Hermaphroditism in fishes: an annotated list of species, phylogeny, and mating system

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Abstract

Fewer than 1% of vertebrate species are hermaphroditic, and essentially all of these are fishes. Four types of hermaphroditism are known in fishes: simultaneous (or synchronous) hermaphroditism (SH), protandry (male-to-female sex change; PA), protogyny (female-to-male sex change; PG), and bidirectional sex change (BS or reversed sex change in protogynous species). Here we present an annotated list of hermaphroditic fish species from a comprehensive review and careful re-examination of all primary literature. We confirmed functional hermaphroditism in more than 450 species in 41 families of 17 teleost orders. PG is the most abundant type (305 species of 20 families), and the others are much less abundant, BS in 66 species of seven families, SH in 55 species of 13 families, and PA in 54 species of 14 families. The recently proposed phylogenetic tree indicated that SH and PA have evolved several times in not-closely related lineages of Teleostei but that PG (and BS) has evolved only in four lineages of Percomorpha. Examination of the relation between hermaphroditism type and mating system in each species mostly supported the size-advantage model that predicts the evolution of sequential hermaphroditism. Finally, intraspecific variations in sexual pattern are discussed in relation to population density, which may cause variation in mating system.

Keywords Bidirectional · Protandry · Protogyny · Sex change · Simultaneous hermaphroditism

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Introduction

Over one-half of the world's living vertebrates (> 60,000 species) are fishes (> 32,000 species; Nelson et al. 2016). Approximately 99% of all vertebrate species consist of separate-sex individuals (gonochorists), i.e., pure males and pure females. The other 1% of vertebrate species are hermaphroditic, and almost all of them are fishes (Avisé 2011; Ashman et al. 2014). Among hermaphroditic fishes, four major types of hermaphroditism are known (Sadovy de Mitcheson and Liu 2008; Munday et al. 2010): simultaneous (or synchronous) hermaphroditism (SH), protandry (PA), protogyny (PG), and bidirectional sex change (BS or reversed sex change in protogynous species; Kuwamura et al. 2014). Simultaneous hermaphrodites produce both mature eggs and sperm in their gonads at the same time, but self-fertilization rarely occurs in fishes (Avisé 2011). In sequential hermaphrodites, either male-to-female sex change (PA) or female-to-male sex change (PG) occurs during the lifetime of an individual. Reports on bidirectional sex change within a species have increased since the 1990s (Kuwamura and Nakashima 1998; Munday et al. 2010), mostly as reversed sex change in

protogynous species when observed in the field (Kuwamura et al. 2014, 2016a).

The evolution of hermaphroditism among animals has been explained by two major hypotheses: the low-density model for simultaneous hermaphroditism and the size-advantage model for sequential hermaphroditism (Ghiselin 1969, 1974). In low-density conditions, few mating opportunities are expected, and mating success will be much higher in simultaneous hermaphrodites than that in gonochorists if random mating occurs (Tomlinson 1966), although hermaphrodites suffer the energetic cost of maintaining two reproductive systems (Heath 1977). Self-fertilization further increases the benefits of simultaneous hermaphroditism under extreme low density with little opportunity to find conspecifics (Tomlinson 1966). In addition, simultaneous hermaphroditism is presumably favored by diminishing fitness return for the investment to one sexual function, e.g., owing to small mating groups or brood space limitation (Charnov 1982).

For sequential hermaphroditism, the size-advantage model (SA model) predicts that the occurrence and direction of sex change are determined by mating system, because the relation between reproductive success and body size of males depends on mating system, while reproductive success of females increases with growth irrespective of mating system (Warner 1975, 1984). For example, in species with random mating regardless of male body size, in which females do not have preference for large males and accept small ones, male reproductive success is not related to body size, and male-to-female sex change (PA) will be favored, because the reproductive success of small males is higher than that of females of the same size, and vice versa in large males and females. By contrast, in species with polygynous mating systems, in which large males monopolize females, male reproductive success sharply increases with growth, and female-to-male sex change (PG) will be favored, because large females can increase reproductive success by changing sex to male. Contrastingly, in species with size-assortative mating or group spawning by one female with multiple males (i.e., intense scramble-type sperm competition), in which reproductive success of males and females increases with growth in a similar fashion, gonochorism will evolve because of the cost of sex change (Warner 1975, 1984). Some mating systems with extensive sperm competition and size–fecundity skew will also reduce or eliminate the size advantage and result in a reduction or even a lack of sex change (Muñoz and Warner 2003, 2004). Bidirectional sex change has recently been regarded as a tactic to secure mating opportunities when mate-search (finding an opposite-sex individual) after the loss of partners is difficult or costly because of low density, and it is suggested to have derived from either protogynous (Kuwamura et al. 2014, 2016a) or gonochoristic ancestors (Sunobe et al. 2017). Large amounts

of evidence supporting the SA model have been reported, especially from coral reef fishes (Nakazono and Kuwamura 1987; Warner 1988; Munday et al. 2006; Sadovy de Mitcheson and Liu 2008; Kazancıoğlu and Alonzo 2010; Erisman et al. 2013). However, the mating systems of many other hermaphroditic fishes are still unknown.

Sadovy de Mitcheson and Liu (2008) published a comprehensive review of functional hermaphroditism in teleost fishes, providing family accounts with a genus-level list of 94 genera in 27 families of seven teleost orders (based on the classification of Nelson 2006) with confirmed functional hermaphroditism. They also listed 31 genera in 21 teleost families that have been suggested as hermaphroditic but not confirmed. Hermaphroditism has evolved in many different fish lineages, predominantly among tropical marine perciforms, in which hermaphroditism expression diversity is the greatest. However, because the sexual pattern and mating system are often highly variable even within a single genus or species (Munday et al. 2006), the genus-level list provided by Sadovy de Mitcheson and Liu (2008) is not sufficient to estimate the evolutionary patterns of sexuality. Although Devlin and Nagahama (2002) provided a list of 259 species in 25 teleost families, they did not make such a clear distinction between functional and non-functional hermaphroditism which is essential to evolutionary/ecological analyses.

The purpose of this study is to present an annotated species-level list of functional hermaphroditism in fishes, which will enable a wide range of interesting analyses, after a comprehensive review and careful re-examination of all primary literature. Frequencies of hermaphroditism in each family and order were summed up, and its distribution on the recently proposed phylogenetic tree (Betancur-R et al. 2017) was examined. Mating systems of hermaphroditic fish species were also reviewed, and the relation between the type of hermaphroditism in each species and its mating system was investigated to test the SA model. Finally, intraspecific variations in sexual pattern are discussed in relation to population density, which may cause variation in mating system.

Materials and methods

Construction of the database of hermaphroditic fishes. We searched original papers on hermaphroditic fish species using references of review papers (e.g., Nakazono and Kuwamura 1987; Devlin and Nagahama 2002; Sadovy de Mitcheson and Liu 2008) and by Internet searches (mainly by Google Scholar) entering keywords such as hermaphroditism, sex change, protogyny, and protandry along with names of known hermaphroditic taxa (orders/families/genera). For each species, we recorded type of hermaphroditism (SH, PA, PG, and BS), methods of confirmation (histology, aquarium or field observations, see below), mating system

(see below), habitat (e.g., deep sea, coral reef), reference, and remarks. Species name and habitat are based on Fish-Base (<https://www.fishbase.in>). The results were compiled into the list based on the fish classification system of Nelson et al. (2016). Then, to avoid overlooking any species, we conducted similar Internet searches for papers reporting hermaphroditism in each of the remaining families of fishes without known cases of hermaphroditism.

Table 1 is a simplified table in which only the type of hermaphroditism and mating system is shown, and detailed records and references are shown in Electronic supplementary material, Table S1 and S2, respectively. In each table, families and orders are arranged following the order of Nelson et al. (2016), and genera and species in alphabetical order within each family and genus, respectively.

To determine if hermaphroditism was confirmed or not in each species, we applied the criteria for functional hermaphroditism following Sadovy and Shapiro (1987) and Sadovy de Mitcheson and Liu (2008), i.e., detailed gonadal histological series ideally illustrated with photomicrographs that show various stages of sexual transition (as examples), simultaneous occurrence of mature testicular and ovarian tissues in gonads, or field or aquarium observations of gamete release and/or sexual characteristics (e.g., shape of urogenital papilla) in identified individuals. Moreover, histological observation on transition of gonad-associated structures could be used to determine the occurrence of sex change (Cole and Shapiro 1990; Sunobe et al. 2017), and microscopic observation of eggs and sperm is also useful to confirm sexual maturation. Species with suggested, but not confirmed functional hermaphroditism were also recorded (Table S1 with remarks, "?" indicates weak evidence), but excluded from Table 1.

