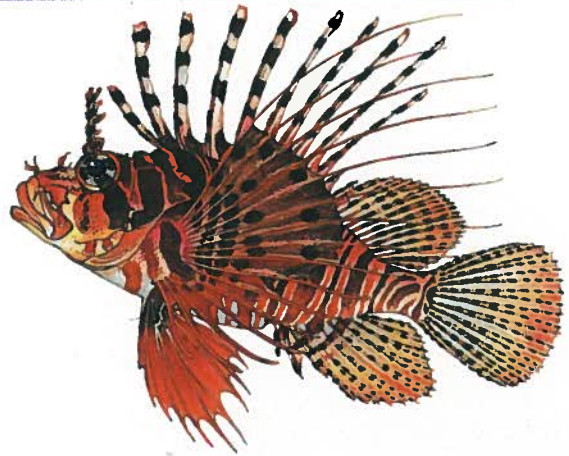# The Diversity of Fishes
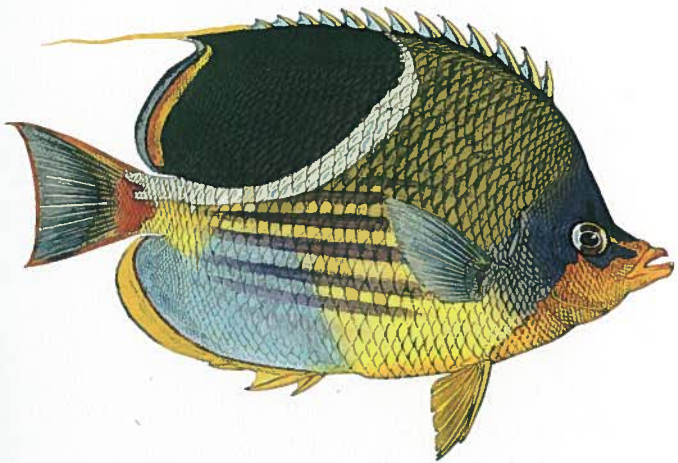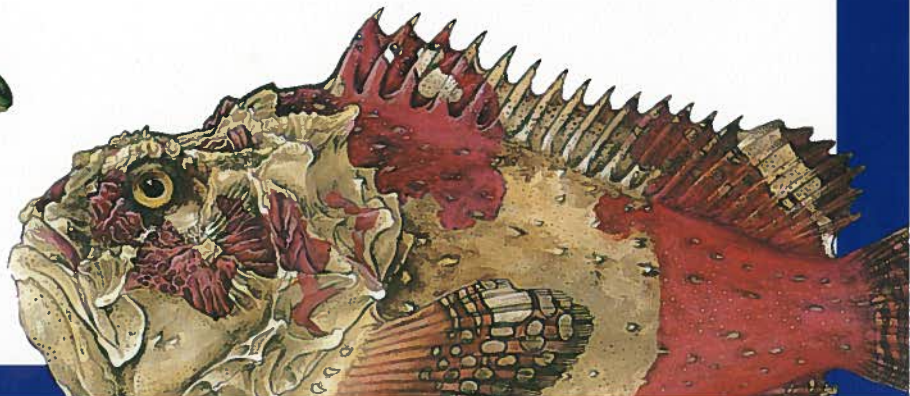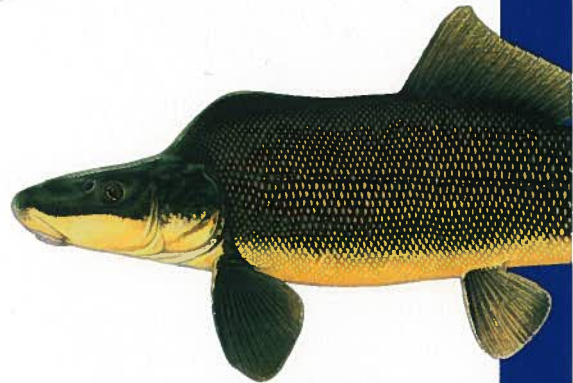
GENE S. HELFMAN

