Phylogenetic Perspectives on the Evolution of Functional Hermaphroditism in Teleost Fishes

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Synopsis Hermaphroditism is taxonomically widespread among teleost fishes and takes on many forms including simultaneous, protogynous, and protandrous hermaphroditism, bidirectional sex change, and androdioecy. The proximate mechanisms that influence the timing, incidence, and forms of hermaphroditism in fishes are supported by numerous theoretical and empirical studies on their mating systems and sexual patterns, but few have examined aspects of sex-allocation theory or the evolution of hermaphroditism for this group within a strict phylogenetic context. Fortunately, species-level phylogenetic reconstructions of the evolutionary history of many lineages of fishes have emerged, providing opportunities for understanding fine-scale evolutionary pathways and transformations of sex allocation. Examinations of several families of fishes with adequate data on phylogeny, patterns of sex allocation, mating systems, and with some form of hermaphroditism reveal that the evolution and expression of protogyny and other forms of sex allocation show little evidence of phylogenetic inertia within specific lineages but rather are associated with particular mating systems in accordance with prevalent theories about sex allocation. Transformations from protogyny to gonochorism in groupers (Epinephelidae), seabasses (Serranidae), and wrasses and parrotfishes (Labridae) are associated with equivalent transformations in the structure of mating groups from spawning of pairs to group spawning and related increases in sperm competition. Similarly, patterns of protandry, androdioecy, simultaneous hermaphroditism, and bidirectional sex change in other lineages (Aulopiformes, Gobiidae, and Pomacentridae) match well with particular mating systems in accordance with sex-allocation theory. Unlike other animals and plants, we did not find evidence that transitions between hermaphroditism and gonochorism required functional intermediates. Two instances in which our general conclusions might not hold include the expression of protandry in the Sparidae and the distribution of simultaneous hermaphroditism. In the Sparidae, the association of hypothesized mating systems and patterns of sex allocation were not always consistent with the size-advantage model (SAM), in that certain protandric sparids show evidence of intense sperm competition that should favor the expression of gonochorism. In the other case, simultaneous hermaphroditism does not occur in some groups of monogamous fishes, which are similar in ecology to the hermaphroditic serranines, suggesting that this form of sex allocation may be more limited by phylogenetic inertia. Overall, this work strongly supports sexual lability within teleost fishes and confirms evolutionary theories of sex allocation in this group of vertebrates.

Introduction Hermaphroditism, or the presence of male and female reproductive functions in the same individual, is relatively common in several lineages of teleost fishes (Atz 1964). Conclusive evidence of functional hermaphroditism has been presented for 94 genera within 27 families and 7 orders, or approximately 6% of teleost families, and there is inconclusive evidence for an additional 31 genera representing 21 families and 6 orders (Sadovy de Mitcheson and Liu 2008). Hermaphroditism can take on a diverse array of forms both within and among various lineages of teleosts, including simultaneous hermaphroditism, protogyny, protandry, bidirectional...
sex change, and androdioecy (Munday et al. 2006a). Moreover, at least one androdioecious species, *Kryptolebias marmoratus*, is known to self-fertilize (Harrington 1961).

Taken within a broad phylogenetic context, the patchy distribution of various forms of hermaphroditism across a wide range of taxa indicates that this mode of sex determination is evolutionary labile and has evolved repeatedly and independently among, and within, several groups of fishes (Smith 1975). Where present, most orders and families are polymorphic with respect to pattern of sexual allocation, with hermaphroditic taxa embedded within largely gonochoric (separate-sexed or dioecious) clades (Sadovy de Mitcheson and Liu 2008). Gonochorism is presumed to be the ancestral condition in fishes due to its pervasiveness among basal clades of fishes and other vertebrate lineages (Atz 1964; Policansky 1982). Hermaphroditism in fishes is thus a polyphyletic and derived condition that likely evolved from a gonochoric ancestral state (Avise and Mank 2009). The independent evolution of hermaphroditism numerous times within fishes is not surprising, given the diversity of other modes of sex-determination displayed by fishes (e.g., chromosomal, polygenic, environmental) that also show multiple independent origins and repeated instances of convergent evolution within, and among, clades (Mank and Avise 2009).

Sex-allocation theory provides explanations for the ways whereby organisms allocate resources to male and female functions (Charnov 1982). The Size-Advantage Model (SAM) represents the most widely recognized theory on the adaptive significance and evolution of sequential hermaphroditism (sex change) in fishes (Ghiselin 1969; Warner 1975), and it proposes that individuals should change sex when the reproductive value of functioning as the opposite sex exceeds that of the current sex (Warner 1988). Differential reproductive expectations related to size are the outcomes of different mating systems. Predictions of the model are well supported by the incidence of protogynous (female to male) sex change and androdioecy (simultaneous hermaphrodite to male), which should occur in polygynous mating systems in which large males tend to monopolize matings and realize a reproductive advantage relative to females, hermaphrodites, and small males (Warner 1984; Petersen 1987). Notably, a large female may not change sex if the combined fecundity of all other females in a local mating group is less than her existing fecundity, and in this circumstance, a smaller female may instead change sex to male (Muñoz and Warner 2003). The model predicts protandrous (male to female) sex change for mating systems in which monopolization of mates is absent and mating consists of random pairing or monogamy in which sexual partners are not matched by size, thereby taking advantage of the relatively high capacity of egg production in larger females. Gonochorism (separate-sexes or dioecy) should be favored when size-specific male and female reproductive expectations do not differ. This can occur in size-matched monogamy, or in mass matings in which sperm competition and a premium on sperm production mean that the reproductive expectations of males increase with size in a fashion similar to expectations of females (Warner 1975).