Taxonomic, phylogenetic, and ecological distributions of hermaphroditism. Frequencies of each type of hermaphroditism, i.e., SH, PA, PG, and BS (reversed sex change), in each family and order were summed up and compared between marine and freshwater families. The phylogenetic tree of Betancur-R et al. (2017), which shows the relationship of major groups (ordinal or supraordinal taxa), was used to examine the distribution of each type of hermaphroditism.

Mating systems in hermaphroditic fishes. To test the SA model (Warner 1975), the relation between the type of hermaphroditism and mating system of each species was investigated. Based on the data cited in Table S1, we classified the mating systems into the following seven types (modified from Kuwamura 1997; Table 1).

1) Random mating: Females mate with males regardless of their body size, without continuing pair bond (i.e., close and lasting association between a male and female).

2) Non-size-assortative monogamy: Pair bonding of a male and a female, which has no preference for male size and accepts a smaller male.

3) Size-assortative monogamy: Pair bonding of a male and a female, in which both prefer larger mates, resulting in pairing of similar-sized mates.

4) Harem polygyny: A large male monopolizes a harem of females.

5) Male-territory-visiting polygamy: Females visit male territories to mate. Males may establish small territories during spawning time even within a multi-male group.

6) Group spawning: Spawning of a single female with multiple males occurs without continuous bonding usually in a spawning aggregation.

7) Spawning aggregation: We used this category when spawning aggregation has been reported, but the detailed mating system is unknown (e.g., neither male territory nor group spawning has been reported).

Facultative monogamy in polygamous species, which may frequently occur in low-density condition (Barlow 1984), is not shown in Table 1.

Results and discussion

Phylogeny and hermaphroditism. We confirmed functional hermaphroditism in more than 450 species of 156 genera in 41 families of 17 teleost orders (based on the classification of Nelson et al. 2016). In Table 1, species with confirmed functional hermaphroditism were listed, indicating the type of hermaphroditism (SH, PA, PG, and BS). A detailed and annotated list of hermaphroditic fish species including additional information and unconfirmed species is provided as Electronic supplementary material Table S1 with a complete reference list of more than 500 papers (S2). We found functional hermaphroditism in 461 species and all of them are teleosts (Infraclass Teleostei). Two types of hermaphroditism, i.e., PG and BS, are reported within a single species in 18 species (Table 1).

We found at least one hermaphroditic species in 41 families (9% of 470 families of Teleostei; Table 2). Percentage of hermaphroditic species in a family widely varied from 0.1% (2 of 1762 species in Cichlidae) to 100% (in both species of Giganturidae and Eginopsidae). Among fish families including over 30 species, the percentage was relatively high in Sparidae (84%), Scaridae (35%), Ipnopidae (28%), Lethrinidae (26%), Pomacanthidae (26%), Labridae (19%), Cirrhitidae (18%), and Serranidae (17%), although these percentages represented the lower limits because sexual patterns of all species have not always been investigated in each family.

PG was the most abundant hermaphroditism type (305 species, 66% of 461 hermaphroditic species), while other types were much less abundant, i.e., BS in 66 species (14%), SH in 55 species (12%), and PA in 54 species (12%) (Table 2). SH, PA, PG, and BS were the most abundant in

Table 1 List of hermaphroditic fish species and their mating systems. Order and family names are arranged following Nelson et al. (2016), and genus and species in alphabetical order within each family and genus, respectively

Order		Sexual pattern	Mating system
Family	Species		
Anguilliformes			
Muraenidae	<i>Gymnothorax griseus</i>	SH	
Muraenidae	<i>Gymnothorax pictus</i>	SH	
Muraenidae	<i>Gymnothorax thyrsoideus</i>	SH	
Muraenidae	<i>Rhinomuraena quaesita</i>	PA	
Clupeiformes			
Clupeidae	<i>Tenualosa macrura</i>	PA	
Clupeidae	<i>Tenualosa toli</i>	PA	
Cypriniformes			
Cobitidae	<i>Cobitis taenia</i>	PA, G	
Stomiiformes			
Gonostomatidae	<i>Cyclothone atraria</i>	PA	
Gonostomatidae	<i>Cyclothone microdon</i>	PA	
Gonostomatidae	<i>Gonostoma elongatum</i>	PA	
Gonostomatidae	<i>Sigmops bathyphilum</i>	PA	
Gonostomatidae	<i>Sigmops gracile</i>	PA	
Aulopiformes			
Ipnopidae	<i>Bathymicrops brevianalis</i>	SH	
Ipnopidae	<i>Bathymicrops regis</i>	SH	
Ipnopidae	<i>Bathypterois grallator</i>	SH	
Ipnopidae	<i>Bathypterois viridensis</i>	SH	
Ipnopidae	<i>Bathypterois quadrifilis</i>	SH, G	
Ipnopidae	<i>Bathypterois mediterraneus</i>	SH	
Ipnopidae	<i>Bathytrophops marionae</i>	SH	
Ipnopidae	<i>Ipnops agassizii</i>	SH	
Ipnopidae	<i>Ipnops meadi</i>	SH	
Giganturidae	<i>Gigantura chuni</i>	SH	
Giganturidae	<i>Gigantura indica</i>	SH, G	
Bathysauridae	<i>Bathysaurus ferox</i>	SH	
Chlorophthalmidae	<i>Chlorophthalmus agassizi</i>	SH	
Chlorophthalmidae	<i>Chlorophthalmus brasiliensis</i>	SH	
Chlorophthalmidae	<i>Parasudis truculenta</i>	SH	
Notosudidae	<i>Ahliesaurus brevis</i>	SH	
Scopelarchidae	<i>Benthalbella infans</i>	SH	
Scopelarchidae	<i>Scopelarchus guentheri</i>	SH	
Paralepididae	<i>Antopterus pharao</i>	SH	
Paralepididae	<i>Lestidium pseudosphyraenoides</i>	SH	
Alepisauridae	<i>Omosudis lowii</i>	SH	
Gobiiformes			
Gobiidae	<i>Coryphopterus alloides</i>	PG	
Gobiidae	<i>Coryphopterus dicrus</i>	PG	
Gobiidae	<i>Coryphopterus eidolon</i>	PG	
Gobiidae	<i>Coryphopterus glaucofraenum</i>	PG	MTV polygamy
Gobiidae	<i>Coryphopterus hyalinus</i>	PG	
Gobiidae	<i>Coryphopterus lipernes</i>	PG	
Gobiidae	<i>Coryphopterus personatus</i>	PG	
Gobiidae	<i>Coryphopterus thrux</i>	PG	
Gobiidae	<i>Coryphopterus urospilus</i>	PG	
Gobiidae	<i>Eviota epiphanes</i>	PG, BS	

Table 1 (continued)

