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Journal

Sexual Development, 3(2-3)

ISSN

1661-5425

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Publication Date

2009

DOI

10.1159/000223079

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Evolutionary Perspectives on Hermaphroditism in Fishes

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Key Words

Mating systems · Outcrossing · Phylogenetics ·
Self-fertilization · Sexual systems

Abstract

Hermaphroditism is a derived and polyphyletic condition in fishes, documented in about 2% of all extant teleost species scattered across more than 20 taxonomic families in 9 orders. It shows a variety of expressions that can be categorized into sequential and synchronous modes. Among the sequential hermaphrodites are protogynous species in which an individual begins reproductive life as a female and later may switch to male, protandrous species in which a fish starts as a male and later may switch to female, and serial bidirectional sex changers. Among the synchronous hermaphrodites (in which an individual can simultaneously produce eggs and sperm) are several outcrossing and one predominantly selfing species. A few species also consist of mixtures of hermaphroditic and single-sex individuals. All of these reproductive categories have been the subject of numerous theoretical and empirical treatments from an evolutionary perspective. Here we highlight some of the major conclusions from these studies, which collectively have been informative on a variety of biological topics related to reproductive modes, gender allocations, sexual conflict and gamesmanship, mating systems, and life-history tradeoffs.

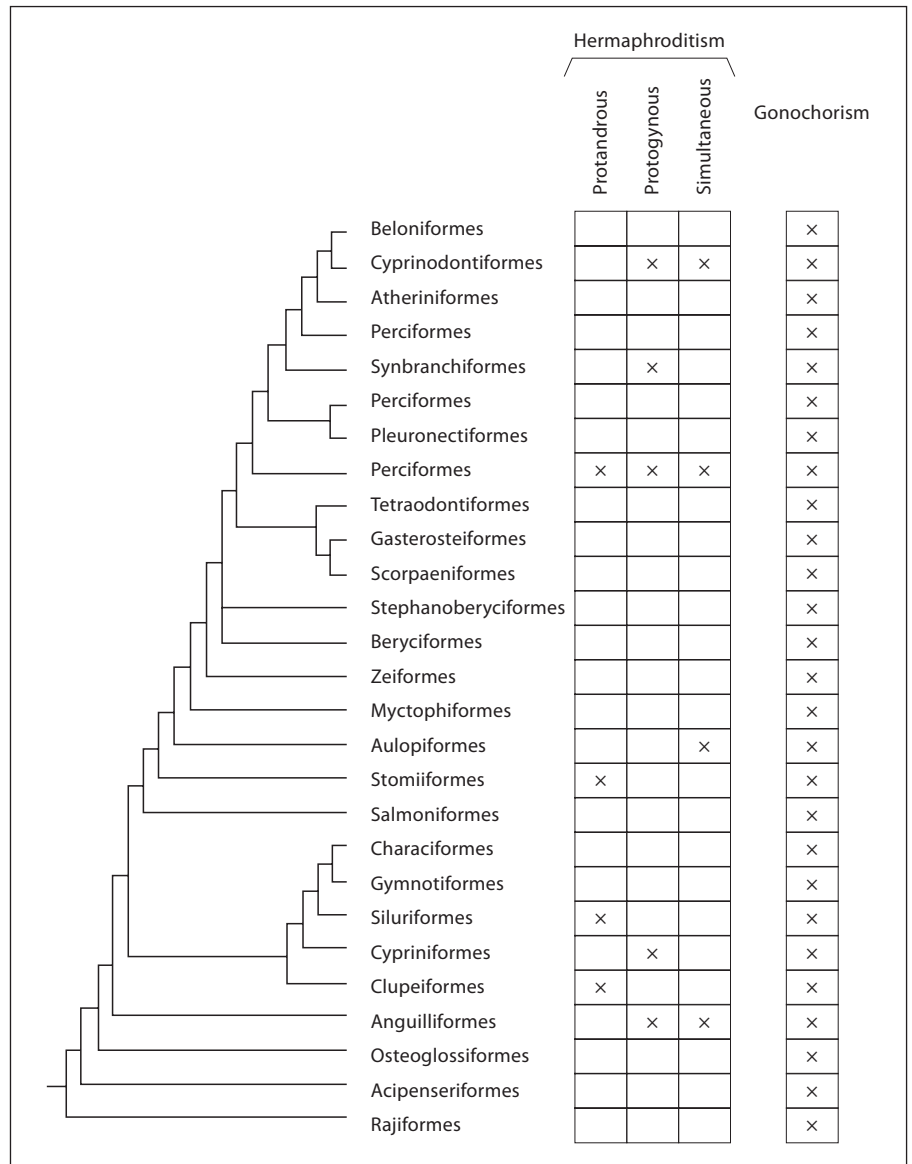
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The ancient Greeks were intrigued in their mythologies by the concept of hermaphroditism, i.e. the expression of both male and female sex within the lifetime of an individual (Box 1). Hermaphroditism also intrigues modern biologists, for several reasons: many real-world plants and animals exhibit the phenomenon [Policansky, 1982]; it is so obviously different from the typical human condition of distinct lifelong sexes; and the adaptation raises many interesting evolutionary questions and scenarios. In fishes, either simultaneous or sequential hermaphroditism has been documented in approximately 500 (2%) of 25,000 extant species [Pauly, 2004] representing more than 20 taxonomic families in 9 orders [Breder and Rosen, 1966; Smith, 1975; Mank et al., 2006]. Sexual differentiation in fishes thus is evolutionarily quite labile as well as developmentally plastic.

