasses and parrotfishes is reflected in a diversity of mating behavior (Fig. 3). Small males either interfere with the mating activities of larger males by darting in to join the spawning couple at the moment sperm is released, a practice called “sneaking,” or they take over a whole spawning site en masse and group-spawn with the females that appear there. In group spawning a single female releases her eggs in the midst of an aggregation of

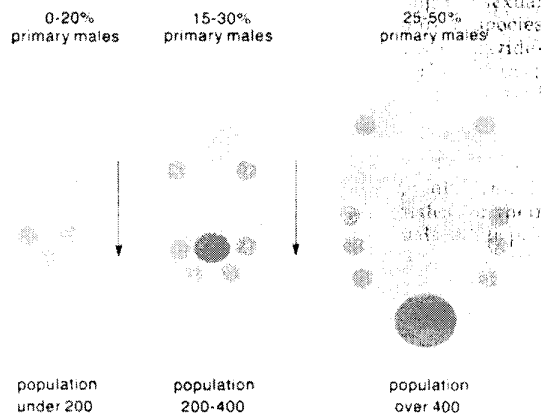


Figure 5. The mating system of the bluehead wrasse, which spends its adult life on a single reef, varies dramatically with the size of the reef. In this diagram of typical mating configurations, the predominant direction of the current is indicated by arrows; sites at the downcurrent end of the reef are preferred by spawning females. On small reefs (2 to 600 m²), mating occurs exclusively with large males in their territories (light blue areas), and primary males are relatively rare. On intermediate-sized reefs (600 to 1,000 m²), territorial males continue to occupy the prime spawning area, but a spawning group of smaller males is active just upcurrent (dark blue area). On the largest reefs (above 1,000 m²), a large spawning group of small males occupies the major downcurrent spawning site, and territorial males are relegated to less productive upcurrent sites. Primary males reach their highest concentrations on such reefs, constituting up to 50% of the population.

males, all of whom participate in fertilization. Spawning groups can contain from two to over a hundred males.

For the size-advantage model to hold, variation in the degree of sex change should correspond to differences in the mating systems. Specifically, sex change should be less common or absent in species where large males have less opportunity to monopolize mating. Hoffman's recent work (1980 diss., 1983) on three closely related wrasses of the genus *Bodianus* provides a clear demonstration of this relationship between sexual expression and mating system (Fig. 4). *Bodianus rufus* of the Caribbean is harem, whereas *B. diplotaenia* of the eastern tropical Pacific defends a spawning site visited by females; thus large males monopolize mating in both species. Correspondingly, small males are absent in both species, and all males are the result of sex change in functional females. On the other hand, the multicolored *B. eclancheri* of the Galapagos Islands is a group-spawner with no apparent pattern of dominance related to size or sex. Hoffman could find no evidence of sex change during adult life in this species. Individuals appear instead to be functional gonochores: change from female to male occurs before maturation, and males are equally common in all size classes of the population. The production of small males through pre-maturational sex change has also been noted in some species of parrotfishes (Robertson and Warner 1978).

What factors lead to changes in the monopolization of mating by large males? We have found that increased population density around spawning sites plays a role in lowering the ability of a male to defend his harem or territory adequately against smaller males (Warner and Hoffman 1980a). In extreme cases, some spawning sites can be undefendable and may be entirely abandoned to group-spawners (Warner and Hoffman 1980b).

A recent study of the wrasses of the Caribbean (genera *Thalassoma*, *Halichoeres*, *Bodianus*, and *Clepticus*) revealed that among species living in similar habitats, those with low population densities tended to have few or no small males (Warner and Robertson 1978). Regardless of whether the mating system was characterized by harems or spawning-site defense, larger males successfully monopolized mating in these species. In species living at greater densities, the proportion of primary males rose as high as 35%. Among these densely distributed species, group spawning as well as territorial mating was seen, with larger males subject to varying amounts of interference from small primary males.