Order		Sexual pattern	Mating system
Family	Species		
Gobiidae	<i>Fusigobius neophytus</i>	PG	MTV polygamy
Gobiidae	<i>Gobiodon erythropsilus</i>	BS	SA monogamy
Gobiidae	<i>Gobiodon histrio</i>	PG, BS	SA monogamy
Gobiidae	<i>Gobiodon micropus</i>	BS	SA monogamy
Gobiidae	<i>Gobiodon oculolineatus</i>	BS	SA monogamy
Gobiidae	<i>Gobiodon okinawae</i>	PG	SA monogamy
Gobiidae	<i>Gobiodon quinquestrigatus</i>	PG, BS	SA monogamy
Gobiidae	<i>Lythrypnus dalli</i>	PG, BS	MTV polygamy
Gobiidae	<i>Lythrypnus nesiotes</i>	PG	
Gobiidae	<i>Lythrypnus phorellus</i>	PG	
Gobiidae	<i>Lythrypnus pulchellus</i>	BS	
Gobiidae	<i>Lythrypnus spilus</i>	PG	
Gobiidae	<i>Lythrypnus zebra</i>	BS	MTV polygamy
Gobiidae	<i>Paragobiodon echinocephalus</i>	PG, BS	SA monogamy
Gobiidae	<i>Paragobiodon xanthosomus</i>	PG	SA monogamy
Gobiidae	<i>Priolepis akihitoi</i>	BS	
Gobiidae	<i>Priolepis borea</i>	BS	
Gobiidae	<i>Priolepis cincta</i>	BS	SA monogamy
Gobiidae	<i>Priolepis eugenius</i>	PG, BS	
Gobiidae	<i>Priolepis fallacincta</i>	BS	
Gobiidae	<i>Priolepis hipoliti</i>	PG, BS	
Gobiidae	<i>Priolepis inhaca</i>	BS	
Gobiidae	<i>Priolepis latifascima</i>	BS	
Gobiidae	<i>Priolepis semidoliata</i>	BS	SA monogamy
Gobiidae	<i>Rhinogobiops nicholsii</i>	PG	
Gobiidae	<i>Trimma annosum</i>	BS	
Gobiidae	<i>Trimma benjamini</i>	BS	
Gobiidae	<i>Trimma caesiura</i>	BS	
Gobiidae	<i>Trimma cana</i>	BS	
Gobiidae	<i>Trimma caudomaculatum</i>	BS	MTV polygamy
Gobiidae	<i>Trimma emeryi</i>	BS	
Gobiidae	<i>Trimma fangi</i>	BS	
Gobiidae	<i>Trimma flammeum</i>	BS	
Gobiidae	<i>Trimma flavatram</i>	BS	
Gobiidae	<i>Trimma fucatum</i>	BS	
Gobiidae	<i>Trimma gigantum</i>	BS	
Gobiidae	<i>Trimma grammistes</i>	BS	Harem
Gobiidae	<i>Trimma kudoii</i>	BS	
Gobiidae	<i>Trimma lantana</i>	BS	
Gobiidae	<i>Trimma macrophthalma</i>	BS	
Gobiidae	<i>Trimma maiandros</i>	BS	
Gobiidae	<i>Trimma marinae</i>	BS	
Gobiidae	<i>Trimma milta</i>	BS	
Gobiidae	<i>Trimma nasa</i>	BS	
Gobiidae	<i>Trimma naudei</i>	BS	
Gobiidae	<i>Trimma necopinum</i>	BS	
Gobiidae	<i>Trimma okinawae</i>	PG, BS	Harem
Gobiidae	<i>Trimma preclarum</i>	BS	
Gobiidae	<i>Trimma rubromaculatum</i>	BS	
Gobiidae	<i>Trimma sheppardi</i>	BS	

Table 1 (continued)

Order		Sexual pattern	Mating system
Family	Species		
Gobiidae	<i>Trimma stobbsi</i>	BS	
Gobiidae	<i>Trimma striatum</i>	BS	
Gobiidae	<i>Trimma tauroculum</i>	BS	
Gobiidae	<i>Trimma taylori</i>	BS	
Gobiidae	<i>Trimma unisquamis</i>	BS	
Gobiidae	<i>Trimma yanagitai</i>	BS	
Uncertain in ovalentaria			
Pomacentridae	<i>Amphiprion akallopisos</i>	PA	NSA monogamy
Pomacentridae	<i>Amphiprion bicinctus</i>	PA	NSA monogamy
Pomacentridae	<i>Amphiprion clarkii</i>	PA	NSA monogamy
Pomacentridae	<i>Amphiprion frenatus</i>	PA	NSA monogamy
Pomacentridae	<i>Amphiprion melanopus</i>	PA	NSA monogamy
Pomacentridae	<i>Amphiprion ocellaris</i>	PA	NSA monogamy
Pomacentridae	<i>Amphiprion percula</i>	PA	NSA monogamy
Pomacentridae	<i>Amphiprion perideraion</i>	PA	NSA monogamy
Pomacentridae	<i>Amphiprion polymnus</i>	PA	NSA monogamy
Pomacentridae	<i>Amphiprion sandaracinos</i>	PA	NSA monogamy
Pomacentridae	<i>Dascyllus ariuanus</i>	PG, BS, G	Harem, MTV polygamy
Pomacentridae	<i>Dascyllus carneus</i>	PG	Harem, MTV polygamy
Pomacentridae	<i>Dascyllus flavicaudus</i>	PG, G	Harem, MTV polygamy
Pomacentridae	<i>Dascyllus marginatus</i>	PG	Harem, MTV polygamy
Pomacentridae	<i>Dascyllus melanurus</i>	PG, G	Harem, MTV polygamy
Pomacentridae	<i>Dascyllus reticulatus</i>	PG, G	Harem, MTV polygamy
Pseudochromidae	<i>Anisochromis straussi</i>	PG	
Pseudochromidae	<i>Ogilbyina queenslandiae</i>	PG	
Pseudochromidae	<i>Pseudochromis flavivertex</i>	BS	
Pseudochromidae	<i>Pseudochromis aldabraensis</i>	BS	
Pseudochromidae	<i>Pseudochromis cyanotaenia</i>	BS	
Pseudochromidae	<i>Pictichromis porphyrea</i>	BS	
Cichliformes			
Cichlidae	<i>Satanoperca jurupari</i>	SH	
Cichlidae	<i>Metriaclima cf. livingstoni</i>	PG	MTV polygamy
Cyprinodontiformes			
Rivulidae	<i>Kryptolebias hermaphroditus</i>	SH, G	
Rivulidae	<i>Kryptolebias marmoratus</i>	SH, G	
Rivulidae	<i>Kryptolebias ocellatus</i>	SH, G	
Poeciliidae	<i>Xiphophorus helleri</i>	PG, G	
Synbranchiformes			
Synbranchidae	<i>Monopterus albus</i>	PG	MTV polygamy
Synbranchidae	<i>Monopterus boueti</i>	PG	
Synbranchidae	<i>Ophisternon bengalense</i>	PG	
Synbranchidae	<i>Synbranchus marmoratus</i>	PG	
Trachiniformes			
Pinguipedidae	<i>Parapercis clathrata</i>	PG	
Pinguipedidae	<i>Parapercis colias</i>	PG	
Pinguipedidae	<i>Parapercis cylindrica</i>	PG	Harem
Pinguipedidae	<i>Parapercis hexophtalma</i>	PG	Harem
Pinguipedidae	<i>Parapercis nebulosa</i>	PG	
Pinguipedidae	<i>Parapercis snyderi</i>	PG	Harem
Pinguipedidae	<i>Parapercis xanthozona</i>	PG	

Table 1 (continued)

Order		Sexual pattern	Mating system
Family	Species		
Trichonotidae	<i>Trichonotus filamentosus</i>	PG	
Creediidae	<i>Crystallodytes cookei</i>	PA	
Creediidae	<i>Limnichthys fasciatus</i>	PA	
Creediidae	<i>Limnichthys nitidus</i>	PA	
Labriformes			
Labridae	<i>Achoerodus gouldii</i>	PG	
Labridae	<i>Achoerodus viridis</i>	PG	
Labridae	<i>Anampses geographicus</i>	PG	
Labridae	<i>Bodianus axillaris</i>	PG	
Labridae	<i>Bodianus diplotaenia</i>	PG	MTV polygamy
Labridae	<i>Bodianus eclancheri</i>	PG	GSP
Labridae	<i>Bodianus frenchii</i>	PG	
Labridae	<i>Bodianus mesothorax</i>	PG	SPA
Labridae	<i>Bodianus rufus</i>	PG	Harem
Labridae	<i>Cheilinus chlorurus</i>	PG	
Labridae	<i>Cheilinus diagrammus</i>	PG	
Labridae	<i>Cheilinus fasciatus</i>	PG	Harem
Labridae	<i>Cheilinus trilobatus</i>	PG	Harem, MTV polygamy
Labridae	<i>Cheilinus undulatus</i>	PG	MTV polygamy
Labridae	<i>Choerodon azurio</i>	PG	
Labridae	<i>Choerodon cauteroma</i>	PG	
Labridae	<i>Choerodon cyanodus</i>	PG	
Labridae	<i>Choerodon fasciatus</i>	PG	
Labridae	<i>Choerodon graphicus</i>	PG	
Labridae	<i>Choerodon rubescens</i>	PG	
Labridae	<i>Choerodon schoenleinii</i>	PG	
Labridae	<i>Choerodon venustus</i>	PG	
Labridae	<i>Cirrhilabrus temmincki</i>	PG	MTV polygamy
Labridae	<i>Clepticus parrae</i>	PG	SPA
Labridae	<i>Coris auricularis</i>	PG	
Labridae	<i>Coris dorsomacula</i>	PG	Harem
Labridae	<i>Coris gaimard</i>	PG	MTV polygamy
Labridae	<i>Coris julis</i>	PG	MTV polygamy
Labridae	<i>Coris variegata</i>	PG	
Labridae	<i>Decodon melasma</i>	PG	
Labridae	<i>Epibulus insidiator</i>	PG	Harem, MTV polygamy
Labridae	<i>Gomphosus varius</i>	PG	MTV polygamy
Labridae	<i>Halichoeres bivittatus</i>	PG	MTV polygamy, GSP
Labridae	<i>Halichoeres garnoti</i>	PG	MTV polygamy
Labridae	<i>Halichoeres maculipinna</i>	PG	MTV polygamy
Labridae	<i>Halichoeres margaritaceus</i>	PG	Harem
Labridae	<i>Halichoeres marginatus</i>	PG	MTV polygamy, GSP
Labridae	<i>Halichoeres melanochir</i>	PG	MTV polygamy
Labridae	<i>Halichoeres melanurus</i>	PG	MTV polygamy
Labridae	<i>Halichoeres miniatus</i>	PG	Harem
Labridae	<i>Halichoeres nebulosus</i>	PG	
Labridae	<i>Halichoeres pictus</i>	PG	
Labridae	<i>Halichoeres poeyi</i>	PG	
Labridae	<i>Halichoeres radiatus</i>	PG	
Labridae	<i>Halichoeres scapularis</i>	PG	