Box 1. Hermaphroditism in Greek Mythology

The word hermaphrodite derives from the Greek myth of Hermaphroditos, a handsome son of Hermes and Aphrodite, the Greek gods of male and female sexuality. At age 15, Hermaphroditos was accosted one day by a lovely nymph – Salmacis – who embraced him, kissed him, and prayed to the gods that they be united forever. Her wish was granted and Hermaphroditos thereafter became simultaneously part male and part

Fig. 1. Distributions of various types of hermaphroditism (male-first or protandrous, female-first or protogynous, and simultaneous) and gonochorism (separate sexes), along extant nodes of a provisional supertree for bony fishes [after Mank et al., 2006]. The supertree is a cladogram (branch lengths are not proportional to divergence time) that represents an amalgamation of several published phylogenies from whole-genome or partial-genome mtDNA sequences. Note that 'Perciformes' is polyphyletic.



female. Tiresias – the blind prophet-priest of Zeus – was another type of hermaphrodite who in this case switched sequentially between male and female. It all began when Tiresias chanced upon a pair of copulating snakes and beat them with a stick. Hera (the wife of Zeus) was infuriated, and punished Tiresias by transforming him into a woman. Seven years later, Tiresias again encountered two mating snakes, but this time left the serpents alone. As a reward, Hera permitted Tiresias to regain a male condition.

Earlier researchers sometimes invoked population-level advantages to rationalize the evolution of hermaph-

roditism. For example, Moe [1969] suggested that sequential hermaphroditism might have evolved as a population control mechanism, with the age of transformation between female and male shifting up or down to compensate for whether a population was too sparse or too dense. Other hypotheses with a group-selection aura posited that hermaphroditism might increase total zygotic production in a population [Smith, 1967] or focus sexual performances into age classes that would maximize a population's reproductive output [Nikolski, 1963].

By contrast, more modern views have emphasized how natural selection and sexual selection might operate, in various social and ecological contexts, on the *differen-*

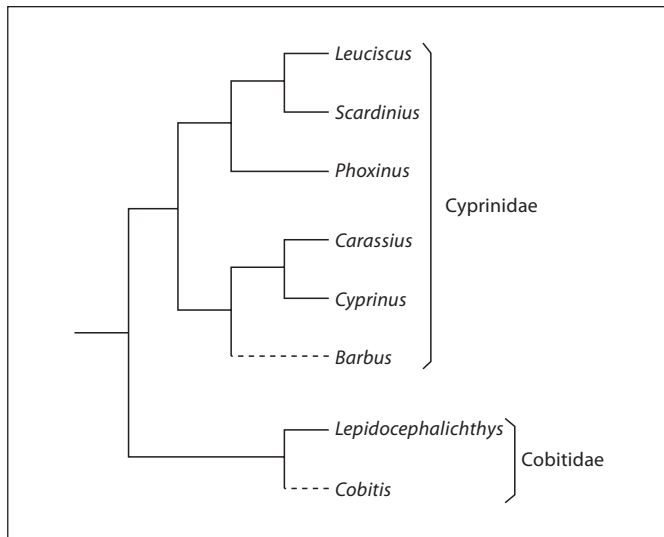


Fig. 2. Phylogenetic position of protogynous hermaphroditism (open branches) within cypriniform fishes [after Mank et al., 2006]. Filled branches reflect gonochorism.

tial fitnesses of individuals who have the capacity to reproduce as males *and* females at various stages of life [Warner, 1975; Shapiro, 1987; Leonard, 2006]. Additionally, there are several different types of hermaphroditism, which can be broadly categorized by whether each individual in a species produces male and female gametes simultaneously (like Hermaphroditos; see Box 1) or whether it switches sex during life but has only one functional sex at any time (like Tiresias; see Box 1). Alternative types of hermaphroditism have different evolutionary paths, and modern evolutionary theory has identified some of the causes and implications.

This review will encapsulate major conclusions – from previous empirical studies and theoretical treatments about the evolution of hermaphroditism in fishes. Endocrinological, physiological, and other ontogenetic mechanics of sex change are also of scientific interest, but these are addressed elsewhere [see Nakamura et al., 2005] and will not be the focus here.

Evolutionary History

Phylogenetic Backdrop. The 9 taxonomic orders of teleosts in which hermaphroditism has been documented are scattered widely across the phylogeny of teleost fishes (fig. 1). No order consists solely of hermaphroditic species, but instead contains gonochoristic (separate-sex, or dioecious) species as well. Indeed, closer phylogenetic inspection of several orders and families that are polymor-

phic for reproductive mode indicates that each hermaphroditic clade typically is embedded within a deeper clade otherwise composed of gonochoristic taxa (example in fig. 2). Extant hermaphroditism in teleost fish is therefore a polyphyletic and derived condition relative to gonochorism. Furthermore, no extant hermaphroditic lineage appears to be evolutionarily ancient (although this should be interpreted in light of the fact that no single sex determining mechanism in fish appears to be ancient [Mank et al., 2006], and thus need not imply that hermaphroditism is any less evolutionarily stable than alternative strategies). The evolutionary flexibility of reproductive modes in fishes also extends to different forms of hermaphroditism (figs. 1, 3), including female-first protogyny and male-first protandry (see beyond).