Bidirectional sex change, in which males and females both can change sex within the same population, and individuals can change sex more than once in their lifetime (Kuwamura and Nakashima 1998), has been experimentally induced in aquaria for several species in multiple families but has only been seen in gobies (Gobiidae) under natural conditions. This pattern appears to be favored in gobies because of the unpredictability of their social circumstances, combined with a high risk of predation due to their small body size (Munday et al. 2010). The incidence and particular direction of sex change in many bidirectional species is consistent with the SAM (Nakashima et al. 1995; Manabe et al. 2008) except for coral-dwelling gobies that form monogamous pairs of equally sized individuals (Munday 2002). In these fishes, the low density of available partners and the high risk of searching for a new partner favor the capacity for sex change in either direction, thereby facilitating the formation of new breeding pairs. According to the risk-of-movement model (Nakashima et al. 1996; Munday et al. 1998), being able to change sex in either direction enables individuals to adjust their sex to mate with any other adult they encounter. Such a strategy also helps to find a mate more quickly and move shorter distances, which minimizes the risk of predation and the loss of reproductive output (Munday et al. 2010).

Simultaneous hermaphroditism refers to a pattern of sex allocation in which individuals possess functional male and female gametic tissue simultaneously and thus can reproduce as either sex during the same reproductive period. All else being equal, simultaneous hermaphroditism is highly adaptive because a mating pair can achieve greater total egg production than a dioecious pair, and still effect cross-fertilization through a relatively small amount of investment in the production of sperm (Charnov 1982). However, the system can be unstable and vulnerable to “cheating” if there are opportunities for
extra-pair matings by individuals that expend more on male function. Thus, simultaneous hermaphroditism tends to be found only in species existing at very low densities (Tomlinson 1966; Ghiselin 1969), or in those species with mechanisms that limit extra-pair matings (Fischer 1980; Charnov 1982).

The proximate mechanisms that influence the timing, incidence, and forms of hermaphroditism in fishes are supported by numerous theoretical and empirical studies of their mating systems and sexual patterns (e.g., Warner 1984; Fischer and Petersen 1987; Munday et al. 2006a). Until recently, examinations of the evolution of hermaphroditism within a strict phylogenetic context to account for patterns of incidence, evolutionary transitions, and ecological or behavioral correlates have been sparse and limited primarily to broader phylogenetic comparisons (Devlin and Nagahama 2002; Sadovy de Mitcheson and Liu 2008; Avise and Mank 2009). The recent emergence of robust, fine-scale information on the interrelationships of species within various lineages (e.g., Labridae, Serranidae, Epinephelidae, Gobiidae) has provided exciting new opportunities to use comparative analyses to elucidate the evolutionary pathways among the diverse sexual allocation patterns of teleost fishes and to provide insights on mechanisms that have shaped the evolution of sex allocation in vertebrates (McCafferty et al. 2002; Erisman et al. 2009; Kazancıçılu and Alonzo 2010).

The purpose of this article is to examine the evolution of hermaphroditism in fishes within an explicit phylogenetic context. We combine our own analyses with the major findings of previous studies on sex allocation and mating systems in several lineages of fishes to draw conclusions about the ancestral conditions within particular lineages and transitional pathways between various patterns. Throughout this article, we focus on a series of important questions posed by Avise and Mank (2009) related to sex allocation and phylogeny in fishes. First, how has hermaphroditism evolved, and does gonochorism ever re-evolve from hermaphroditism? Next, does hermaphroditism show phylogenetic inertia (i.e., driven by common ancestry) or is it influenced by exogenous (environmental, social) factors in accordance with sex-allocation theory? Finally, do evolutionary transformations between hermaphroditism and gonochorism in fishes require functional intermediates (e.g., gynodioecy and androdioecy)? In the discussion, we address these questions and the general question of why sexuality in fishes is so labile compared with that of other vertebrate groups.

Results

Epinephelidae

Fishes in the family Epinephelidae include the groupers, soapfishes, and their relatives. Although traditionally these fishes have been combined with seabasses, anhinees, and hamlets in the family Serranidae, recent work by Smith and Craig (2007) has shown these to be separate lineages. Observations on the patterns of sex allocation of epinephelid fishes date back to those by Aristotle and represent the earliest research on hermaphroditism in animals (Atz 1964). Most species are protogynous hermaphrodites; some (diandry) or all (monandry) individuals within populations reproduce first as females and change sex later in their lifetime to reproduce as males (Sadovy de Mitcheson and Liu 2008; Erisman et al. 2010). Bidirectional sex change has been induced under laboratory conditions, but as yet there is no evidence that this pattern occurs in wild populations (Tanaka et al. 1990; Liu and Sadovy 2004). A few species have a gonochoric pattern and show no evidence of post-maturational sex change (Sadovy and Colin 1995; Erisman et al. 2008).

Protogyny is widespread in the Epinephelidae, and phylogenetic reconstructions indicate it as the ancestral condition in the clade (Erisman et al. 2009). Protogyny, including both monandry and diandry, is reported for 45 species of groupers and 2 outgroup species of soapfishes and related fishes (tribes Liopropomini, Grammistini, and Diploprioni). Functional gonochorism has been confirmed in five species of groupers from three genera (Epinephelus, Mycteroperca, and Paranthias), and it is reported but unconfirmed in Epinephelus itajara and two species of basslets in the genus Liopropoma. Protogynous sex change was reported to occur in two individuals held in captivity in the functional gonochore Mycteroperca rosacea (Kiewek-Martinez et al. 2010). Phylogenetic reconstructions using both parsimony and maximum likelihood methods indicate four to five independent transitions from protogyny to gonochorism in this group. In addition, there is also some evidence of an evolutionary reversal from gonochorism to protogyny in E. fuscoguttatus, and simultaneous hermaphroditism may have evolved once from protogyny in Pseudogramma gregoryi (Erisman et al. 2009).