BRUCE B. COLLETTE

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## Mating Systems

Mating systems are defined by the number of mating partners an individual has during a breeding season (see Table 20.1). The three most common categories are promiscuous, polygamous, and monogamous. **Promiscuous** breeders are those in which little or no obvious mate choice occurs and in which both males and females spawn with multiple partners, either at one time or over a short period. Such spawning has been documented for the Baltic herring (Clupeidae), guppies (Poeciliidae), Nassau groupers (Serranidae), humbug damselfish colonies (Pomacentridae), cichlids, and the Creole wrasse (Labridae) (Thresher 1984; Barlow 1991; Turner 1994).

Polygamy, in which only one sex has multiple partners, takes multiple forms. **Polyandry**, in which one female mates with several males (and presumably not vice versa) is relatively uncommon, so far documented only in an anemonefish (Pomacentridae) (Moyer and Sawyers 1973). Polyandry might also be descriptive of female ceratioid anglerfishes that have more than one male attached (see Chap. 17, The Deep Sea). **Polygyny** is the most common form, involving males as the polygamous sex. Territorial males that care for eggs and young are frequently visited by several females, as in sculpins, sunfishes, darters, damselfishes, and two cichlids. Polygyny can also develop into harem formation, in which a male has exclusive breeding rights to a number of females that he may guard. Harems have been observed in numerous cichlids and in several coral reef families (e.g., tilefishes, damselfishes, wrasses, parrotfishes, surgeonfishes, triggerfishes).

Many polygynous animals form leks, which are traditional areas where several males congregate for the sole purpose of displaying to females (Emlen and Oring 1977). Females are often attracted to a male in response to his central position within the lekking ground or to the vigor of his display and bright plumage. Lekking is common in birds and mammals, in which only the female provides parental care. Some African cichlids come closest to forming true leks. Large numbers (ca. 50,000) of male *Cyrtocara eucinostomus* congregate along a shallow 4-km-long shelf in Lake Malawi and build sand nests and display to passing females each morning. Females spawn and then mouth brood eggs elsewhere. The male aggregations break up each afternoon, when fish feed (McKaye 1983, 1991). Some fishes form leklike aggregations of males (e.g., damselfishes, wrasses, parrotfishes, surgeonfishes), but the display ground is also an appropriate place for launching or caring for eggs, which stretches the definition of lekking (Loiselle and Barlow 1978; Moyer and Yogo 1982). In a unique variation on leklike behavior, female triggerfish (*Odonus niger*, Balistidae) form a communal display ground for 1 day before spawning, after which they all mate with a single, nearby male (Fricke 1980).

In **monogamous** systems, fish live in pairs that stay together and mate, or mate with the same individual repeatedly and exclusively, regardless of pairing at nonmating times. Strongly pairing species include North American freshwater catfishes, many butterflyfishes, most substrate-guarding and some mouth-brooding cichlids, and anemonefishes; in the butterflyfishes, pairs may remain together for several years and probably mate for life (Reese 1975). Monogamous coral reef fishes commonly spawn with the same partner on a daily basis over an extended period without ensuing care of young, whereas freshwater species such as cichlids spawn over a limited time and then both parents typically care for the young. Monogamy is also known in freshwater bonytongues, bagrid and airsac catfishes, and snakeheads, and among marine pipefishes, sea horses, jawfishes, damselfishes, blennies, gobies, surgeonfishes, triggerfishes, filefishes, pufferfishes, and hermaphroditic hamlets (Barlow 1984, 1986; Thresher 1984; Turner 1986).

## Gender Roles in Fishes

Although the vast majority of fishes are gonochoristic, with sex determined at an early age and remaining fixed as male or female, a significant number of fishes can function as males and/or females simultaneously or sequentially (see also Chap. 10, Determination, Differentiation, and Maturation). The environmental correlates and evolutionary causes of sex change in fishes have been the subject of considerable study and speculation (Box 20.1).