The most thoroughly studied species in this group is the bluehead wrasse, *Thalassoma bifasciatum*. In this species, large males normally control the spawning sites on smaller reefs where the density of the mating population is low, and small males are nearly absent from these local populations (Fig. 5). On large reefs, where spawning sites are much more crowded, group-spawning aggregations occupy the major sites and small males are relatively common (Warner and Hoffman 1980b). Since individuals arrive on reefs as drifting planktonic larvae, the precise mechanisms leading to the distribution of small males are not known, but this example serves as a useful illustration of how density can affect the sex-changing strategy.

Not surprisingly, the effect on monopolization of mating is most pronounced at extreme densities. *T. lucasanum* of the eastern tropical Pacific is the most densely

Figure 6. The most adaptive direction for sex change can depend on the size of the social group. When the group consists of a single pair, both individuals profit if the larger member of the pair is a female, since she could produce more eggs than a smaller individual. Protandry is most adaptive in this case, and is found in the strictly monogamous anemonefishes of the genus *Amphiprion* (top). In larger social groups, the combined egg production of smaller members can easily exceed the egg production of the largest individual, and thus his output is maximized by functioning as a male. Protogyny would be expected here, and is found in the group-living damselfishes of the genus *Dascyllus* (bottom), which are closely related to anemonefishes. (Photo at top by H. Fricke; photo at bottom by F. Bam.)



distributed wrasse thus far studied; its population is essentially gonochoristic, with about 50% primary males (Warner 1982). Large territorial males are rather rare and only moderately successful in this species, and nearly all mating takes place in groups.

Certain characteristics of the habitat that allow access to spawning sites by small males apt to engage in "sneaking" should also affect mate monopolization. These characteristics are difficult to measure in a quantitative fashion, but some trends are evident. For example, small parrotfishes that live in beds of sea grass near coral reefs have a higher proportion of small males than species that exist in similar densities on the reefs themselves (Robertson and Warner 1978). In one grass-dwelling species, sex change appears to be entirely absent (Robertson et al. 1982). Sea grasses offer abundant hiding places for small fishes, and dominant males in these habitats suffer interference from smaller males in a high proportion of their matings.

Perhaps the most telling variation within a family occurs in the damselfishes (Pomacentridae), where sex change was only recently discovered (Fricke and Fricke, 1977). Small damselfishes called clownfishes or anemonefishes (genus *Amphiprion*) live in or near large stinging anemones in reef areas and thus have extremely limited home ranges. They appear to be unaffected by the stinging cells of the anemone, and may enjoy a certain amount of protection from the close association (Allen 1972). An anemonefish society consists of two mature individuals and a variable number of juveniles. The species are protandrous; the largest individual is a female, the smaller adult a male (Fricke and Fricke 1977; Moyer and Nakazono 1978b). The per capita production of fertilized eggs is higher when the larger individual of a mating pair is the female, and protandry is thus advantageous to both adults (Warner 1978).

Note that the advantage of protandry in this case

depends on the fact that the social group is rigidly limited to two adults. If more adults were present, the most adaptive sexual pattern could instead be protogyny. This is because the largest individual, as a male, might be able to fertilize more eggs than it could produce as a female. In accordance with this, protogyny appears in some related damselfishes (genus *Dascyllus*) in which the social groups of adults are larger (Fig. 6; Fricke and Holzberg 1974; Swarz 1980 and pers. com.; Coates 1982).

Social control of sex change

Another way of testing the size-advantage model is through an investigation of the dynamics of sex change within a species. So far, I have stressed the importance of the mating system in determining the advantage of a given sex and size. Within a mating system, it is often relative rather than absolute size that determines reproductive expectations. For example, when dominance depends on size, the probable mating success of a particular male is determined by the sizes of the other males

in the local population. It would be most adaptive for individuals to be able to change from female to male when their expectations of successful reproduction as a male increase considerably. Thus the removal of a large, dominant male from a population should result in a change of sex in the next largest individual, but no change should be expected in the rest of the local population.

Such social control of sex change has been noted in several species of protogynous coral-reef fishes. Because harem species exist in small, localized groups, they have proved to be exceptionally good candidates for studies of this kind. In the cleaner-wrasse *L. dimidiatus*, Robertson (1972) found that if the male is removed from the harem, the largest female rapidly changes sex and takes over the role of harem-master. Within a few hours she adopts male behaviors, including spawning with the females. Within ten days this new male is producing active sperm. By contrast, the other females in the harem remain unchanged.