Table 1 (continued)

Order		Sexual pattern	Mating system
Family	Species		
Labridae	<i>Halichoeres semicinctus</i>	PG	MTV polygamy, GSP
Labridae	<i>Halichoeres tenuispinnis</i>	PG	MTV polygamy
Labridae	<i>Halichoeres trimaculatus</i>	PG, BS	MTV polygamy, GSP
Labridae	<i>Hemigymnus melapterus</i>	PG	
Labridae	<i>Hologymnosus annulatus</i>	PG	
Labridae	<i>Iniistius dea</i>	PG	
Labridae	<i>Iniistius geisha</i>	PG	
Labridae	<i>Iniistius pentadactylus</i>	PG	Harem
Labridae	<i>Labrichthys unilineatus</i>	PG	Harem
Labridae	<i>Labroides dimidiatus</i>	PG, BS	Harem
Labridae	<i>Labrus bergylta</i>	PG	
Labridae	<i>Labrus merula</i>	PG	
Labridae	<i>Labrus mixtus</i>	PG	
Labridae	<i>Labrus viridis</i>	PG	
Labridae	<i>Lachnolaimus maximus</i>	PG	Harem
Labridae	<i>Macropharyngodon moyeri</i>	PG	Harem
Labridae	<i>Notolabrus celidotus</i>	PG	MTV polygamy
Labridae	<i>Notolabrus gymnogenis</i>	PG	
Labridae	<i>Notolabrus parilus</i>	PG	
Labridae	<i>Notolabrus tetricus</i>	PG	MTV polygamy
Labridae	<i>Ophthalmolepis lineolatus</i>	PG	
Labridae	<i>Parajulis poecilepterus</i>	PG	GSP
Labridae	<i>Pictilabrus laticlavus</i>	PG	MTV polygamy
Labridae	<i>Pseudocheilinus ataenia</i>	PG	
Labridae	<i>Pseudocheilinus evanidus</i>	PG	
Labridae	<i>Pseudocheilinus hexataenia</i>	PG	Harem
Labridae	<i>Pseudolabrus guentheri</i>	PG	
Labridae	<i>Pseudolabrus rubicundus</i>	PG	MTV polygamy
Labridae	<i>Pseudolabrus sieboldi</i>	PG	MTV polygamy
Labridae	<i>Pteragogus aurigarius</i>	PG	MTV polygamy
Labridae	<i>Semicossyphus darwini</i>	PG	
Labridae	<i>Semicossyphus pulcher</i>	PG	MTV polygamy
Labridae	<i>Semicossyphus reticulatus</i>	PG	
Labridae	<i>Stethojulis balteata</i>	PG	
Labridae	<i>Stethojulis interrupta</i>	PG	MTV polygamy
Labridae	<i>Stethojulis strigiventer</i>	PG	
Labridae	<i>Stethojulis trilineata</i>	PG	MTV polygamy
Labridae	<i>Suezichthys ornatus</i>	PG	MTV polygamy
Labridae	<i>Symphodus melanocercus</i>	PG	MTV polygamy
Labridae	<i>Symphodus tinca</i>	PG, G	MTV polygamy
Labridae	<i>Thalassoma bifasciatum</i>	PG	MTV polygamy, GSP
Labridae	<i>Thalassoma cupido</i>	PG	MTV polygamy, GSP
Labridae	<i>Thalassoma duperrey</i>	PG	MTV polygamy, GSP
Labridae	<i>Thalassoma hardwicke</i>	PG	MTV polygamy, GSP
Labridae	<i>Thalassoma janssenii</i>	PG	MTV polygamy, GSP
Labridae	<i>Thalassoma lucasanum</i>	PG	MTV polygamy, GSP
Labridae	<i>Thalassoma lunare</i>	PG	MTV polygamy, GSP
Labridae	<i>Thalassoma lutescens</i>	PG	MTV polygamy, GSP
Labridae	<i>Thalassoma pavo</i>	PG	MTV polygamy, GSP
Labridae	<i>Thalassoma purpurum</i>	PG	

Table 1 (continued)

Order		Sexual pattern	Mating system
Family	Species		
Labridae	<i>Thalassoma quinquevittatum</i>	PG	MTV polygamy, GSP
Labridae	<i>Xyrichtys martinicensis</i>	PG	Harem
Labridae	<i>Xyrichtys novacula</i>	PG	Harem
Odacidae	<i>Odax pullus</i>	PG	
Scaridae	<i>Calotomus carolinus</i>	PG	MTV polygamy
Scaridae	<i>Calotomus japonicus</i>	PG	MTV polygamy
Scaridae	<i>Calotomus spinidens</i>	PG	MTV polygamy
Scaridae	<i>Cetoscarus bicolor</i>	PG	
Scaridae	<i>Chlorurus sordidus</i>	PG	MTV polygamy
Scaridae	<i>Chlorurus spilurus</i>	PG	
Scaridae	<i>Cryptotomus roseus</i>	PG	MTV polygamy
Scaridae	<i>Hipposcarus harid</i>	PG	
Scaridae	<i>Scarus ferrugineus</i>	PG	
Scaridae	<i>Scarus festivus</i>	PG	
Scaridae	<i>Scarus forsteni</i>	PG	MTV polygamy
Scaridae	<i>Scarus frenatus</i>	PG	Harem
Scaridae	<i>Scarus ghobban</i>	PG	
Scaridae	<i>Scarus globiceps</i>	PG	MTV polygamy, GSP
Scaridae	<i>Scarus iseri</i>	PG	Harem, GSP
Scaridae	<i>Scarus niger</i>	PG	MTV polygamy, GSP
Scaridae	<i>Scarus oviceps</i>	PG	MTV polygamy
Scaridae	<i>Scarus psittacus</i>	PG	MTV polygamy
Scaridae	<i>Scarus rivulatus</i>	PG	MTV polygamy
Scaridae	<i>Scarus rubroviolaceus</i>	PG	
Scaridae	<i>Scarus russelii</i>	PG	
Scaridae	<i>Scarus scaber</i>	PG	
Scaridae	<i>Scarus schlegeli</i>	PG	MTV polygamy
Scaridae	<i>Scarus spinus</i>	PG	
Scaridae	<i>Scarus taeniopterus</i>	PG	
Scaridae	<i>Scarus tricolor</i>	PG	
Scaridae	<i>Scarus vetula</i>	PG	Harem, MTV polygamy
Scaridae	<i>Scarus viridifucatus</i>	PG	
Scaridae	<i>Sparisoma atomarium</i>	PG	Harem
Scaridae	<i>Sparisoma aurofrenatum</i>	PG	Harem
Scaridae	<i>Sparisoma chrysopteron</i>	PG	MTV polygamy
Scaridae	<i>Sparisoma cretense</i>	PG, G	Harem
Scaridae	<i>Sparisoma radians</i>	PG	Harem, MTV polygamy, GSP
Scaridae	<i>Sparisoma rubripinne</i>	PG	MTV polygamy, GSP
Scaridae	<i>Sparisoma viride</i>	PG	MTV polygamy
Perciformes			
Centropomidae	<i>Centropomus undecimalis</i>	PA	
Latidae	<i>Lates calcarifer</i>	PA	
Polynemidae	<i>Galeoides decadactylus</i>	PA, G	
Polynemidae	<i>Filimanus heptadactyla</i>	SH, G	
Polynemidae	<i>Polydactylus macrochir</i>	PA	
Polynemidae	<i>Polydactylus microstomus</i>	SH, G	
Polynemidae	<i>Polydactylus quadrifilis</i>	PA	
Terapontidae	<i>Bidyanus bidyanus</i>	PA	
Terapontidae	<i>Mesopristes cancellatus</i>	PA	
Serranidae (Epinephelinae)	<i>Cephalopholis argus</i>	PG	Harem