Sex reversal has evolved, apparently independently, in at least 23 families belonging to seven teleostean orders, including moray eels (Anguilliformes), loaches (Cypriniformes), lightfishes (Stomiiformes), killifishes (Atheriniformes), swamp eels (Synbranchiformes), flatheads (Scorpaeniformes), and 14 perciform families (snooks, sea basses, soapfishes, emperors, rovers, porgies, threadfins, angelfishes, bandfishes, cichlids, damselfishes, wrasses, parrotfishes, and gobies). Sex changers can be either 1) **simultaneous hermaphrodites**, capable of releasing viable eggs or sperm during the same spawning, or 2) **sequential hermaphrodites**, functioning as males during one life phase, and as females during another. Among sequential hermaphrodites, **protandrous** fishes develop first as males and then later change to females, whereas **protogynous** fishes mature first as females and then later become males. Variations on these patterns exist, such as protogynous populations with some males that develop directly from juveniles, or simultaneous hermaphrodites that lose the ability to function as one sex (Smith 1975; Warner 1978; Sadovy and Shapiro 1987).

Protogyny is by far the most common form of hermaphroditism. In a classic study, Robertson (1972) found that the Indo-Pacific cleaner wrasse, *Labroides dimidiatus*, formed harems of one large male and up to 10 females. Breeding access to the male was determined by a behavioral dominance hierarchy, or peck order, with the largest female dominating the next smallest and so on. If the top (alpha) female was removed, the next largest female assumed her role, and everyone else moved up a step. If the male was removed, the alpha female began courting females within an hour and developed functional testes within 2 weeks (see also Kuwamura 1984).

Protogyny in wrasses can take other forms. In the Caribbean bluehead wrasse, *Thalassoma bifasciatum*, fish usually begin life as predominantly yellow females or

## BOX 20.1 "When the Going Gets Tough, the Tough Change Sex"[1]: The Evolution of Sex Change in Fishes

The topic of sex or gender change and its relationship to hermaphroditism has sparked a great deal of debate among biologists. Two questions dominate the discussion of sex-changing fishes (and of sex allocation in organisms in general). The questions are "Why change sex?" and "When to change?" Answers lie primarily in the ecologies of individual species, greatly influenced by the relative reproductive success of males versus females at different sizes. Animals change gender when, at a given size, the reproductive success of one gender becomes higher than if the individual remained the other gender (Ghiselin 1969; Warner 1975). The value of changing gender is reduced by the costs of changing, such as lost reproductive opportunities while undergoing the change and metabolic costs of altering gonads.

This size **advantage model** assumes indeterminate growth and increased fecundity with increasing size. Reproductive success in females is generally limited by gamete production, whereas males are limited by the number of mates they can acquire (Bateman's principle). Males, including small males, generally produce a surplus of sperm, most of which never encounter an egg. In contrast, egg production increases with growth in females, and each egg is likely to be fertilized. These circumstances would dictate that sex changers be protandrous: Small females produce very few eggs, but small males can fertilize many eggs. Such conditions would select for fish that began life as small but functional males and changed to female when they were large enough to produce more eggs than a small male could fertilize. For example, in pair-spawning, monogamous anemonefish, lifetime egg production of the pair is maximized by having the larger fish a female.

However, male fish often compete for females (see below), and the outcome of such competition is frequently determined by body size, with larger males winning. Hence one large, behaviorally dominant male can monopolize many females and fertilize their eggs, as in the bluehead wrasse and *Anthias* examples mentioned earlier. Under these circumstances, the greatest advantage accrues to the largest males, and the tactic to follow is to be a female first (since small males have such limited competitive and therefore reproductive success) and then change to male because of the advantage conferred upon large males. The age or size at which an individual should change sex is probably determined by an interaction between body size and social structure (numbers of males and females, dominance hierarchies) of the population (Shapiro 1987). Social control also explains protogynous sex change in the Midas cichlid, *Cichlasoma citrinellum*, one of the few freshwater changers. Large fish tend to be male, smaller fish are female. Growth rate depends on behavioral interactions of juveniles, with dominant fish growing faster. The size advantage model again explains the course of change, since female Midas cichlids mate preferentially with larger males. This preference is adaptive, because the male has primary responsibility for defending the breeding site and larger males are better defenders (Francis and Barlow 1993).