A review of empirical data for groupers shows a remarkable congruence between the mating systems and sexual patterns of groupers and the principles of the SAM (Fig. 1). As outlined above, the model proposes that protogyny is adaptive when the expected reproductive success of large males is higher than
that of both females and small males. This should occur in mating systems in which large males monopolize matings with females and exclude smaller males from spawning, often through aggressive behavior (Warner 1984, 1988). Most species of grouper are protogynous, with polygynous mating systems whereby large males establish mating territories and frequently engage in bouts of aggression with other males; mating occurs in pairs, with large males often monopolizing matings with several females; and males have relatively small testes, indicative of low levels of sperm competition and the absence of group mating (e.g., Sadovy et al. 1994; Donaldson 1995; Mackie 2007). Also as outlined above, the SAM predicts that gonochorism is adaptive when the sexes show a similar increase in reproductive success with size, and this may happen in mating systems characterized by group-spawning and sperm competition (Warner 1982; Muñoz and Warner 2003). In accordance with these predictions, spawning in gonochoric species occurs in groups with several males and one or more females, male territorial behavior is rare or absent, and males have relatively large testes (a high gonosomatic index [GSI], expressed as the percentage of body weight devoted to gonad) indicative of sperm competition (Sadovy and Colin 1995; Erisman et al. 2007).

Placement of data on GSI and the structure of mating groups within a phylogenetic context provides additional support for the model and demonstrates the influence of these factors on the evolution of patterns of sex allocation in groupers. Reconstruction of the evolutionary history of reproduction in groupers shows that shifts in sexual pattern from protogyny to gonochorism are not restricted to certain branches of the phylogenetic tree, but rather they occur independently in several genera and are correlated with equivalent shifts in

Fig. 1. Most parsimonious reconstructions of the transformations in character states for sexual pattern and mating behavior in epinephelid fishes, modified from Erisman et al. (2009).
mating behavior from spawning by pairs to group spawning (Erisman et al. 2009). Moreover, transformations in mating behavior occur prior to, or simultaneously with, transformations in sexual pattern, suggesting the loss of sex change is associated with a change from spawning by pairs to group spawning. Related to this view, comparative analyses of GSI and sexual pattern suggest that sperm competition is significantly higher in gonochoric species than in protogynous species (Erisman et al. 2009).

**Serranidae**

The serranid fishes have a long history of investigations on hermaphroditism dating back more than a century (e.g., Dufossé 1856; Van Oordt 1929). The family includes two separate lineages, the Anthiinae (anthiines or basslets) and the Serraninae (seabasses, hamlets, and relatives). Four sexual patterns have been documented and confirmed (gonochorism, protogyny, simultaneous hermaphroditism, and androdioecy). Within the Anthiinae, sexual patterns have been documented for at least 17 species, and all but two are protogynous hermaphrodites. *Epinephelides armatus* and *Lepidoperca aurantia* are reportedly gonochoric (Roberts 1989; Moore et al. 2007), but their phylogenetic relationship to other anthiines has not been hypothesized. Sexual patterns within the Serraninae are diverse and include protogynous hermaphroditism (*Chelidoperca* and *Centropristis*), simultaneous hermaphroditism (*Bullisichthys, Diplectrum, Hypopectrus, Serranus*, and *Serraniculus*), androdioecy (*Serranus baldwini* and *Serranus psittacinus*), and gonochorism (*Paralabrax*). Most species of *Paralabrax* have been confirmed as functional gonochores (Sadovy and Domeier 2005), but there is evidence that individuals within some populations of *Paralabrax maculatofasciatus* may undergo protogynous sex change and thus are diandric (Hastings 1989; Hovey and Allen 2000). Although most species of *Serranus* are simultaneous hermaphrodites, *S. psittacinus* and *S. baldwini* are androdioecious: most individuals possess ovotestes and function as simultaneous hermaphrodites, and the largest fish have only testicular tissue and function only as males (Hastings and Petersen 1986; Petersen 2006).

Phylogenetic reconstructions of the evolution of patterns of sex allocation indicate that the common ancestor of the Serranidae was protogynous (Erisman and Hastings 2011; Fig. 2), and that protogyny likely represents a synapomorphy within this family nested within clades of otherwise gonochoric fishes (Smith and Craig 2007). Protogyny was retained among most species in the Anthiinae and basal members of the Serraninae. Although phylogenetic information is lacking, available evidence suggests that gonochorism evolved independently at least once, and possibly twice, within the Anthiinae. Within the Serraninae, gonochorism evolved from protogyny in the genus *Paralabrax*, whereas simultaneous hermaphroditism evolved once from protogyny in the lineage that includes species of *Hypopectrus, Serranus, Serraniculus*, and *Diplectrum*. Finally, androdioecy evolved once from simultaneous hermaphroditism in two species of *Serranus* (Erisman and Hastings 2011).