Transitional States. Far less certain, however, are answers to the following questions. How exactly does hermaphroditism evolve from gonochorism? And, does gonochorism ever re-emerge from phylogenetically localized instances of ancestral hermaphroditism? Some insight can be gleaned from the plant literature, where theoretical and empirical methods have been used to elucidate the evolutionary history of hermaphroditism. In principle, gonochorism and synchronous hermaphroditism are evolutionary endpoints on a reproductive spectrum that includes intermediate mixed-sex modalities (fig. 4): gynodioecy (a population mixture of females and hermaphrodites), androdioecy (a mixture of males and hermaphrodites), and trioecy (males, females, and hermaphrodites). Trioecy is extremely rare in the biological world and androdioecy is only slightly less so [Weeks et al., 2006], but gynodioecy is rather common (especially in plants, where >500 species in 50 families display the phenomenon) [Jacobs and Wade, 2003]. Theoretical models addressing these biological patterns (again, primarily in plants) have a long history [Lloyd, 1975; Charlesworth and Charlesworth, 1978; Charnov, 1982; Charlesworth, 1984; Barrett, 1998; Jarne and Charlesworth, 1993; Pannell, 2000; Wolf and Takebayashi, 2004], and they generally suggest the following.

During an evolutionary transition between separate-sex and purely hermaphroditic reproduction, typically one sex at a time is either lost (in a transition from gonochorism to hermaphroditism) or gained (in a transition from hermaphroditism to gonochorism). This factor alone (a step-by-step transition) probably helps to account for the rarity of trioecy. Furthermore, in an evolutionary transition from gonochorism to hermaphroditism (or vice versa), gynodioecy has been deemed theoretically more likely than androdioecy because, ulti-