Table 1 (continued)

Order		Sexual pattern	Mating system
Family	Species		
Serranidae (Epinephelinae)	<i>Cephalopholis boenak</i>	PG, BS	
Serranidae (Epinephelinae)	<i>Cephalopholis cruentata</i>	PG	Harem
Serranidae (Epinephelinae)	<i>Cephalopholis cyanostigma</i>	PG	Harem
Serranidae (Epinephelinae)	<i>Cephalopholis fulva</i>	PG	Harem
Serranidae (Epinephelinae)	<i>Cephalopholis hemistiktos</i>	PG	Harem
Serranidae (Epinephelinae)	<i>Cephalopholis miniata</i>	PG	Harem
Serranidae (Epinephelinae)	<i>Cephalopholis panamensis</i>	PG	Harem
Serranidae (Epinephelinae)	<i>Cephalopholis taeniops</i>	PG	
Serranidae (Epinephelinae)	<i>Cephalopholis urodeta</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus adscensionis</i>	PG	Harem
Serranidae (Epinephelinae)	<i>Epinephelus aeneus</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus akaara</i>	PG, BS	
Serranidae (Epinephelinae)	<i>Epinephelus andersoni</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus bruneus</i>	PG, BS	
Serranidae (Epinephelinae)	<i>Epinephelus chlorostigma</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus coioides</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus diacanthus</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus drummondhayi</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus fasciatus</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus fuscoguttatus</i>	PG	SPA
Serranidae (Epinephelinae)	<i>Epinephelus guttatus</i>	PG	SPA
Serranidae (Epinephelinae)	<i>Epinephelus itajara</i>	PG, G	GSP
Serranidae (Epinephelinae)	<i>Epinephelus labriformis</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus malabaricus</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus marginatus</i>	PG	MTV polygamy
Serranidae (Epinephelinae)	<i>Epinephelus merra</i>	PG	SPA
Serranidae (Epinephelinae)	<i>Epinephelus morio</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus ongus</i>	PG	SPA
Serranidae (Epinephelinae)	<i>Epinephelus rivulatus</i>	PG	
Serranidae (Epinephelinae)	<i>Epinephelus striatus</i>	PG, G	GSP
Serranidae (Epinephelinae)	<i>Epinephelus tauvina</i>	PG	
Serranidae (Epinephelinae)	<i>Hyporthodus flavolimatus</i>	PG	
Serranidae (Epinephelinae)	<i>Hyporthodus niveatus</i>	PG	
Serranidae (Epinephelinae)	<i>Hyporthodus quernus</i>	PG	
Serranidae (Epinephelinae)	<i>Mycteroperca bonaci</i>	PG	
Serranidae (Epinephelinae)	<i>Mycteroperca interstitialis</i>	PG	
Serranidae (Epinephelinae)	<i>Mycteroperca microlepis</i>	PG	SPA
Serranidae (Epinephelinae)	<i>Mycteroperca olfax</i>	PG	SPA
Serranidae (Epinephelinae)	<i>Mycteroperca phenax</i>	PG	SPA
Serranidae (Epinephelinae)	<i>Mycteroperca rubra</i>	PG	SPA
Serranidae (Epinephelinae)	<i>Mycteroperca venenosa</i>	PG	GSP
Serranidae (Epinephelinae)	<i>Plectropomus laevis</i>	PG	
Serranidae (Epinephelinae)	<i>Plectropomus leopardus</i>	PG	SPA
Serranidae (Epinephelinae)	<i>Plectropomus maculatus</i>	PG	
Serranidae (Serraninae)	<i>Bullisichthys caribbaeus</i>	SH	
Serranidae (Serraninae)	<i>Centropristis striata</i>	PG	
Serranidae (Serraninae)	<i>Centropristis ocyurus</i>	PG	
Serranidae (Serraninae)	<i>Chelidoperca hirundinacea</i>	PG	
Serranidae (Serraninae)	<i>Diplectrum bivittatum</i>	SH	
Serranidae (Serraninae)	<i>Diplectrum formosum</i>	SH	

Table 1 (continued)

Order		Sexual pattern	Mating system
Family	Species		
Serranidae (Serraninae)	<i>Diplectrum macropoma</i>	SH	
Serranidae (Serraninae)	<i>Diplectrum pacificum</i>	SH	
Serranidae (Serraninae)	<i>Diplectrum rostrum</i>	SH	
Serranidae (Serraninae)	<i>Hypoplectrus aberrans</i>	SH	SA monogamy
Serranidae (Serraninae)	<i>Hypoplectrus chlorurus</i>	SH	SA monogamy
Serranidae (Serraninae)	<i>Hypoplectrus nigricans</i>	SH	SA monogamy
Serranidae (Serraninae)	<i>Hypoplectrus puella</i>	SH	SA monogamy
Serranidae (Serraninae)	<i>Hypoplectrus unicolor</i>	SH	SA monogamy
Serranidae (Serraninae)	<i>Paralabrax maculatofasciatus</i>	PG, G	
Serranidae (Serraninae)	<i>Serraniculus pumilio</i>	SH	
Serranidae (Serraninae)	<i>Serranus annularis</i>	SH	
Serranidae (Serraninae)	<i>Serranus atricauda</i>	SH	
Serranidae (Serraninae)	<i>Serranus auriga</i>	SH	
Serranidae (Serraninae)	<i>Serranus baldwini</i>	SH	Harem
Serranidae (Serraninae)	<i>Serranus cabrilla</i>	SH	
Serranidae (Serraninae)	<i>Serranus hepatus</i>	SH	
Serranidae (Serraninae)	<i>Serranus phoebe</i>	SH	
Serranidae (Serraninae)	<i>Serranus psittacinus</i>	SH	Harem
Serranidae (Serraninae)	<i>Serranus scriba</i>	SH	
Serranidae (Serraninae)	<i>Serranus subligarius</i>	SH	SA monogamy
Serranidae (Serraninae)	<i>Serranus tabacarius</i>	SH	SA monogamy
Serranidae (Serraninae)	<i>Serranus tigrinus</i>	SH	SA monogamy
Serranidae (Serraninae)	<i>Serranus tortugarum</i>	SH	SA monogamy
Serranidae (Grammistini)	<i>Pseudogramma gregoryi</i>	SH	
Serranidae (Grammistini)	<i>Rypticus saponaceus</i>	PG	
Serranidae (Grammistini)	<i>Rypticus subbifrenatus</i>	PG	
Serranidae (Anthiinae)	<i>Anthias anthias</i>	PG	
Serranidae (Anthiinae)	<i>Anthias nicholsi</i>	PG	
Serranidae (Anthiinae)	<i>Anthias noeli</i>	PG	
Serranidae (Anthiinae)	<i>Baldwinella vivanus</i>	PG	
Serranidae (Anthiinae)	<i>Hemanthias leptus</i>	PG	
Serranidae (Anthiinae)	<i>Hemanthias peruanus</i>	PG	
Serranidae (Anthiinae)	<i>Hypoplectrodes huntii</i>	PG	
Serranidae (Anthiinae)	<i>Hypoplectrodes maccullochi</i>	PG	
Serranidae (Anthiinae)	<i>Pronotogrammus martinicensis</i>	PG	
Serranidae (Anthiinae)	<i>Pseudanthias conspicuus</i>	PG	
Serranidae (Anthiinae)	<i>Pseudanthias elongatus</i>	PG	
Serranidae (Anthiinae)	<i>Pseudanthias pleurotaenia</i>	PG	
Serranidae (Anthiinae)	<i>Pseudanthias rubrizonatus</i>	PG	
Serranidae (Anthiinae)	<i>Pseudanthias squamipinnis</i>	PG	MTV polygamy
Serranidae (Anthiinae)	<i>Sacura margaritacea</i>	PG	
Pomacanthidae	<i>Centropyge acanthops</i>	PG, BS	
Pomacanthidae	<i>Centropyge bicolor</i>	PG	Harem
Pomacanthidae	<i>Centropyge ferrugata</i>	PG, BS	Harem
Pomacanthidae	<i>Centropyge fisheri</i>	PG, BS	
Pomacanthidae	<i>Centropyge flavissimus</i>	BS	Harem
Pomacanthidae	<i>Centropyge heraldi</i>	PG	Harem
Pomacanthidae	<i>Centropyge interruptus</i>	PG	Harem
Pomacanthidae	<i>Centropyge multispinus</i>	PG	
Pomacanthidae	<i>Centropyge potteri</i>	PG	Harem