Studies on mating behavior and sperm competition in serranid fishes are restricted to a few groups and preclude an analysis similar to that applied to groupers; however, these factors do seem congruent with the distribution of patterns of sex allocations within the family. Specifically, gonochorism evolved from protogyny at least once in the Serraninae (Erisman and Hastings 2011), in which it is associated with the evolution of group spawning and sperm competition (Sadovy and Domeier 2005; Erisman and Allen 2006; Miller and Allen 2006). Among simultaneously hermaphroditic serranids, male reproductive specialization is limited behaviorally by a form of reciprocal fertilization, called egg-trading, wherein individuals parcel their daily clutches and require reciprocal egg release from a partner to continue spawning (Fischer 1980). This pattern is stable within the low levels of sperm competition evident within this clade. Although larger hermaphroditic individuals typically have higher ratios of male to female reproductive success, simultaneous hermaphroditism appears to be an Evolutionary Stable Strategy for these species (Petersen 2006). The evolution of androdioecy from simultaneous hermaphroditism in the genus *Serranus* is associated with an increase in population density and a change in the mating system from monogamous egg-trading to harem-defense polygyny in which large, pure males restrict interactions among conspecifics, monopolize male matings of individuals within their territories, and gain an advantage in reproductive success by losing female function and specializing as males (Petersen 2006). Interestingly, isolated pairs of individuals in *S. psittacinus* do not exhibit androdioecy and reciprocally spawn as simultaneous hermaphrodites (Petersen 1990).

Overall, evolutionary patterns of sex allocation in the Serranidae show evidence of potential phylogenetic inertia, as different patterns seem restricted to certain lineages. However, the expression of various
forms also conforms to theories of sex allocation. We suspect that the expression of forms within certain lineages, such as within the anthiines, will prove to be much more diverse once more species and populations are examined for sexual patterns, mating systems, and phylogenetic relationships.

Labridae

Recent work (Clements et al. 2004; Westneat and Alfaro 2005) recognizes both wrasses and parrotfishes as part of the family Labridae. Studies on the mating and sexual systems of labrid fishes have produced some of the most important theoretical and empirical insights into the evolution and selective advantages of sequential hermaphroditism in fishes (e.g., Robertson 1972; Warner and Robertson 1978; Warner 1982; Mun˜oz and Warner 2004). Protogyny is the pervasive pattern of sex allocation among various lineages of wrasses and parrotfishes, and has been confirmed for at least one species within 26 different genera, supporting it as the ancestral condition in labrids (Sadovy de Mitcheson and Liu 2008; Kazancıog˘lu and Alonzo 2010). Among protogynous species, both monandry and diandry have been widely reported. Gonochorism has been confirmed in nine different genera, and phylogenetic reconstructions indicate that it has evolved from protogyny at least six times independently, with at least three reversals back to protogyny from gonochorism (Fig. 3). Bidirectional sex change has been induced in Labroides dimidiatus and Halichoeres trimaculatus, two species believed to be functionally protogynous in the wild (Kuwamura et al. 2002, 2007).

Comparative analyses within the Labridae support the prediction of the SAM that males’ advantage in size drives the evolution of protogynous sex change. For example, Kazancıog˘lu and Alonzo (2010) found a significant correlation between the incidence of sequential hermaphroditism and the degree of size-related reproductive skew (i.e., strength of the size

Fig. 2. Most parsimonious reconstructions of the transformations in character states for sexual pattern in serranid fishes, from Erisman and Hastings (2011).
advantage). Similarly, they found that phylogenetic expression of hermaphroditism in the Labridae is associated both with sexual size dimorphism and the presence of mate-guarding behavior in males.

Evolutionary transformations in pattern of sex allocation from protogyny to gonochorism in wrasses and parrotfishes are predicted to be more likely when the size-advantage of large males is weak (Kazancioglu and Alonzo 2010). Such transitions appear to be associated with shifts to one of two kinds of mating systems. First, a shift to group spawning in certain genera (e.g., Bodianus, Sparisoma), in which there is high sperm competition, corresponds with a loss of sex change (Robertson and Warner 1978; Hoffman 1985). Interestingly, the prevalence of sex change in local populations of some species of Thalassoma depends on the local mating system in an analogous fashion: sex change is rare when group spawning is common (Warner and Hoffman 1980; Warner 1982). Second, a shift in mating system to benthic eggs and paternal care in some species of Symphodus also is associated with a loss of sex change. In this group, a nesting male may still mate with multiple females, but his overall rate of mating is reduced because of long periods of egg guarding, during which mating does not occur (Warner and Lejeune 1985). Protogynous sex change in this group has only been confirmed in one species, Symphodus melanocercus, which does not engage in paternal care and has a correspondingly high reproductive rate for large males. Evidence of a low frequency of sex change is reported but not confirmed for Symphodus tinca, in which males invest only limited energy on tending eggs, and large males spawn at a higher rate relative to smaller males (Warner and Lejeune 1985).

**Pomacentridae**

The damselfishes are a species-rich family of reef fishes with a wide geographic distribution both in temperate and tropical nearshore waters (Nelson 2006). All damselfishes reproduce by laying demersal eggs, and the social and mating systems of most species are characterized by permanent territoriality and paternal care for eggs (Petersen 1995). The sexual systems of many species have been studied, with
Amphiprion fishes (once within the monophyletic group of anemonefishes (Amphiprion and Premnas) (Sadovy de Mitcheson and Liu 2008; Cooper et al. 2009). Clear evidence of functional protandry has been found for 10 species of anemonefishes, and it is always associated with monogamous mating systems (Fricke and Fricke 1977; Godwin 1994). Social groups include either a single pair or a pair of larger, sexually mature individuals and several smaller juveniles that occupy a sea anemone. Within the pair of sexually mature individuals, the larger individual is female and the smaller is male. A size-dependent aggressive hierarchy often exists, whereby the breeding male prevents all others from mating with the female (Fricke 1979; Buxton 2004). Protandry is the most adaptive pattern of sex allocation in this case; it allows the reproductive success of the mating pair to benefit from the increased production of eggs by the large female, since egg production tends to be correlated with body size in fishes (Warner 1984).