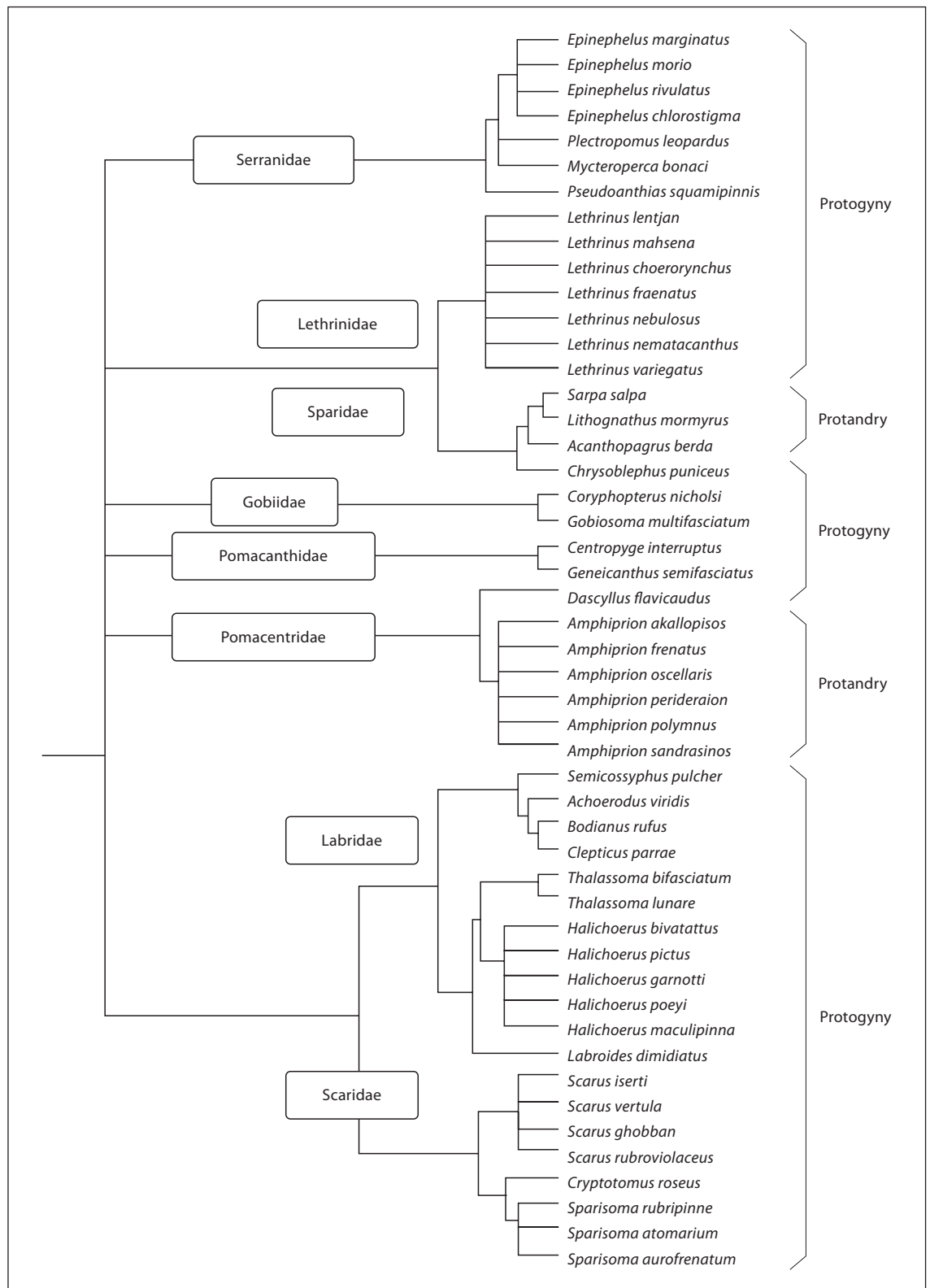


Fig. 3. Phylogenetic interspersion of protogyny and protandry in Perciformes [after Allsop and West, 2003]. The diagram shows only hermaphroditic species; many other species in this traditional taxonomic order (which itself is polyphyletic, with family relationships often poorly known) are gonochoristic.

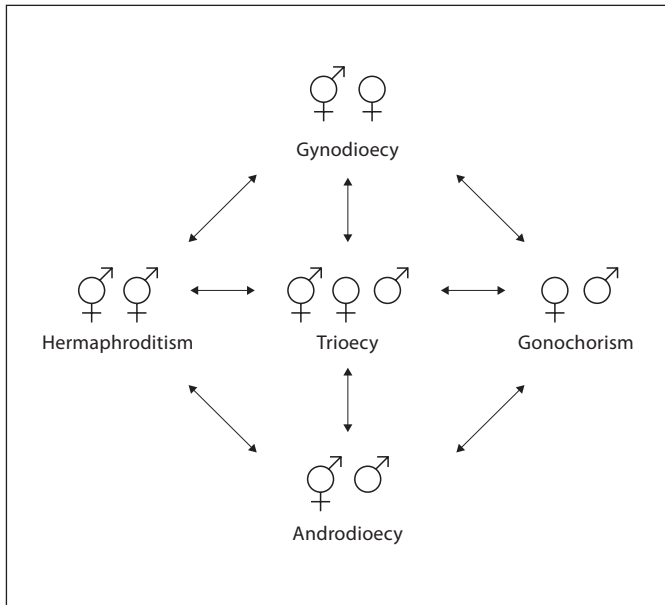


Fig. 4. Reproductive systems that in principle could be evolutionarily transitional between gonochorism and hermaphroditism in plants [modified from Weeks et al., 2006].

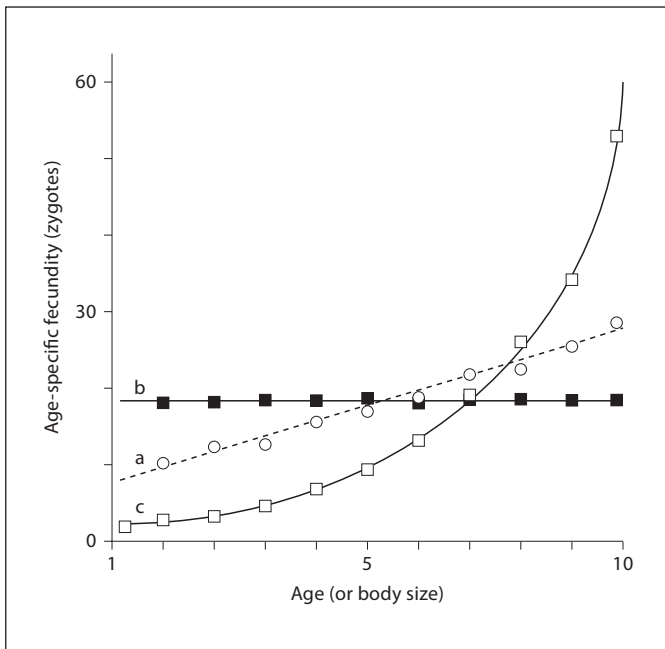


Fig. 5. Age-specific reproductive outputs for a hypothetical population of fishes [after Warner, 1975]. Curve *a* is for females; curve *b* is for males in a population where mating is random; and curve *c* is for males in a population where females mate only with same-age or older males (as might tend to be true in male-territorial or harem species, for example; but see also Taborsky [2008]).

mately, male gametes are far more abundant than female gametes. Thus, especially if hermaphrodites can self-fertilize, with regard to reproductive success a pure female in a gynodioecious population should be more competitive than a male in an androdioecious population, assuming that male gametes from hermaphrodites can be used to fertilize a female's eggs. Once females have arisen in an otherwise hermaphroditic species, they may also gain a reproductive benefit by virtue of engaging in outcrosses only, whereas some lineages of self-fertilizing hermaphrodites might suffer from inbreeding depression.