Table 1 (continued)

Order		Sexual pattern	Mating system
Family	Species		
Pomacanthidae	<i>Centropyge tibicen</i>	PG	Harem
Pomacanthidae	<i>Centropyge vrolicki</i>	PG	Harem
Pomacanthidae	<i>Chaetodontoplus septentrionalis</i>	PG	Harem
Pomacanthidae	<i>Genicanthus bellus</i>	PG	
Pomacanthidae	<i>Genicanthus caudovittatus</i>	PG	Harem
Pomacanthidae	<i>Genicanthus lamarck</i>	PG	Harem
Pomacanthidae	<i>Genicanthus melanospilos</i>	PG	Harem
Pomacanthidae	<i>Genicanthus personatus</i>	PG	Harem
Pomacanthidae	<i>Genicanthus semifasciatus</i>	PG	Harem
Pomacanthidae	<i>Genicanthus watanabei</i>	PG	
Pomacanthidae	<i>Holacanthus passer</i>	PG, G	Harem
Pomacanthidae	<i>Holacanthus tricolor</i>	PG	Harem
Pomacanthidae	<i>Pomacanthus zonipectus</i>	PG	
Pomacanthidae	<i>Apothemichthys trimaculatus</i>	PG	
Malacanthidae	<i>Malacanthus plumieri</i>	PG	Harem
Cirrhitidae	<i>Amblycirrhitus pinos</i>	PG	
Cirrhitidae	<i>Cirrhitichthys aprinus</i>	PG	Harem
Cirrhitidae	<i>Cirrhitichthys aureus</i>	PG, BS	
Cirrhitidae	<i>Cirrhitichthys falco</i>	PG, BS	Harem
Cirrhitidae	<i>Cirrhitichthys oxycephalus</i>	PG	Harem
Cirrhitidae	<i>Neocirrhites armatus</i>	PG	Harem
Eleginopsidae	<i>Eleginops maclovinus</i>	PA	
Scorpaeniformes			
Platycephalidae	<i>Cociella crocodila</i>	PA	
Platycephalidae	<i>Inegocia japonica</i>	PA	Random mating
Platycephalidae	<i>Kumococius rodericensis</i>	PA	
Platycephalidae	<i>Onigocia macrolepis</i>	PA	
Platycephalidae	<i>Platycephalus</i> sp.	PA	Random mating
Platycephalidae	<i>Sugggrundus meerdervoorti</i>	PA	
Platycephalidae	<i>Thysanophrys celebica</i>	PA	Random mating
Scorpaenidae	<i>Caracanthus unipinna</i>	PG	Harem
Moroniformes			
Moronidae	<i>Morone saxatilis</i>	PA	
Spariformes			
Nemipteridae	<i>Scolopsis monogramma</i>	PG	
Nemipteridae	<i>Scolopsis taenioptera</i>	PG	
Lethrinidae	<i>Lethrinus nebulosus</i>	PG, G	
Lethrinidae	<i>Lethrinus genivittatus</i>	PG	
Lethrinidae	<i>Lethrinus lentjan</i>	PG	
Lethrinidae	<i>Lethrinus variegatus</i>	PG	
Lethrinidae	<i>Lethrinus miniatus</i>	PG	
Lethrinidae	<i>Lethrinus rubrioperculatus</i>	PG	
Lethrinidae	<i>Lethrinus atkinsoni</i>	PG	
Lethrinidae	<i>Lethrinus harak</i>	PG	
Lethrinidae	<i>Lethrinus ornatus</i>	PG	
Lethrinidae	<i>Lethrinus ravus</i>	PG	
Sparidae	<i>Acanthopagrus australis</i>	PA	
Sparidae	<i>Acanthopagrus berda</i>	PA	SPA
Sparidae	<i>Acanthopagrus schlegelii</i>	PA	
Sparidae	<i>Acanthopagrus latus</i>	PA	

Table 1 (continued)

Order		Sexual pattern	Mating system
Family	Species		
Sparidae	<i>Calamus leucosteus</i>	PG	
Sparidae	<i>Chrysoblephus cristiceps</i>	PG	
Sparidae	<i>Chrysoblephus puniceus</i>	PG	
Sparidae	<i>Chrysoblephus laticeps</i>	PG	
Sparidae	<i>Dentex gibbosus</i>	PG	
Sparidae	<i>Dentex tumifrons</i>	PG	
Sparidae	<i>Diplodus annularis</i>	PA, G	
Sparidae	<i>Diplodus capensis</i>	PA, G	
Sparidae	<i>Diplodus puntazzo</i>	PA, G	
Sparidae	<i>Diplodus sargus</i>	PA, G	
Sparidae	<i>Diplodus vulgaris</i>	PA, G	
Sparidae	<i>Lithognathus mormyrus</i>	PA, G	
Sparidae	<i>Pagellus acarne</i>	PA, G	
Sparidae	<i>Pagellus bogaraveo</i>	PA, G	
Sparidae	<i>Pagellus erythrinus</i>	PG	
Sparidae	<i>Pagrus auriga</i>	PG	
Sparidae	<i>Pagrus caeruleostictus</i>	PG	
Sparidae	<i>Pagrus ehrenbergii</i>	PG, G	
Sparidae	<i>Pagrus major</i>	PG, G	
Sparidae	<i>Pagrus pagrus</i>	PG	
Sparidae	<i>Rhabdosargus sarba</i>	PA, G	
Sparidae	<i>Sarpa salpa</i>	PA, G	SPA
Sparidae	<i>Sparidentex hasta</i>	PA	
Sparidae	<i>Sparus aurata</i>	PA	GSP
Sparidae	<i>Spicara chryselis</i>	PG	
Sparidae	<i>Spicara smaris</i>	PG	
Sparidae	<i>Spicara maena</i>	PG	
Sparidae	<i>Spondylisoma cantharus</i>	PG	
Tetraodontiformes			
Balistidae	<i>Sufflamen chrysopterus</i>	PG	Harem

SH simultaneous hermaphroditism, PA protandry, PG protogyny, BS bidirectional sex change or reversed sex change in protogynous species, G gonochorism, SA monogamy size-assortative monogamy, NSA monogamy non-size-assortative monogamy, Harem harem polygyny, MTV polygamy male-territory-visiting polygamy, GSP group spawning, SPA spawning aggregation unknown detailed mating system, blank unknown. Facultative monogamy in polygamous species is not shown. If intraspecific variation has been reported in sexual pattern or mating system, two or more types are shown. Detailed data of each species and references are given in Table S1 and S2, respectively

Serranidae, Sparidae, Labridae, and Gobiidae, respectively (26, 16, 98, and 50 spp., respectively). Most cases of BS in Gobiidae have been determined by gonad histology or aquarium experiments (e.g., Sunobe et al. 2017; Table S1), and the frequency of each sex change direction in the field is known only in a few species (Kuwamura et al. 1994; Manabe et al. 2007).

Three types of hermaphroditism were found in Pomacentridae (PA, PG, and BS) and Serranidae (SH, PG, and BS) (Table 2), while two types were found in Muraenidae and Polynemidae (SH and PA), Cichlidae (SH and PG), Sparidae (PA and PG), and Gobiidae, Pseudochromidae, Labridae, Pomacanthidae, and Cirrhitidae (PG and BS). This indicated that different types of hermaphroditism have appeared in

different lineages repeatedly (see Mank et al. 2006), and the sexual pattern is often highly variable in expression within a single family.