Protogyny has evolved at least once in Dascyllus, in which it occurs in at least 5, and perhaps in as many as 7, of the 10 species in the genus (Coates 1982; Godwin 1995; McCafferty et al. 2002). While there is some evidence of phylogenetic inertia in the expression of protogyny within this group (Godwin 1995), characteristics of the mating system appear to provide a better explanation. Specifically, those species that live in close association with discontinuous or discrete units of branching corals (e.g., Dascyllus aruanus, Dascyllus carneus, Dascyllus reticulatus) have mating systems characterized by resource-defense polygyny in which males are able to defend the habitat and a harem of females, and these species are protogynous (reviewed by McCafferty et al. 2002). In D. aruanus, sex change is frequent in populations consisting of small isolated groups (Cole 2002), whereas it is less frequent in populations that consist of large aggregations (Asoh 2003). Conversely, in species such as Dascyllus albisella and Dascyllus trimaculatus that occupy habitats that are less patchy and have a more continuous distribution on reefs, males and females show overlapping habitat ranges and sex ratios, males do not defend females or restrict their movement, and mating is promiscuous between females and males that defend nest sites, much like the mating systems of other damselfishes (Petersen 1995). In these species, we see a reversal from protogyny back to gonochorism (MacCafferty et al. 2002).

The advantage of protandry in anemonefishes depends on the fact that the social group is rigidly limited to two reproductive adults of different sizes, which in turn is due to the small size of the host anemone or, for species living in groups, dominance hierarchies (Buxton 2003, 2004). However, in the case of Dascyllus, more adults may be present, which favors protogyny since large males may be able to fertilize and guard more eggs than they could produce as a female. However, when reproductive output of large males is constrained by investment in paternal care and in preventing females from mating with other males, selection for sex change breaks down in a manner similar to that suggested for the Symphodus labruses (Warner and Lejeune 1985).

Sparidae

Porgies, sea breams, and related fishes in the family Sparidae are one of the most diverse families of teleosts with respect to patterns of sex allocation (Buxton and Garratt 1990). Different species exhibit gonochorism, protogyny, and protandry. Both diandry (protogyny) and digyny (protandry), in which only some individuals change sex within a population, have been reported for some species of sequential hermaphrodites. There is some evidence that simultaneous hermaphroditism may occur in populations of Pagellus bogaraveo and Sparus aurata although only protandry has been confirmed (Sadovy de Mitcheson and Liu 2008). Moreover, a few species (e.g., Boops boops, Sarpa salpa) have been variously described as protogynous, protandrous, or gonochoric due to the variations in gonadal configurations that make diagnosis of sexual pattern in these fishes particularly challenging.

The diversity in patterns of sex allocation is even more striking when placed within a phylogenetic context (Chiba et al. 2009). Multiple patterns occur within single genera, and evolutionary transformations from protandry to gonochorism, protogyny to gonochorism, and even protandry to protogyny to gonochorism are predicted (Fig. 4). As a result of this diversity, and perhaps because of uncertainty in the identification of sexual patterns in particular species, reconstructions of the ancestral states of characters of sex allocation are for the most part equivocal.
Studies on the mating systems of sparid fishes are rare, because many species inhabit deeper or offshore habitats, but the information that exists for a few shallow-water species provides some insights into the relationships between mating and sexual systems in the family. For example, the polygynous mating systems and protogynous condition in *Chrysoblephus laticeps* and *Spondyliosoma emarginatum* support the SAM. In both species, males are territorial and monopolize matings with a harem of females, spawning occurs in pairs, and sperm competition is relatively low as indicated by GSIs of approximately 1% (Buxton and Garratt 1990). The gonochoric species *Cheimerius nufar* also offers some support for sex-allocation theory, because mating occurs within spawning aggregations and the incidence of streak spawning or group spawning is relatively common (Buxton and Garratt 1990; Sheaves et al. 1999). However, despite direct observations of spawning by multiple males that indicate sperm competition in this species, male GSI appears to be relatively low (1%). The mating system of the protandrous hermaphrodite *Acanthopagrus berda* is even more intriguing in its lack of concordance with the SAM, which predicts that protandry should be favored when sperm competition is low and when mating occurs between members of monogamous pairs or those of random pairs (Warner 1988). This species forms spawning aggregations; spawning occurs in groups, and hence sperm competition should be quite high (Garratt 1993; Sheaves et al. 1999).

A wider examination of levels of male GSI among sparid fishes reveals patterns not currently predicted by sex-allocation theory (Table 1). Fittingly, gonochoric species show higher male GSI levels that suggest greater levels of sperm competition than in protogynous species. However, GSI among protandrous species is highly variable (range = 0.5–10%) and comparable to that observed in gonochoric species. As mentioned above, sperm competition is expected to lead to similar reproductive expectations of size for males and females, which would select for gonochorism but against protandry.

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**Fig. 4.** Most parsimonious reconstructions of the transformations in character states for sexual pattern in sparid fishes. Phylogeny from Chiba et al. (2009).
We are unsure why this group does not show the expected association of male GSI and sexual pattern. Male GSI is correlated with mating system and degree of sperm competition among fish taxa, although there is substantial variation in GSI across species with similar mating systems, especially among species with more intense sperm competition (Petersen and Warner 1998). As mentioned above, sparid gonadal anatomy and sex allocation is notoriously variable and hard to classify, and most species are temperate, seasonal breeders. This can lead to uncertainty both in estimates of sexual pattern and GSI. Note also that GSI is an indication of energy devoted to the production of gametes, and may vary across species for reasons unrelated to sperm competition. Thus, it is not an infallible guide to the mating system or patterns of males’ reproductive success, particularly across species. It is possible that other exogenous factors influence sexual expression in sparid fishes, such as sex-related differences in growth or mortality (Garratt 1993). At this point, we can only say that more careful characterizations of sparid sexual patterns and mating systems may reveal a major challenge to the SAM.