Social control of sex change has also been found in other harem species (Moyer and Nakazono 1978a; Hoffman 1980; Coates 1982), as well as in species that live in bigger groups with several large males present (Fishelson 1970; Warner et al. 1975; Shapiro 1979; Warner 1982; Ross et al. 1983). In all cases, it is always the

largest remaining individuals that undergo sex change when the opportunity presents itself. Even when experimental groups consist entirely of small individuals, sex change can still be induced in the largest individuals present, in spite of the fact that they may be far smaller than the size at which sex change normally occurs (Hoffman 1980; Warner 1982; Ross et al. 1983).

The exact behavioral cues used to trigger sex change appear to differ among species. Ross and his co-workers have shown experimentally that the sex-change response in the Hawaiian wrasse *T. dipercus* depends solely on relative size and is independent of the sex and coloration of the other individuals in a group, whereas Shapiro and Lubbock (1980) have suggested that the local sex ratio is the critical factor in the bass *Anthus squamipinnis*. While it is still unclear how sex change is regulated in fishes that live in large groups, the mechanisms appear to operate with some precision. Shapiro (1980) found that the simultaneous removal of up to nine male *Anthus* from a group led to a change of sex in an equivalent number of females.

Social control of sex change occurs in protandrous fishes as well, and in a pattern consistent with the size-advantage model. A resident male anemonefish will change sex if the female is removed (Fricke and Fricke 1977; Moyer and Nakazono 1978b). One of the juveniles—who apparently are otherwise repressed from maturing—then becomes a functional male and the adult couple is reconstituted.

Simultaneous hermaphroditism

In one sense, the adaptive significance of simultaneous hermaphroditism is obvious: by putting most of their energy into egg production and producing just enough sperm to ensure fertilization, a hermaphroditic mating couple can achieve a much higher output of young than a male-female pair (Fig. 7; Leigh 1977; Fischer 1981). The problem, however, rests with the maintenance of simultaneous hermaphroditism in the face of an alternative male strategy. Consider an individual that fertilizes the eggs of a hermaphrodite, but does not reciprocate by producing eggs of its own. Instead, this individual uses the energy thus saved to find and fertilize other hermaphrodites. This strategy would spread rapidly in a purely hermaphroditic population, effectively forcing it to become gonochoristic. It would therefore appear that where simultaneous hermaphroditism is present, there should exist some means of preventing this kind of "cheating" (Leigh 1977; Fischer 1981).

Among the small coral-reef basses (serranidae) that are known to be simultaneous hermaphrodites, two types of possible antichecking behavior have been observed. The hamlets, small basses common on Caribbean coral reefs (genus *Hypoplectrus*), appear to ensure that investments in eggs are kept nearly even between the members of a spawning pair by what Fischer (1980) has called "egg trading." In this behavior, a pair alternates sex roles over the course of mating (Fig. 8). Each time an individual functions as a female, it extrudes some, but not all, of its eggs. As a male, it fertilizes the eggs of its partner, who also parcels out eggs in several batches. Thus both individuals are forced to demonstrate their commitment to egg production, and neither has the chance for an unreciprocated fertilization of a large batch of eggs.

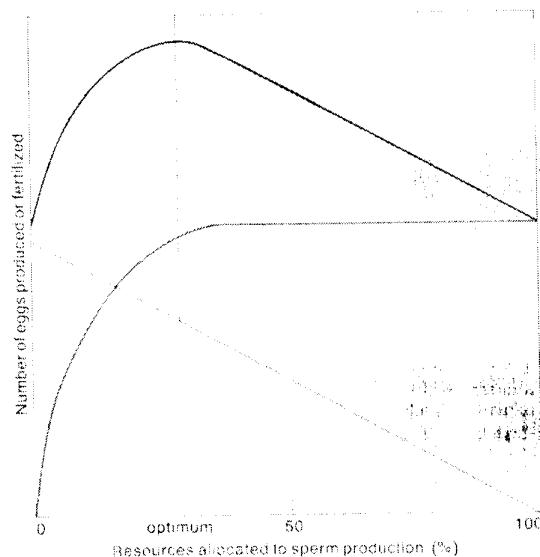


Figure 7. The number of eggs produced by an individual is normally directly related to the amount of energy devoted to their manufacture (gray line). In the case of sperm, however, a relatively low output can often produce maximum success (colored line)—that is, a small amount of sperm can fertilize all of a partner's eggs, and further investments are superfluous. Natural selection favors the individual with the highest overall reproductive rate combining male and female functions (black line), and in this case the optimum result is obtained by putting most of the energy into egg production. A simultaneous hermaphrodite following this strategy has a much higher reproductive success than an individual that is exclusively male or female. (After Fischer 1981.)