Left unanswered is why more species of fishes and other vertebrates do not change sex. Ideas on this subject focus on the relative costs of changing sex in different taxa, the existence of dimorphic sex chromosomes (which are generally lacking in fishes), and differences in sex determination mechanisms (Warner 1978). Add to these the realization that evolution is predominantly a conservative process. Biological systems are complex, which is certainly a description of the reproductive systems of fishes, given the behavioral, ecological, physiological, and anatomic components involved. Alterations to complex systems are likely to destroy the homeostasis that has evolved among the components. Hence the advantages of sex change would have to be very large to overcome fitness losses due to disruption of the co-evolved gene complexes that code for the systems. Sex change then becomes an alternative to gonochorism, but one that does not offer a sufficiently large advantage to overcome the costs of refitting the reproductive systems of most fishes. Gonochorism obviously works well for most species; since it is not broken, there is little selective advantage in fixing it.

[1] Warner 1982, 43.

similarly colored males (initial-phase coloration). Any of the initial-phase fish can change into larger, terminal-phase males, which develop a blue head, a black-and-white midbody saddle, and a green posterior region. Large males set up territories over coral heads that females pre- fer as spawning sites. Some females are intercepted by and spawn with groups of up to 15 smaller males, but the largest, pair-spawning males have the highest spawning success. A territory-holding male may receive 40 to 100 spawnings per day, whereas a nearby group-spawning

male may receive only 1 or 2 matings, and his sperm will often be diluted by the gamete output of other males in the group (Warner et al. 1975; Warner 1991).

Other well-studied protogynous species include the anthiine serranid, *Anthias squamipinnis*, a pair-spawning species that forms large aggregations in which females may outnumber males by 36:1. The precision of social control of sex change in this species is remarkable: If nine males are removed from a large group, nine females change sex to replace them. Sex change to male in *Anthias* also occurs if the female-male ratio exceeds a threshold value (Shapiro 1979, 1987). The commonness of protogyny probably reflects the fact that most teleosts, including gonochoristic species, differentiate first as nonfunctional females.

Protandry has been reported in moray eels, loaches, lightfishes, platycephalids, snooks, porgies, threadfins, and damselfishes. The popular clown- or anemonefishes (*Amphiprion* spp., Pomacentridae) live in groups of two large and several small individuals in an anemone. Only the two largest fish in an anemone are sexually mature, the largest individual being female and the next largest being male. Although smaller fish may be as old as the spawning individuals, the behavioral dominance of the mature pair keeps these smaller males from maturing and growing, and a dominance hierarchy exists among the smaller males. In essence, "low ranking males are psychophysiologically castrated" (Fricke and Fricke 1977, 830). If the female dies, the male changes sex to female, and the next largest fish in the group takes over his former role and grows rapidly (Allen 1975; Moyer and Nakazano 1978).

Simultaneous hermaphroditism (cosexuality) is known from only 3 shallow-water families and 11 of the 12 families in the deep-sea order Aulopiformes (lizardfishes, Synodontidae, are the exception) (Smith 1975; Warner 1978). Three species of New World cyprinodontiform rivulines (Aplocheilidae) are capable of self-fertilization (*Cynolebias* spp. of South America and the mangrove rivuline, *Rivulus marmoratus*, of North and Central America). Self-fertilization in *Rivulus* is internal, producing clonal populations of homozygous, genetically identical hermaphroditic fish. Functional males can be produced, depending on temperature and day length (Harrington 1971, 1975). Cyprinodontiform fishes are often colonists of small streams on islands and other seasonally adverse habitats (see Chap. 17). Self-fertilization may be one means of assuring mates in low-density populations that frequently become isolated, a scenario that could also be applied to the deep-sea aulopiforms.