**Aulopiformes**

The order Aulopiformes comprises approximately 236 species of lizardfishes and relatives that occupy habitats ranging from coastal waters to the deep sea (Nelson 2006). More than two-thirds of aulopiform fishes (approximately 158 species) are reported to be simultaneous hermaphrodites (Baldwin and Johnson 1996). Both likelihood and parsimony reconstructions of evolutionary history of patterns of sex allocation in the Aulopiformes indicate gonochorism (which is present throughout the suborders Aulopoidei and Paraulopoidei) as the ancestral condition (Fig. 5) (Davis and Fielitz 2010). Simultaneous hermaphroditism is hypothesized to have evolved a single time in the stem species of the Alepisauroidei during the early Cretaceous, which represents the oldest known date and lineage for the evolution of simultaneous hermaphroditism among vertebrates (Davis and Fielitz 2010).

Mating systems of lizardfishes and their relatives remain poorly understood, which precludes a thorough evaluation of the relative influence of phylogenetic inertia versus social factors on the evolution of sexual patterns.
patterns of sex allocation. However, the pervasiveness of gonochorism in lineages inhabiting shallow water (e.g., *Synodus*, *Aulopus*) and the evolution of simultaneous hermaphroditism in lineages occupying deep water (>200 m depth) are congruent with the low-density model (Tomlinson 1966; Ghiselin 1969), if we assume that shallow-water species occur in high population densities whereas those in the deep sea are more sparsely distributed. Specifically, simultaneous hermaphroditism should be unstable at high population densities when extra-pair matings are possible, but advantageous for species that occupy deep-sea habitats in which population densities are extremely low and thus the probability of finding a mate is low as well. In this case, by allocating most energy toward production of eggs and a much smaller amount to male function, individuals maximize their reproductive output and have the capacity to mate with any other individual they meet (Ghiselin 1969; Charnov et al. 1976).

In contrast, these aspects of the mating system may not occur in gonochoric species that often occur in higher densities in shallow water. In the lizardfish (Synodontidae) *Synodus dermatogenys*, males compete for females through aggressive behavior, and both sexes are promiscuous, spawning multiple times with different mates during the reproductive period (Donaldson 1990). Sperm competition is also present; courtship begins in pairs, but during the spawning rush, several additional males usually join the pair.

**Gobiidae**

The family Gobiidae includes more than 1400 species of fishes distributed worldwide both in tropical and temperate habitats (Nelson 2006). Protogyny is confirmed in one or more species within eight genera and reported, but unconfirmed, in an additional six genera (reviewed by Sadovy de Mitcheson and Liu 2008). Bidirectional sex change is confirmed in several species of *Lythrypnus* and *Gobiodon* as well as in *Paragobiodon echinocephalus* and *Trimma okinawae* (Nakashima et al. 1996; Munday et al. 1998;
However, individuals tend to only act as one sex at a time, and they can switch to the opposite sex multiple times. The mating systems of most hermaphroditic species of gobies, including both protogynous and bidirectional species, are consistent with predictions of the SAM (Nakashima et al. 1993; Manabe et al. 2008). Many are polygynous, and have female harems (e.g., Trimma okinawae, L. dalli), with the largest individual being male (St Mary 1994; Munday et al. 2006b). The direction of sex change generally tends to be from female to male, as large males may realize an advantage in reproductive success due to defense of nest-sites or females but with occasional instances of males reverting to functional females when it is favorable, such as when a solitary male enters a new social group that already contains a dominant male (Kuwamura et al. 1994; Munday et al. 2010). Similar to theories on the evolution of simultaneous hermaphroditism, the evolution of bidirectional sex change in gobies “may offer the advantage of increased mating opportunities among adult conspecifics that are otherwise constrained by small size, limited mobility, highly specific microhabitat requirements, and/or a short life span” (Cole 2010). However, bidirectional sex change in the subset of coral-dwelling gobies (Gobiodon and Paragobiodon) is not well explained by the SAM, because no differences exist between males and females in the rate at which reproductive success increases with size (Kuwamura et al. 1993; Munday 2002). These small fishes are pair-forming and monogamous, and the reproductive success of a breeding pair depends on the size of both the male and female, with the result that both individuals are approximately the same size (Munday et al. 2006b). For these gobies, the advantage of bidirectional sex change is that they may need to move among hosts to find a new partner following the loss of a breeding partner or the death of their host colony of corals. Given the low density of available partners and the high risk of predation associated with searching for a new partner, the ability to change sex in either direction enables an individual to adjust its sex to mate with any other adult it encounters (Munday 2002). Such a strategy also helps to find a mate more quickly and move shorter distances, minimizing the risks of predation and of loss of reproductive output (Munday et al. 2010).

**Discussion**

We refer here to the three overarching questions posed by Avise and Mank (2009) about the evolution of hermaphroditism in fishes and one broader...
question about sexual lability in fishes compared to other vertebrates:

How does hermaphroditism evolve, and does gonochorism ever re-evolve from hermaphroditism?

Although various forms of hermaphroditism in teleost fishes are embedded within a deeper clade composed primarily of gonochoric taxa, comparative phylogenetic analyses for numerous families of fishes that express multiple forms of sex allocation demonstrate that sexual patterns of fishes have the potential to evolve in a variety of directions and that gonochorism has indeed evolved repeatedly within hermaphroditic lineages. For example, protogyny is likely the ancestral pattern of sex allocation in labrids, serranids, and epinephelids from which gonochorism has evolved multiple times independently. Conversely, in pomacentrids, gobids, and aulopiform fishes, various forms of hermaphroditism evolved from gonochorism one or more times within specific lineages. In sparid fishes, we observe an incredible diversity in patterns of sex allocation and evidence of multiple, independent origins of protogyny, protandry, and gonochorism.