Most of the theoretical models underlying these conclusions have incorporated biological assumptions that apply to plants (and perhaps some invertebrate animals) but may have less relevance to fish. For example, the assumption that male gametes from hermaphrodites are physically available to fertilize the eggs of pure females may hold for many pollinated plants and free-spawning marine invertebrates, but may be inappropriate for fish species with elaborate courtship and spawning rituals; and self-fertilization is unknown in fishes, except in one androdioecious species (*Kryptolebias marmoratus*, to be discussed later). Furthermore, some of the biological phenomena in plants (such as the prevalence of gynodioecy over androdioecy) that motivated the available models on evolutionary transitions between dioecy and hermaphroditism do not seem to apply to fishes. Indeed, the conditions of gynodioecy and androdioecy are only rarely reported in fish [Petersen and Fischer, 1986; Robertson et al., 1982].

Sexual Lability. Another reservation about applying the theory developed for plants to fishes involves the implicit assumption that reproductive states transitional to gonochorism and hermaphroditism are genetically hard-wired and thus directly responsive to natural or sexual selection. Instead, sexual differentiation in fish is remarkably plastic developmentally, and subject to environmental influences [Francis, 1992; see also several articles in the current issue]. For example, in the otherwise hermaphroditic mangrove killifish, males can be experimentally induced by exposure to particular environmental conditions [Harrington and Kallman, 1967]; and in nature, developmental switches between male and female have long been known to be socially mediated in several fish species that are sequentially hermaphroditic [Fishelson, 1970; Robertson, 1972; Fricke and Fricke, 1977; Shapiro, 1979]. These broad norms of reaction with respect to gender reflect the fact that testes and ovaries in teleosts derive during ontogeny from a single precursor tissue that can differentiate rather flexibly during an individu-

al's lifetime (unlike the case in birds and mammals, for example). This is not to imply that selection plays no role in the evolution of reproductive modes in fish, or that fish reproductive operations have no genetic basis. To the contrary, proximate environmental factors that influence sexual expression in a fish population are likely to alter selection pressures that ultimately influence the evolution of underlying sex-influencing mechanisms (including, in some species, the genetic and developmental scope for hermaphroditism).

In any event, the apparent paucity of gynodioecy and androdioecy in extant fishes suggests that these transitional states tend to be evolutionarily highly ephemeral and rare at best, perhaps because the set of fitness conditions favoring the stability of mixtures of hermaphroditic and gonochoristic systems is restrictive [Charnov et al., 1976]. In part for this reason, most of the available evolutionary theory regarding hermaphroditism in fish has addressed selective factors that might promote the expression of different forms of hermaphroditism in various taxa.

Sequential Hermaphroditism

If we assume that the mechanism controlling induction of sex change has evolved to permit individuals to change sex only when it is to their reproductive advantage to do so, then a satisfying, evolutionary explanation should be capable of predicting correctly when individuals should change sex and when they should not.

Shapiro, 1987

Most non-gonochoristic fish species are sequential as opposed to simultaneous (synchronous) hermaphrodites. Sequential hermaphroditism comes in 3 primary forms: protogyny, in which an individual begins reproductive life as a female and then later may switch to male; protandry, in which an individual begins reproductive life as a male and later may switch to female; and serial bi-directional sex change, in which an individual may switch back and forth between functional male and female. Protogyny is the most common pattern in nature [Warner, 1984], but the fact that all 3 forms of sequential hermaphroditism have been documented in marine fishes (most commonly in reef-dwelling species) argues that no universal fitness advantage invariably attends being either a female first, or a male first, in a fish's life.

Some ichthyologists of past decades assumed that each sequential hermaphrodite automatically changes sex upon reaching a threshold body size or critical age. How-

ever, laboratory and field observations have demonstrated that social and behavioral factors typically trigger each switch from one sex to the other [Shapiro, 1987]. For example, removal of a dominant male from a social group of protogynous fish, or removal of a female from a protandric group, may induce one or more remaining individuals to change sex. Empirically, fish typically change sex when they reach about 80% of their maximum body size and are about 2.5 times their initial age at sexual maturity [Allsop and West, 2003]. Considerable effort has gone into analyzing possible ecological and demographic conditions that proximately trigger such sex changes and that ultimately have led to protogyny, protandry, or serial switching in various fish species.

One of the earliest evolutionary models for sex change – the 'size-advantage' hypothesis – today remains a singularly powerful explanation for sequential hermaphroditism [Ghiselin, 2006]. As originally phrased by Ghiselin [1969], 'Suppose that the reproductive functions of one sex were better discharged by a small animal, or those of the other sex by a large one. An animal which, as it grew, assumed the sex advantageous to its current size would thereby increase its reproductive potential.' This life-history notion was formalized by Warner [1975] and Warner et al. [1975] who showed that if age-specific reproductive output increases more rapidly with age (or body size) for one sex than the other, and if the curves relating fecundity to age cross for the two sexes, then in principle an age or body size exists at which an individual could reproductively profit by switching gender (fig. 5). In other words, 'individuals should change sex when the reproductive prospects of functioning as the opposite sex exceed the expectations of the current sex' [Warner and Swearer, 1991].