The frequency of hermaphroditic fish families in each order is presented in Table 3. We found hermaphrodites in 17 orders (27% of 63 orders of Teleostei). Two families in Series Ovalentaria, Pomacentridae and Pseudochromidae, are not classified into orders by Nelson et al. (2016), but were counted as belonging to the same order here, for convenience. Among 17 orders, PG was the most abundant (20 families, 49% of 41 hermaphroditic families), BS the least abundant (7 families, 17%), and SH and PA had similar abundances (13 and 14 families, 32% and 34%, respectively). The tendency was somewhat different from that of

Table 2 Frequency of hermaphroditic fish species in each family. Order and family names are arranged following Nelson et al. (2016). Summed up from Table 1

Order	Family	Number of hermaphroditic species						Total number of species	Habitat**
		SH	PA	PG	BS	Total	%*		
Anguilliformes	Muraenidae	3	1	0	0	4	2.0	200	M
Clupeiformes	Clupeidae	0	2	0	0	2	0.9	218	M
Cypriniformes	Cobitidae	0	1	0	0	1	0.5	195	F
Stomiiformes	Gonostomatidae	0	5	0	0	5	16.1	31	M
Aulopiformes	Ipnopidae	9	0	0	0	9	28.1	32	M
	Giganturidae	2	0	0	0	2	100.0	2	M
	Bathysauridae	1	0	0	0	1	50.0	2	M
	Chlorophthalmidae	3	0	0	0	3	17.6	17	M
	Notosudidae	1	0	0	0	1	5.9	17	M
	Scopelarchidae	2	0	0	0	2	11.1	18	M
	Paralepididae	1	0	0	0	1	3.7	27	M
	Alepisauridae	1	0	0	0	1	11.1	9	M
Gobiiformes	Gobiidae	0	0	24	50	66	4.9	1359	M(&F)
Uncertain in ovalentaria	Pomacentridae	0	10	6	1	16	4.1	387	M
	Pseudochromidae	0	0	2	4	6	3.9	152	M
Cichliformes	Cichlidae	1	0	1	0	2	0.1	1762	F
Cyprinodontiformes	Rivulidae	3	0	0	0	3	0.8	370	F
	Poeciliidae	0	0	1	0	1	0.3	353	F
Synbranchiformes	Synbranchidae	0	0	4	0	4	17.4	23	F
Trachiniformes	Pinguipedidae	0	0	7	0	7	8.5	82	M
	Trichonotidae	0	0	1	0	1	10.0	10	M
	Creediidae	0	3	0	0	3	16.7	18	M
Labriiformes	Labridae	0	0	98	2	98	18.9	519	M
	Odacidae	0	0	1	0	1	8.3	12	M
	Scaridae	0	0	35	0	35	35.4	99	M
Perciformes	Centropomidae	0	1	0	0	1	8.3	12	M&F
	Latidae	0	1	0	0	1	7.7	13	M&F
	Polynemidae	2	3	0	0	5	11.9	42	M
	Terapontidae	0	2	0	0	2	3.8	52	(M&)F
	Serranidae	26	0	66	3	92	17.1	538	M
	Pomacanthidae	0	0	22	4	23	25.8	89	M
	Malacanthidae	0	0	1	0	1	2.2	45	M
	Cirrhitidae	0	0	6	2	6	18.2	33	M
	Eleginopsidae	0	1	0	0	1	100.0	1	M
Scorpaeniformes	Platycephalidae	0	7	0	0	7	8.8	80	M
	Scorpaenidae	0	0	1	0	1	0.2	454	M
Moroniformes	Moronidae	0	1	0	0	1	25.0	4	M&F
Spariiformes	Nemipteridae	0	0	2	0	2	3.0	67	M
	Lethrinidae	0	0	10	0	10	26.3	38	M
	Sparidae	0	16	16	0	32	84.2	38	M
Tetraodontiformes	Balistidae	0	0	1	0	1	2.4	42	M
Total number of species		55	54	305	66	461			

SH simultaneous hermaphroditism, PA protandry, PG protogyny, BS bidirectional sex change or reversed sex change in protogynous species. When two or more types are reported within a species, we counted them in each column

*Percentage of hermaphroditic species in each family (total number of species after Nelson et al. 2016)

**M marine, F fresh water (after Nelson et al. 2016). In parentheses if no hermaphrodites have been reported from the habitat

Table 3 Frequency of hermaphroditic fish families in each order. Order names are arranged following Nelson et al. (2016). Summed up from Table 2

Order	Number of families including hermaphrodites						Total number of families	Group names in Fig. 1
	SH	PA	PG	BS	Total	%*		
Anguilliformes	1	1	0	0	1	5.3	19	Elopomorpha
Clupeiformes	0	1	0	0	1	20.0	5	Clupeiformes
Cypriniformes	0	1	0	0	1	7.7	13	Cypriniformes
Stomiiformes	0	1	0	0	1	20.0	5	Stomiatiformes
Aulopiformes	8	0	0	0	8	53.3	15	Aulopiformes
Gobiiformes	0	0	1	1	1	12.5	8	Gobiaria
Uncertain** in ovalentaria	0	1	2	2	2	25.0	8	Ovalentaria
Cichliformes	1	0	1	0	1	50.0	2	Ovalentaria
Cyprinodontiformes	1	0	1	0	2	20.0	10	Ovalentaria
Synbranchiformes	0	0	1	0	1	33.3	3	Anabantaria
Trachiniformes	0	1	2	0	3	27.3	11	Eupercaria
Labriiformes	0	0	3	1	3	100.0	3	Eupercaria
Perciformes	2	5	4	3	9	14.5	62	Eupercaria
Scorpaeniformes	0	1	1	0	2	4.9	41	Eupercaria
Moroniformes	0	1	0	0	1	33.3	3	Eupercaria
Spariformes	0	1	3	0	3	50.0	6	Eupercaria
Tetraodontiformes	0	0	1	0	1	10.0	10	Eupercaria
Total number of families	13	14	20	7	41			

SH simultaneous hermaphroditism, PA protandry, PG protogyny, BS bidirectional sex change or reversed sex change in protogynous species. When two or more types are reported within a family, we counted them in each column

*Percentage of hermaphroditic families in each order (total number of families after Nelson et al. 2016)

**Treated as one order for convenience

the number of species. The number of species with BS was higher than that with SH or PA because of the extensive surveys on BS species of Gobiidae (Table 2, S1). The percentage of hermaphroditic families in an order varied widely from 4.9% (2 out of 41 families in Scorpaeniformes) to 100% (all three families in Labriiformes) (Table 3). All four types were only found in Perciformes, and three types (PA, PG, and BS) in the tentative order (Pomacentridae–Pseudochromidae) in Ovalentaria.

By combining our list with the phylogenetic tree of Betancur-R et al. (2017), it was indicated that SH and PA have evolved several times in not-closely related lineages; SH in Elopomorpha, Aulopiformes, Ovalentaria, and Eupercaria, and PA in Elopomorpha, Clupeiformes, Cypriniformes, Stomiatiformes, Ovalentaria, and Eupercaria (Fig. 1). For Elopomorpha, PG was suggested by Fishelson (1992) in nine species of Muraenidae based on gonad histology of few samples (Table S1), but functional protogynous sex change has not been confirmed (Sadovy de Mitcheson and Liu 2008). Therefore, it is suggested that PG (and BS) has evolved only in four lineages (Gobiaria, Anabantaria, Ovalentaria, and Eupercaria) of Percomorpha relatively recently (Fig. 1). The different distribution patterns in the phylogenetic tree of the former two types (SH and PA) and the latter (PG and BS)

are interesting, and may also be related to the difference in mating systems.

Habitat (marine or freshwater) and hermaphroditism.

Among hermaphroditic fishes, the number of families only inhabiting freshwater (6 families, 15% of all hermaphroditic families) was much lower than that of marine only families (32 families, 78%) (Table 2). All four types of hermaphroditism were found in marine families, while three types (except BS) were found in freshwater families. In freshwater families, the number of species of each type was similar (SH, 4; PA, 3; PG, 6), and the total number of freshwater hermaphroditic species (13 spp., 3% of all hermaphroditic species) was much lower than that in marine families (445 spp., 97%). The percentage of freshwater species in hermaphroditic species (3%) was significantly lower than that of the freshwater species in all fishes (about 43%; Nelson et al. 2016) ($\chi^2 = 294$, $P < 0.001$), although phylogenetic distribution of marine and freshwater species should be considered for a sophisticated test of the different likelihood of hermaphroditism evolution between habitats.

Regarding this hermaphroditism absence from most freshwater habitats, it has been suggested that the relatively large eggs or young produced by many freshwater species tend to accentuate the physical differences in male

Fig. 1 Phylogeny of fishes and occurrence of hermaphroditism. The phylogenetic tree was processed from Fig. 1 of Betancur-R et al. (2017). SH simultaneous hermaphroditism, PA protandry, PG protogyny, BS bidirectional sex change or reversed sex change in protogynous species. For group names and orders, see Table 3

Table 4 Relation between hermaphroditism and mating system. Summed up from Table 1

Mating system*	Number of species in each type of sexual pattern**									
	SH	SH, G	PA	PA, G	PG	PG, G	PG, G, BS	PG, BS	BS	Total
Random mating			3							3
Non-size-assortative monogamy			10							10
Size-assortative monogamy	9				2			3	5	19
Harem polygyny	2				45	2		4	2	55
Harem, GSP					1					1
Harem, MTV polygamy					5	3	1			9
Harem, MTV polygamy, GSP					1					1
MTV polygamy					40	1		1	2	44
MTV polygamy, GSP					16			1		17
Group spawning			1		3	2				6
Spawning aggregation			1	1	11					13
Unknown***	37	7	27	11	150	5	0	8	38	283

**Harem* harem polygyny, *MTV polygamy* male-territory-visiting polygamy, *GSP* group spawning

***SH* simultaneous hermaphroditism, *PA* protandry, *PG* protogyny, *BS* bidirectional sex change or reversed sex change in protogynous species, *G* gonochorism

***Mating systems of hermaphroditic species are completely unknown in 26 families (see Table 1)

and female anatomy, possibly forming a barrier or physical constraint to hermaphroditism (Warner 1978) and that fewer and larger eggs and more parental care may reduce the size advantage (Sadovy de Mitcheson and Liu 2008). Moreover, mating systems of freshwater fish should also be taken into consideration.