Does hermaphroditism show phylogenetic inertia (i.e., driven by common ancestry) or is it influenced by exogenous (environmental, social) factors in accordance with sex-allocation theory?

George Williams (1975) postulated that phylogeny was a better predictor than ecology for explaining distributions of sexual systems (i.e., patterns of gender expression) across the animal kingdom. Within large, distinctive clades, this appears to be the case, since mode of sexuality is invariant in many large lineages (Ghiselin 1974; Leonard 1990). As shown above, however, our findings for several clades of teleost fishes do not support William’s hypothesis, in that there is little evidence for phylogenetic inertia affecting the distribution of hermaphroditism in many groups. Instead, hermaphroditism appears to be reliably associated with particular social/mating systems (which can affect the size-specific reproductive expectations of males and females) or with changes in habitat and population density (which can affect the probability of mating multiple times), and transitions to and from various forms of hermaphroditism occur in concert with changes in these features.

Although William’s hypothesis does not match the pattern within taxa with hermaphroditic representatives, hermaphroditism only occurs in a minority of fish families (Sadovy de Mitcheson and Liu 2008). For those families that are exclusively gonochoric, his ideas might still hold if we found evidence of conditions that would favor hermaphroditism, but without its actual evolution. Such a review is beyond the scope of this article, but examining at least one recent review, there is surprisingly little evidence supporting William’s idea. In a recent paper, Walker and McCormick (2009) included a table reviewing the sexual patterns and behavior of known haremic reef fishes, and found that the vast majority of species that had harems also had evidence of protogynous hermaphroditism. The only clade that appeared to possibly break this pattern was the Tetraodontiformes, in which harem polygyny was reported for several species, but protogynous hermaphroditism was only reported for one species. Whether or not this pattern will remain after more data emerge on sex allocation and mating systems in these less-studied fishes is unclear. However, for several well-studied clades with hermaphroditic representatives, we find strong evidence for exogenous factors affecting sex allocation and do not find evidence of phylogenetic inertia.

The one exception to this rule may be the evolution of simultaneous hermaphroditism. In the Serranidae, simultaneous hermaphroditism has evolved in species that are monogamous and have no parental care, a mating system that exists in other taxae of fishes. For example, this mating system is widespread in chaetodontids and pomacentrids in which species are gonochoric (Barlow 1984; Whiteman and Coté 1999). Simultaneous hermaphroditism appears to have a clear selective advantage over gonochorism in such mating systems (Petersen 2006), but this pattern has only evolved in one clade in the Serranidae. Its rarity in other species known to have this mating system may be due to some form of phylogenetic inertia.

Several recent studies on other animal phyla mirror the polyphyletic evolution of various forms of hermaphroditism in response to exogenous factors, as we found for teleost fishes. Ophryotrocha worms exhibit multiple sexual patterns within single genera (dioecy, simultaneous and sequential hermaphroditism) (Dahlgren et al. 2001), and the incidence of hermaphroditism is labile in response to population density and its subsequent relationship to mating opportunities (Di bona et al. 2010). Similarly, barnacles (Cirripedia) and marine gastropods (e.g., Patellagastropoda, Heterobranchia, Caenogastropoda) each exhibit a diversity of patterns of sex allocation with independent, evolutionary transitions occurring repeatedly among lineages, driven by changes in population density or in size.
of the mating group (via local competition for mates and sperm) rather than driven by common ancestry (Collin et al. 2005; Yusa et al. 2012, 2013). These groups suggest that our results of high degrees of lability in the patterns of sex allocation within selected lineages of fishes may be general for a wide range of taxa.

Within lineages of teleosts that show a diversity of patterns of sex allocation, individuals maintain the ability for gonadal differentiation in any direction throughout their lifetime and can adjust their sex when it is likely to increase their potential for reproductive success under the particular social circumstances and environmental conditions they encounter (Munday et al. 2006a; Avise 2011). Such plasticity is evidenced by the fact that sex change can be induced in gonochoric species (Kiewek-Martínez et al. 2010) or protandry in protogynous species (Kuwamura et al. 2007) when in captivity. While sex change tends to be unidirectional in most groups, but some species and clades have evolved the capacity to change sex in either direction because their local social or environmental conditions can change dramatically and unpredictably in a way that favors repeated changes of sex. This suggests that the proximate mechanisms that control sex allocation and sex expression are sensitive to these conditions, and that individuals are able to assess their immediate environment and make “decisions” about the costs and benefits of changing sex, or not (Munday et al. 2010).

Do evolutionary transitions from hermaphroditism to gonochorism (or even between forms of hermaphroditism) require functional intermediates?

Although there appears to be ample evidence that other groups of plants and animals commonly show functional intermediates between hermaphroditism and gonochorism (Charlesworth and Charlesworth 1978; Lorenzi and Sella 2008; Barrett 2010; Avise 2011), we observe little evidence for such intermediate forms in fishes. Comparative phylogenetic analyses suggest that functionally intermediate sexual patterns are not required, or at least are not of long duration, during the transition between common patterns of sex allocation. Moreover, while it may be logical to hypothesize that a sexual pattern such as androdioecy, with mature simultaneous hermaphrodites and pure males, represents an intermediate evolutionary transition between simultaneous and protogynous hermaphroditism (Hastings and Petersen 1986; Sadovy and Domeier 2005; Avise and Mank 2009), patterns of evolutionary transformations in the Serranidae demonstrate that: (1) protogynous hermaphroditic and simultaneous hermaphroditic species are sister taxa with no extant intermediate form and (2) androdioecy (the functional intermediate between simultaneous hermaphroditism and protogyny) is derived from simultaneous hermaphroditism, and its evolution is unrelated to protogyny. These results are contrary to hypotheses arguing that gonochorism and synchronous hermaphroditism are evolutionary endpoints on a reproductive spectrum that includes intermediate mixed modalities (e.g., androdioecy, gynodioecy) (see Weeks et al. 2006; Avise and Mank 2009).