Following these seminal treatments, most subsequent empirical appraisals and theoretical analyses of sequential hermaphroditism can be considered refinements that have taken into account additional factors (beyond body size per se) that might impact age-specific fecundity and mortality curves in ways that affect individuals' expectations for reproductive success as a function of gender. The kinds of complicating (and often interacting) factors that have been addressed include population density [Warner and Hoffman, 1980; Lutnesky, 1994], population body-size ratios [Ross et al., 1983], sex ratios and mating patterns [Shapiro and Lubbock, 1980; Warner, 1982], sperm competition and reproductive skew [Muñoz and Warner, 2003, 2004], immediate physiologic or other costs (including missed mating opportunities) of sex change per se [Hoffman et al., 1985; Iwasa, 1991; Munday and Molo-

ny, 2002], or other life-history tradeoffs [Charnov, 1986]. Each such factor has been considered in the context of how it might alter age-specific reproduction (and hence selection pressures for the timing and direction of sex change) in one species or another of sequentially hermaphroditic fish.

Protogyny

This form of hermaphroditism characterizes many wrasses (Labridae) [Warner and Robertson, 1978], parrotfishes (Scaridae) [Robertson and Warner, 1978], and other reef fishes. The bluehead wrasse (*Thalassoma bifasciatum*) provides a well-studied example [Warner and Swearer, 1991]. Females and juvenile males display an initial phase (IP) coloration with a yellow dorsal stripe and a series of lateral green blotches separated by white bars; large breeding males show a striking terminal phase (TP) with a bright blue head and green body. The IP males are 'primary' males, whereas those in the non-reversible TP are 'secondary' males who arose either from IP males or from particular females who changed sex (typically within a few days following the loss of TP males from a locale). Many other protogynous species, such as the angelfish *Centropyge potteri*, have similar lifestyles but are monandric: i.e., all males derive from sex-changed females [Lutnesky, 1994].

Protogyny is predicted to be evolutionarily favored when the reproductive output of males increases, as a function of size or age, faster than that of females. Thus, protogyny should also often be associated with sexual selection on males. Male size advantage is especially likely when large males tend to monopolize matings [Warner, 1988], as for example in species where territorial or otherwise ruling males control reproductive access to females [Lutnesky, 1994; Ross, 1990]. Thus, it is probably no mere coincidence that protogynous life histories are observed most frequently in fishes with harem social systems in which most of the mating events are instrumented by large, dominant males (although it may be difficult to determine whether protogyny is the cause or the effect in this association).

Although the size-advantage model generally has proved powerful in explaining sex-change patterns in hermaphroditic fish species, not all field observations seem easily accommodated under this model. For example, in some protogynous species the largest females do not always change sex when given the opportunity [Lutnesky, 1994; Cole and Shapiro, 1995]. To address this conundrum, Muñoz and Warner [2004] conducted field observations and experiments on a Caribbean popula-

tion of bucktooth parrotfish (*Sparisoma radians*). The authors found that pronounced size-related skews in female fecundity, coupled with dilutions of paternity via intermale sperm competition, set up population conditions in which, for the largest females, expected reproductive success as a male was actually lower than continued reproduction as a female. Factoring in these complications helped to make sense of the observation that smaller females were often the sex changers in this species. This study illustrates how suitable modifications to the size-advantage model have sometimes proved useful in understanding the peculiarities of particular protogynous systems.

Protandry

In the popular cartoon movie *Finding Nemo*, a male anemonefish loses his mate and must struggle alone to raise his offspring Nemo. In real life, Nemo's father likely would have switched gender following his mate's death and then paired with a male. Anemonefish such as *Amphiprion clarkii* (Pomacentridae) are among the few marine fish that begin reproductive life as a functional male and later switch to female [Miura et al., 2003]. The black porgy (*Acanthopagrus schlegelii*; Sparidae) is another example [Wu et al., 2005]. In the case of *Amphiprion*, a local breeding community typically consists of one dominant female and several smaller males and juveniles, and if the breeding female dies a male then transforms to take her place.

Perhaps the most surprising aspect of protandry is its rarity relative to protogyny. In most fish species, female fecundity increases dramatically with age and body size, whereas even small mature males can produce enough sperm to fertilize countless eggs. Thus, selection pressures might generally seem to favor a male-first-in-life strategy (all else being equal). However, protandry typically produces a male-biased sex ratio, further exacerbating the sperm excess that is expected even in populations with a balanced sex ratio. Thus, where male competition exists for mating opportunities, protandry would be generally maladaptive. Additionally, for many fish species the slopes in the regressions of age-specific fecundity on body size (fig. 5) are probably rather similar in males and females when mating is either random or monogamous (compared to the great disparity in these slopes, especially in later age cohorts, when large males are highly polygynous and can monopolize matings with many females). By these lines of reasoning, the rarity of protandry relative to protogyny might not be so unexpected after all.

Serial Bidirectional Sex Change

Although most sequential hermaphrodites change sex only once in a lifetime, individuals in several goby species (Gobiidae) are known to display serial sex changes in both directions [Sunobe and Nakazono, 1993; Kuwamura et al., 1994; St Mary, 1994, 1997]. Examples are provided by obligate coral-dwelling gobies in the genera *Gobiodon* and *Paragobiodon*. These reef fish live among the protective branches of live corals, often as single breeding pairs but sometimes in larger social groups in which only the biggest 2 or 3 individuals are reproductively active [Cole and Hoese, 2001].