The other species of simultaneous hermaphrodites occur among the small hamlets (*Hypoplectrus*, *Serranus*). Each individual is physiologically capable of producing sperm and eggs at the same time, but behaviorally these fishes function as only one sex at a time during a spawning bout. In Caribbean hamlets (*Hypoplectrus*), spawning bouts can last for several hours, during which time members of a pair alternate sex roles, one fish first behaving as the female and releasing eggs and then behaving as the male and releasing sperm (Pressley 1981; Fischer and Petersen 1987). The eastern Pacific *Serranus fasciatus* is haremic, sex-changing, and simultaneous: One male guards and spawns with several hermaphrodites that act as females. If the male is

removed, the largest hermaphrodite changes into a male (Fischer and Petersen 1987). Serranines have separate external openings for the release of eggs and sperm (in addition to an anus), which may prevent internal or accidental self-fertilization. Self-fertilization may occur in some serranines, but only in aquaria (Thresher 1984).

One additional group of fishes departs from normal gonochoristic gender roles. Livebearers in Mexico and Texas include parthenogenetic "species" that are all-female but require sperm from males of other species to activate cell division in their eggs. Parthenogenesis in livebearers takes two forms: gynogenesis and hybridogenesis (Fig. 20.1). **Gynogenetic** females are usually triploid and produce eggs that are also 3n. These eggs are activated by sperm from other species, but no sperm material is incorporated; hence daughters are genetically identical to their mothers. **Hybridogenetic** females, in contrast, are diploid and produce haploid eggs that, during the reduction division of meiosis, keep maternal genes and discard paternal genes. Upon mating, these eggs unite with sperm from males of another species, forming a new, diploid hybrid daughter (no sons are produced). When the daughter mates, she again produces eggs that are haploid and "female." Hence the maternal lineage is conserved, and the male's genetic contribution is lost after one generation. These parthenogenetic "species" are thought to have arisen originally as hybrids between *Poeciliopsis monacha* females and males of four congeners, *P. lucida*, *P. occidentalis*, *P. latidens*, and *P. viriosa*. The males of the four species are the usual sperm donors during mating. An additional species, the Amazon molly, *Poecilia formosa*, is diploid and gynogenetic. Sperm from two other species (*P. mexicana* and *P. latipinna*) activate the eggs but contribute no genetic material (Schultz 1971, 1977; Vrijenhoek 1984). Natural gynogenesis has also been reported for the cyprinid *Cyprinus auratus gibelio* (Price 1984).

An immediate question that arises is how natural selection maintains males that waste gametes so wantonly. Apparently, dominance hierarchies among donor-male populations of livebearers exclude many males from mating with conspecific females. These are often the males that participate in the parasitized, heterospecific spawnings. Satellite or peripheral males that have very low reproductive output are characteristic of many vertebrate species (these are often the sneakers and streakers discussed below), providing an abundance of otherwise unused sperm (Moore 1984). Additionally, laboratory tests of mate preferences in sexual females show that sexual females are more attracted to males that the females observed courting gynogenetic females. Apparently, a male can increase his chances of mating with a sexual female if he spends time courting asexual females, because sexual females copy the choices made by female gynogens. It is not known whether sexual females prefer males that mate with sexual females over those that mate with gynogenetic females (Schlupp et al. 1994).

Certain generalities arise from surveys of sex change in shallow-water fishes, as do exceptions. Sex change is largely a tropical and subtropical, marine phenomenon (Policansky 1982c; Warner 1982). Cool temperate and freshwater sex changers are known (e.g., loaches, swamp