The nonrequirement of functional intermediates during transitions between gonochorism and hermaphroditism, or among various forms of hermaphroditism, in fishes becomes easier to visualize when one considers that diagnoses of sexual patterns in teleosts merely represent population-level integrations of individual responses. In reality, the phenotypic end states (e.g., ability to change sex) are already present within populations at the level of the individual, and changes in sex allocation patterns can occur rapidly when triggered by the appropriate social conditions (Munday et al. 2010). Clear evidence of this can be found in the fact that patterns of sex allocation within a single species can differ at opposite ends of the same reef (e.g., Thalassoma bifasciatum; Warner 1984) and that multiple patterns of sex allocation can be induced experimentally in species not known to do so under natural conditions (Tanaka et al. 1990; Kuwamura et al. 2002).

Why is sexuality so labile in teleost fishes compared with other vertebrate groups?

Throughout this article, we have shown how labile and diverse sexuality is within clades of fishes; this situation lies in stark contrast to the near ubiquity of gonochorism in the rest of the vertebrates. There are three reasons that have been given in the literature to account for this pattern, and they have to do with patterns of sexual differentiation, reproductive biology, and sex determination. First, it is possible that teleosts’ sexual lability is a product of inherent plasticity in gonadal differentiation and development that is absent in other vertebrates (Nakamura et al. 1998; Baroiller et al. 2009; Kobayashi et al. 2013). In both sexes of teleost fishes, the gonad is derived from the cortex of the gonadal primordium only, unlike other vertebrates in which the testis develops from the medulla (Devlin and Nagahama 2002). For that reason, bisexual juveniles are prevalent in many
groups of teleost fishes, independent of their eventual functional sexual pattern (D’Ancona 1949; Yamamoto 1969). Similarly, in both hermaphroditic and gonochoristic taxa, nonfunctional tissue of the nonfunctional sex is often present in adult fish and can be induced to develop under laboratory conditions (Kuwamura et al. 2007; Munday et al. 2010).

Second, hermaphroditism is more common in externally fertilizing clades of fishes, possibly because the fixed costs of changing sex are lower in species that do not have to produce specialized reproductive tracts for copulation and internal insemination (Warner 1978). The oviduct of externally fertilizing fishes is a simple, often transient, canal connecting the ovarian lumen with the urogenital opening, and may be occluded in nonspawning individuals (Hastings and Bortone 1980). Similarly, the vas deferens is often a simple structure carrying sperm directly from sperm sinuses to the tip of the genital papilla. Thus, the structures responsible for the delivery of gametes of externally fertilizing fishes are relatively simple, perhaps reducing the costs of functional transitions between the sexes. A final possibility to explain the extreme sexual lability of teleosts is the diversity and rapid turnover of sex-determining mechanisms in fishes compared with other vertebrates, which is a product of fishes’ dynamic genome (Devlin and Nagahama 2002; Mank et al. 2006; Mank and Avise 2009). None of these mechanisms is mutually exclusive, but in some combination these, and possibly other, mechanisms have led to increased lability in patterns of sex allocation within and among species. These patterns of sex allocation appear extremely responsive to selective forces determined by the ecological influences on the social and mating systems of these species.

Conclusions

This review demonstrates that within several diverse lineages of teleosts with at least some hermaphroditic species, patterns of sex allocation show a strong fit to models for the evolution of hermaphroditism and agree well with the SAM of sex change. This is especially true for transitions to and from gonochorism and protogyny. These models also appear to explain multiple, independent, evolutionary instances of protandry, androdioecy, and bidirectional sex change, although at least one group, the sparids, provide some ambiguous results that require further examination. The evolution of simultaneous hermaphroditism also appears adaptive where it appears in these hermaphroditic clades, although it is less clear what restricts the instances of this form of sexuality.

We found little evidence for phylogenetic inertia for a particular type of sex allocation in these groups, and there is a tight correlation between mating systems and sexual patterns. After over 40 years of fieldwork, the initial models of sex allocation proposed by Tomlinson, Ghiselin, Warner, Charnov, and subsequent authors continue to be robust, and the emergence of analyses with detailed phylogenies for many fish taxa has only strengthened their initial conclusions.

This review lends support to existing theories on the evolution of sex allocation in teleost fishes; however, many opportunities remain to challenge current paradigms and search for additional patterns. Perhaps the lowest hanging fruit occurs in the Tetraodontiformes, a group of fishes with a diversity of mating systems and reproductive patterns on par with hermaphroditic lineages but which lack conclusive evidence of functional hermaphroditism (Sadovy de Mitcheson and Liu 2008; but see Takamoto et al. 2003). Since tetraodontiform fishes are found in shallow, tropical habitats, studies that combine phylogenetic, behavioral, and life-history information are logistically feasible for testing theories on phylogenetic constraints in the evolution of sex-allocation in bony fishes. Alternatively, the sparids represent a challenging group to test predictions of the SAM for protandrous systems, both theoretically with several species possibly not fitting the predictions of sex-allocation theory, and logistically due to the difficulty of studying fishes common on deep, offshore habitats, with seasonal spawning, and a relatively low-degree of site fidelity.

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References


Evolution of hermaphroditism in teleosts