Two evolutionary hypotheses have been advanced to account for bi-directional sex change. Under the 'risk-of-movement' model [Nakashima et al., 1996; Munday et al., 1998], intense predation pressures on patch-structured reefs make mate-searching movements very risky for small and sparsely distributed fish like gobies, thus giving a selective advantage to any stay-at-home individual who could facultatively switch gender as the need arises (such as when a mate dies or when the sex ratio is highly skewed in the local environs). A different (but somewhat overlapping) hypothesis – the 'growth-rate-advantage' model [Kuwamura et al., 1993; Nakashima et al., 1995] – incorporates the observation that female gobies grow faster than males, yet reproductive success may increase equally with body size in both sexes (because larger females produce more eggs and larger males can better defend egg clutches). Under this biological set-up, when two potential mates meet, selection should favor different kinds of sex change: protogyny when the initial pair consists of two females, protandry when the pair consists of two males, and sex reversal when the female initially is larger than the male in a heterosexual pair [Munday, 2002]. The two competing models – risk-of-movement and growth-rate-advantage – were put to test using manipulative field experiments for the Australian goby *Gobiodon histrio*, and for this species the risk-of-movement hypotheses proved to match the observations most closely [Munday, 2002].

Synchronous Hermaphroditism

In a relatively small number of fish species, an individual is capable of producing both male and female gametes simultaneously [Fischer and Petersen, 1987; Cole, 1990; Kobayashi and Suzuki, 1992]. 'Cosexuality' of this form is known in representatives of about a dozen fish families, most notably in the Serranidae, Cirrhitidae, and

Gobiidae. The rarity of synchronous hermaphroditism in fishes is probably due in part to inherent antagonisms between male and female hormonal or other physiological systems [Bull and Charnov, 1985], and perhaps to high fixed costs for each sexual function [Heath, 1977]. Additionally, for outcrossing simultaneous hermaphrodites, the higher cost of producing female gametes creates an inherent risk: without some mechanism to ensure that mates contribute equal amounts of both gametes, cheating strategies might easily evolve and lead to the loss of simultaneous hermaphroditism in a lineage.

With a single documented exception (the mangrove killifish, Cyprinodontidae; see beyond), all synchronously hermaphroditic fish species are thought to outcross rather than self-fertilize. In some species such as the chalk bass (*Serranus tortugarum*), an individual typically alternates sexual roles in close succession, spawning serially during an encounter as a male and as a female. In other species such as the blue-banded goby (*Lythrypnus dalli*), an individual reportedly can have competent male and female gonadal tissue simultaneously but nonetheless act only as male or female at each stage in life, thus partly decoupling physiological and behavioral aspects of synchronous hermaphroditism [St Mary, 1993]. Thus, such species might best be considered sequential hermaphrodites. And in a few species including the barred serrano (*Serranus fasciatus*), specimens mature as simultaneous hermaphrodites but larger individuals later may lose female function and become functional males [Petersen, 1990]. Such species could be deemed androdioecious.

One basic ecological and evolutionary consideration for synchronous (but not all sequential) hermaphrodites is encapsulated in the 'low-density' model, which notes that individuals who produce male and female gametes at the same time have less difficulty than gonochorists in finding mates, especially when populations are sparse [Tomlinson, 1966]. This advantage should hold both for outcrossing hermaphrodites (who need to encounter only one other individual to mate) and self-fertilizing hermaphrodites (who need not encounter any partner). In this mate-acquisition regard, some of the possible selective advantages for synchronous hermaphrodites can overlap those for sequential hermaphrodites under the risk-of-movement model described above.

Outcrossing

Small reef-dwelling seabasses in the family Serranidae illustrate the standard types of mating behavior in synchronous hermaphrodites. In the black hamlet (*Hypo-*

plectrus nigricans), 2 otherwise solitary individuals pair up (typically in the late afternoon) to spawn in a process called egg trading that consists of a 3-step behavioral sequence [Fischer and Petersen, 1987]: (a) each fish packages an entire day's clutch of eggs into parcels; (b) courtship is initiated by the individual that will first release eggs; and (c) partners take turns releasing an egg parcel every few minutes and externally fertilizing their mate's released parcel. Hamlet partners are usually faithful during the episode but occasionally switch partners on different days, so the mating system approximates serial monogamy. In the harlequin bass (*Serranus tigrinus*), the process is similar except that clutches are not parceled and the mating system is thought to be permanent monogamy. And, in the barred serrano – a rare example of an androdioecious species [Hastings and Petersen, 1986] – the mating system (harem-style polygyny) is similar to that of some protogynous wrasses described earlier.

In effect, an outcrossing synchronous hermaphrodite faces sex-role decisions within a spawning episode or season that are analogous to the sex-role choices faced by sequential hermaphrodites across a lifetime: namely, how best to allot male versus female function so as to maximize expectations for reproductive success [Fischer, 1981, 1984; St Mary, 1994; Petersen and Fischer, 1996]. Thus, sex-allocation theory – which addresses how a hermaphrodite should in principle divide its reproductive portfolio between male and female effort [Petersen, 1991] – is again relevant, and many similar considerations that arose for sequential hermaphrodites reappear in this new context. For example, in the androdioecious barred serrano – a species with female harems – a late-life switch from hermaphrodite to male can be rationalized by the size-advantage hypothesis, using the same basic argument (disproportionate mating success for larger males) that applied to harem species of protogynous hermaphrodites [Petersen, 1987].