Mating system and the evolution of hermaphroditism. In the field, mating systems have been reported in less than 40% of hermaphroditic species (Table 4), and most of them were shallow coral reef fishes (Table S1). Mating system is known only from 11 species with SH (20% of 55 spp.), i.e., small serranids living on coral reefs (Table 1, S1). Reciprocal pair spawning (i.e., egg trading) occurs in monogamous pairs (9 spp., e.g., Fischer 1981), or a large male (secondary male derived from hermaphrodite) controls a harem of simultaneous hermaphrodites (3 spp., e.g., Petersen and Fischer 1986). Mating systems of the other 80% of species with SH, including deep-sea species (e.g., Aulopiformes), remain unknown. SH in deep-sea fishes are often regarded as evidence for the low-density model (Tomlinson 1966; Ghiselin 1969), because population density is generally low in the deep sea. Although the study of mating behavior in deep-sea fishes is extremely difficult, underwater video tape recordings and the distribution of the number of fish caught have recently suggested pair bonding in two deep-sea SH species of Giganturidae (Kupchik et al. 2018). Another example of hermaphroditism is found in androdioecious (i.e., SH and males) killifish of genus *Kryptolebias*, in which hermaphrodites never mate with other hermaphrodites (Furness et al. 2015), but reproduce via selfing or mating with males.

The mating system has only been reported in 16 species with PA (30% of 54 spp.; Table 4). Non-size-assortative

monogamy (i.e., females accept smaller males as in random mating) is known from 10 species of anemonefishes (Pomacentridae; Table 1; e.g., Fricke and Fricke 1977), and random mating from three species of Platycephalidae (Table 1; e.g., Sunobe et al. 2016). These mating systems support the SA model prediction about PA being favored in species with random mating or non-size-assortative monogamy in which females accept smaller males (Warner 1975, 1984). Spawning aggregation and group spawning have also been reported (in two and one species, respectively, of Sparidae; Table 1; e.g., van der Walt and Mann 1998), but whether random mating occurs in the aggregation remains unknown.

Mating systems have been reported from 142 species with PG (47% of 305 spp.; Table 4). Harem polygyny and male-territory-visiting polygamy (62 and 69 spp., respectively) were the prevailing systems (adding up to 85% of 142 spp.; Table 4), e.g., Labridae, Scaridae, and Pomacanthidae (Table 1). This supports the SA model prediction of PG being favored in polygynous species with large males monopolizing females (Warner 1975). Size-assortative monogamy has been reported from five species with PG (Table 4). All five species belong to Gobiidae, and BS was also confirmed in three of them (Table 1) and suggested in another one (Table S1). The tendency of PG with BS in the monogamous goby *Paragobiodon echinocephalus* has been explained by the growth-rate advantage in females (Kuwamura et al. 1994): the difference between sexes in growth rate favors the evolution of sex changer even if the size advantage is the same between the two sexes. For the other exceptional cases of group spawning in two labrid and three serranids, and spawning aggregation in one sparid, two labrids, and nine serranids (Table 1, 4), further observations

are needed because group spawning is also known in species with male-territory-visiting polygamy (Table 4; Warner and Hoffman 1980; Suzuki et al. 2010).

Mating system has been reported from 19 species with BS (29% of 66 spp.; Table 4). Size-assortative monogamy is known in eight species (Gobiidae), harem polygyny in seven species (Gobiidae, Pomacentridae, Labridae, Pomacanthidae, and Cirrhitidae), and male-territory-visiting polygamy in five species (Gobiidae, Pomacentridae, and Labridae) (Table 1). BS in the monogamous coral-dwelling gobies has been explained by the risk-of-movement hypothesis (Munday et al. 2010). BS in protogynous and polygynous species can be explained by the low-density hypothesis for the reversed sex change, because facultative monogamy occurs at low-density conditions in polygynous species (Kuwamura et al. 2014, 2016a). Contrastingly, the reversed (female-to-male) sex change does not occur even at very low density in the protandrous anemonefishes (Fricke and Fricke 1977; Kuwamura and Nakashima 1998; T. Kuwamura, unpublished data) or PA species with random mating (Table 1).

Mating system is only known in two of 13 freshwater hermaphroditic species, one in Cichlidae and the other in Synbranchidae (Table 2). Both species are PG with male-territory-visiting polygamy (Table 1), supporting the SA model. Although group spawning is common, mating systems of freshwater gonochorists are as various as in marine species (Taborsky 2008). For example, both monogamy and polygyny are known in cichlid fishes (Kuwamura 1997), but functional hermaphroditism is almost unknown, probably owing to biparental care or prolonged parental care of juveniles, which may reduce the difference in reproductive success between the sexes (Warner and Lejeune 1985).

Effect of population density on mating system and sexual pattern. Intraspecific variations in sexual pattern (including gonochorism) and mating system (excluding facultative monogamy in many polygamous species) have been reported in at least 50 and 28 species, respectively (Tables 1 and 4), which may be partly explained by differences in population density. It is well known that mating system may vary depending on population density (Fricke 1980; Warner and Hoffman 1980; Barlow 1984; Petersen 2006). Accordingly, the low-density hypothesis for the evolution of reversed sex change in polygynous and protogynous species has been proposed and tested (Kuwamura et al. 2002, 2011, 2014, 2016a), predicting that facultative monogamy and reversed sex change may occur under low-density condition in polygynous species. For example, in a coral-dwelling damselfish *Dascyllus aruanus* (Pomacentridae), female-to-male sex change (PG) occurs in harems on isolated corals as the SA model predicts, and reversed sex change (BS) occurs when widowed males meet under experimental low-density conditions at which facultative

monogamy occurs (Kuwamura et al. 2016a). In contrast, sex change rarely occurs (i.e., gonochorism) in high-density populations living in continuous coral-covered habitats, where females can choose mates with low risk of movement (Kuwamura et al. 2016a). Moreover, in another pomacentrid, the monogamous and protandrous anemonefish *Amphiprion clarkii*, sex change rarely occurs in a high-density population with low risk of movement (Ochi 1989).

The effect of population density has also been reported from protogynous labrids. Two types of males (diandry) and alternative male mating tactics are well known in Labridae (Warner and Robertson 1978; Kuwamura et al. 2016b). Primary males mature and remain as males, i.e., gonochorists, and secondary males have changed sex from female (PG). Small IP (initial phase) males participate in group spawning or sneaking, and large TP (terminal phase) males establish mating territories and pair spawn with visiting females. The percentage of IP males (primary males) and the frequency of group spawning increase with population density (Warner and Hoffman 1980; Suzuki et al. 2010), and sex change rarely occurs under high densities (Warner 1982). Contrastingly, reversed (male-to-female) sex change has been reported in low-density populations of *Halichoeres trimaculatus* (Kuwamura et al. 2007). Reversed sex change in facultatively monogamous pairs in low-density conditions has also been confirmed in a harem wrasse *Labroides dimidiatus* (Kuwamura et al. 2014).

These examples suggest that different population densities can cause intraspecific variation in sexual pattern through variations in the mating system. Protogynous species become gonochoristic in high-density conditions and reversed sex change may occur in low-density conditions. In protandrous species; however, reversed sex change has not been reported in low-density conditions and further investigations are needed. In Sparidae, for example, both hermaphroditism (PA or PG) and gonochorism are known in at least 12 species (Table 1, S1). Although their mating systems are almost unknown at present, they will be a good subject to examine the relationship between population density and sexual pattern.

There is much more work to be done to investigate the effects of population density and mating system on interspecific variations in sexual pattern, and we hope that the database presented here should allow for many future comparative tests. To further facilitate this work, we need to create a database of the mating systems of gonochoristic fish species similar to that presented here for hermaphroditic species. We can then proceed to make comparative tests with closely related groups that differ even more strongly in sexual pattern.

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