Figure 8. Simultaneous hermaphrodites among fishes include the hamlet (genus *Hypoplectrus*), a small bass that may alternate sexual roles as many as four times in the course of a single mating, by turns offering eggs to be fertilized and fertilizing its partner's eggs. Here the fish acting as the male curves its body around the relatively motionless female, cupping the upward-floating eggs as he fertilizes them. The strategy of parceling out eggs in a number of batches means that the egg contributions of the two partners are roughly equal, and reduces the rewards of "cheating" by fertilizing a large batch of eggs and then refusing to offer eggs for fertilization in return. (Photo by S. G. Hoffman.)



Another method of preventing desertion is to reduce the opportunities of your partner to find another mate. Some simultaneously hermaphroditic species of the genus *Serranus* delay their mating until late dusk, just before nightfall. These species do not engage in egg-trading, but presumably the onset of darkness means that time is quite limited before shelter must be taken for the night, and thus further mating is impossible (Pressley 1981).

Although these antichecking behaviors are fascinating in their own right, they give us little insight into the origin of the sexual pattern itself. Simultaneous hermaphroditism has been viewed as an adaptation to extremely low population density: if finding mates is difficult, it helps a great deal to be able to mate with whomever you meet (Tomlinson 1966; Ghiselin 1969). Thus many deep-sea fishes, sparsely distributed in their habitat, are simultaneous hermaphrodites (Mead et al. 1964). Perhaps the small serranids evolved from ancestors who lived at low densities, and developed their antichecking behaviors at a later stage when densities were higher. Alternatively, and perhaps more likely, the existence of late-dusk spawning behavior could have allowed the development of hermaphroditism. Unfortunately, we again run up against the problem of untestability and limited predictive power: several other coral-reef fishes mate late in the day, but they are not simultaneous hermaphrodites.

Broader patterns

The contrast between sex change and simultaneous hermaphroditism is intriguing: sex change, particularly protogyny, appears to be a specific adaptation to certain mating systems that happen to be common on coral reefs. These mating systems may be prevalent in coral habitats because clear water, relatively low mobility, and the absence of paternal care allow a greater degree of dominance by large males. Simultaneous hermaphroditism, on the other hand, is theoretically adaptive in a wider variety of circumstances, but is evolutionarily unstable unless male-type cheating can be prevented. While the wide dispersion of deep-sea fishes automati-

cally works against cheating, I can see no reason why coral reefs are particularly good places for such prevention to come about.

Among hermaphroditic groups other than tropical marine fishes, our knowledge of behavior and ecology is generally insufficient to carry out a similar analysis of the relationship of sexual pattern to mating system. Broad surveys of vertebrates (Warner 1978) or organisms in general (Policansky 1982) have shown large-scale tendencies toward hermaphroditism in some groups, sporadic appearance of the phenomenon in others, and a total lack of sexual flexibility in still others. While major features such as the greater complexity of terrestrial reproduction may help to explain the lack of hermaphroditism in some large groups (Warner 1978), many others must await more thorough investigation of the life histories and behavior of the organisms in question.

On this point, Policansky (1982) has suggested that a major problem of sex-change theory is that among closely related species with similar life histories, some change sex and some do not. In light of this review, I am not yet ready to take such a dim view of the size-advantage model. Sexual expression in fishes is extraordinarily adaptable, and closely related species can have quite different sexual patterns that appear to be predictable from their different mating systems. For the fishes, at least, divergent sexual expressions may be no more surprising than differences in coloration. Detailed considerations of the mating systems and life histories of other sexually labile groups are needed to test the hypothesis further.

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