With respect to egg-trading behavior in the serially monogamous seabasses, a 'tit-for-tat' model has been applied [Fischer and Petersen, 1987; Petersen, 1995]. The basic idea is that by releasing a clutch gradually and waiting for a partner to reciprocate, a pair-mating fish can better evaluate the mating situation and cut its losses if its partner deserts. In the harlequin bass, by contrast, egg parceling is presumably less critical because the monogamous pair bond has greater permanency. Such tit-for-tat scenarios are merely one aspect of the 'hermaphrodite's dilemma' [Leonard, 1990] that envisions inevitable sexual conflict (differences of interest between male and female

partners) [Leonard, 1993] in any reproductive interaction involving reciprocity with possible cheating. In turn, the interactive reproductive games played by hermaphroditic fish are just one subset of the longstanding topic of how cooperative interactions evolve [Axelrod and Hamilton, 1981].

Self-Fertilization

The necessity to reproduce at all costs should favor the development of selfing wherever the environment is such that the transfer of gametes between individuals is hindered. Ghiselin, 1969

Only one hermaphroditic species – the mangrove killifish, *Kryptolebias* (formerly *Rivulus*) *marmoratus*; Cyprinodontidae – is documented to self-fertilize routinely. Most mature individuals have an internal ovotestis that produces sperm and eggs that typically unite inside a fish's body, after which zygotes are laid into the environment. In some populations, selfing rates are so high that nearly all fish belong to highly inbred lineages that have near-zero heterozygosities and thus, in effect, are clonal. Also present in this species are pure males who appear to mediate occasional outcross events. This happens when a hermaphrodite sheds some unfertilized eggs onto which a male (who has no intromittent organ) releases sperm. Thus, *K. marmoratus* can be described as an androdioecious species with a mixed-mating system [selfing and outcrossing; Mackiewicz et al., 2006a, b]. This remarkable reproductive system, which was discovered a half-century ago [Harrington, 1961] and has been the subject of many genetic and evolutionary analyses [review in Avise, 2008], is unique among vertebrates.

Mixed-mating systems are common, however, in plants [Goodwillie et al., 2005] and invertebrate animals [Jarne and Auld, 2006], for which various hypotheses have been advanced for why selfing is tolerated given what otherwise would seem to be a serious potential problem: inbreeding depression (low genetic fitness in the progeny of matings between close kin). In principle, one compensating evolutionary advantage to selfing is that a selfer transmits two sets of genes to each offspring whereas an outcrosser transmits only one set. Another evolutionary idea is that a mixed-mating system converts the inbreeding dilemma of constitutive selfing into a best-of-two-worlds adaptive strategy that combines many of the advantages of sexual and clonal reproduction [Allard, 1975]. In particular, consistent selfing might often be advantageous in the ecological short-term because it can yield progeny with identical copies of potentially co-adapted multi-locus genotypes that nature already has field-tested for genetic fitness (in parental lineages) in a

particular habitat. However outcrossing is important as well, especially when habitats change over time or show spatial heterogeneity, as it produces genetically diverse progeny, some of which may be well suited to the new environment.

Although such considerations may have played a role in the evolution of selfing as part of the mixed-mating system in *K. marmoratus*, we suspect that another factor has been more important. By virtue of producing both eggs and sperm simultaneously, each self-fertilizing individual has automatic 'fertilization insurance'. Baker [1955] was the first to promote the notion that the capacities for self-fertilization and for long-distance dispersal are positively correlated across species of plants and invertebrate animals, and that a plausible explanation involves the reproductive assurance that comes from being a selfing hermaphrodite, since even a single individual can be a successful colonist. The empirical association between selfing and colonization potential (or 'weediness') has become known as Baker's rule.

The behavior and natural history of the mangrove killifish can be interpreted as consistent with Baker's rule in several regards: the species has a large geographic range, extending from southern Brazil to Florida and including many Caribbean islands; a tendency for individuals to occupy mangrove litter and termite cavities in rotting logs may predispose this species to occasional long-distance dispersal via floating forest litter (e.g., following storms); adults can survive out of water for up to 10 weeks; fertilized ova are well suited for dispersal because they

too can survive out of water for long periods; and many killifish individuals tend to lead rather isolated, independent lives. All of these attributes would favor self-fertilization as a routine alternative to outcrossing in *K. marmoratus*. The mixed-mating system could thus be interpreted to combine the long-term and short-term advantages of outcrossing (continued genetic health and adaptability) with the immediate benefits of selfing (including fertilization insurance).

Synopsis

This review has merely delved into some of the evolutionary considerations that apply to various fish species in which individuals can reproduce as both male and female. Nevertheless, even this cursory treatment should make it clear that hermaphroditism in vertebrates is a phenomenon rich in conceptual and empirical content for many arenas in ecology, ethology, genetics, and evolutionary biology.

Acknowledgments

The laboratory of JCA is supported by funds from the University of California at Irvine. JEM is supported in part by a Wenner-Gren Foundation Fellowship. We thank Felipe Barreto, Rosemary Byrne, Andrei Tatarenkov, and Vimoksalehi Lukoschek for helpful comments on an early draft of the manuscript.

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