**FIGURE 20.1.** *Parthenogenesis in Mexican livebearers. (A) In gynogenesis, a triploid female (designated MLL, shorthand for* Poeciliopsis monacha-lucida-lucida) *produces 3n eggs that are activated but not fertilized by sperm from a male P. lucida (L'). A daughter identical to the mother is produced. (B) In hybridogenesis, a diploid mother (ML, for P. monacha-lucida) produces haploid eggs (M) that contain only the maternal genome. Sperm from P. lucida (L') combine to form a diploid daughter (ML'), but this male component will be discarded again during the next round of gamete production, and all future eggs will continue to have solely* monacha *genes.*
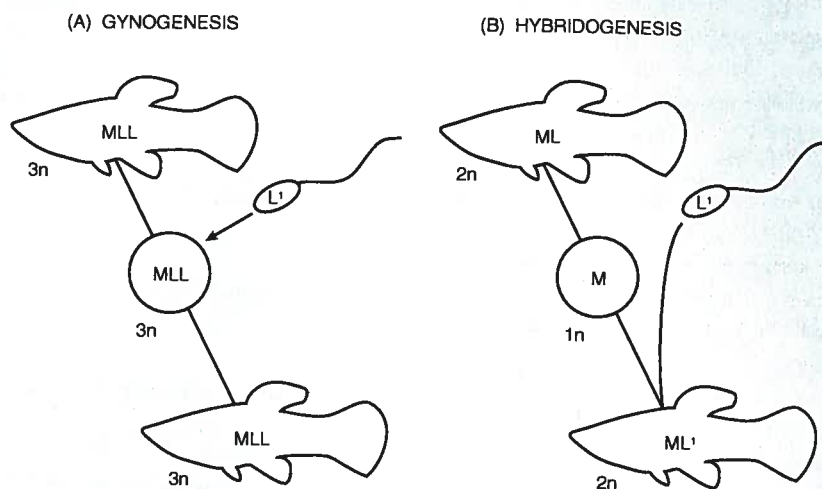


After Vrijenhoek 1984 and Allendorf and Ferguson 1990.

eels, wrasses, gobies, cichlids) but are relatively uncommon compared with tropical marine hermaphrodites. Patterns often follow familial lines, all members of a family being either protandrous or protogynous. Exceptions include the protogynous or simultaneously hermaphroditic sea basses (a family that is probably polyphyletic) and the protandrous or protogynous porgies. However, population differences are becoming increasingly well known in sex-changing fishes. The cleaner wrasse, *Labroides dimidiatus*, is haremic under some conditions but forms pairs under others. Bluehead wrasse, *Thalassoma bifasciatum*, are dominated by territorial-spawning males on small reefs with small populations, but by group-spawning males on large reefs with dense populations. Resource limitation—either food availability or reef size—and population size are frequent determinants of variation in mating systems. Clearly, sex change and mating systems respond to environmental variability (see Thresher 1984; Shapiro 1991; Warner 1991).

## COURTSHIP AND SPAWNING

### Sexual Selection, Dimorphism, and Mate Choice

Some traits of an animal function primarily to attract mates or to aid in battles between members of one sex for access to the other sex. Such **sexually selected** traits confer a mating advantage on an individual; they are a subset of natural selection, which usually involves traits that confer a survival advantage. Sexually selected traits may serve no other purpose than mating and may even

handicap the possessor with respect to other, fitness-influencing activities. However, sexually selected traits can also confer a positive survival advantage, such as large size in males, which provides a physical defense from predators and is also favored by females during mating (Box 20.2). Sexually selected traits are often referred to as **secondary** sexual characteristics. **Primary** characteristics include ovipositors, genitalia, and other copulatory structures such as claspers in elasmobranchs, gonopodia or priapia in livebearers and phallostethids, or brood patches or pouches and other structures used in parental care. In some instances, a character may be both secondary and primary, serving both in mate attraction and in copulation or parental care. In sticklebacks, males are attracted to females with swollen bellies, but the swelling results from the female's ripe ovaries (Wootton 1976).

Secondary sexual characteristics have four general attributes: 1) They are restricted to or are expressed differentially in one sex (usually the male), 2) they do not appear until maturation, 3) they often develop during a breeding season and then regress, and 4) they generally do not enhance survival. Secondary characteristics take the form of **sexual dimorphisms** (differences in body parts between sexes), such as differences in body size, head shape, fin shape, dentition, and body ornamentation, or as dichromatisms (differences in coloration). We know comparatively little about electrical, chemical, and acoustic differences between the sexes, although differences in anatomy and physiology associated with these sensory modes are common (e.g., in elephantfishes, salmons, minnows, gymnotid knifefishes, toadfishes, croakers, damselfishes, and gobies). For example, males of the plainfin