Chapter 1
Evolution of Hermaphroditism in Fishes: Phylogeny and Theory

Tetsuo Kuwamura

Abstract This chapter introduces the main features of functional hermaphroditism in fishes. It has been reported in 481 fish species belonging to 41 families of 17 teleost orders. Simultaneous hermaphroditism (or synchronous hermaphroditism) is known in 57 species of 13 families, and among species exhibiting sequential hermaphroditism, protogyny is much more common (314 species of 20 families) than protandry (62 species of 14 families) or bidirectional sex change (69 species of seven families). Recent phylogenetic trees have indicated that simultaneous hermaphroditism and protandry have evolved several times in not closely related lineages of Teleostei, whereas protogyny and bidirectional sex change have evolved only in Percomorphaceae. The evolution of hermaphroditism has been successfully explained by individual fitness, with two major hypotheses: the low-density model for simultaneous hermaphroditism and the size-advantage model for sequential hermaphroditism. The mating system of a species is one of the important drivers of the evolution of hermaphroditism, and the relationship between mating systems and hermaphroditism will be focused on in the following chapters. Additionally, sex change is socially controlled in many fishes, and its physiological mechanisms are briefly summarized.

Keywords Bidirectional sex change · Low density · Protandry · Protogyny · Simultaneous hermaphroditism · Size-advantage

This chapter introduces the main features of functional hermaphroditism in fishes, with discussions of the four types of hermaphroditism and their frequencies, phylogenetic relationships and habitats, evolutionary theories, mating systems and social control, and an overview of physiological mechanisms. The details of each type of hermaphroditism are described in the following chapters.

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1.1 Types and Frequencies of Hermaphroditism in Fishes

Both sexual and asexual reproductions are seen in living organisms. Sexual reproduction has many associated costs to the individual compared with asexual reproduction, but it has evolved in all organisms except viruses because it increases genetic diversity among offspring which allow them to more successfully adapt to environmental changes, such as the mutations of parasites (Hamilton et al. 1990; Lehtonen et al. 2012). Only two sexes, i.e., males that produce a large number of small sperm and females that produce a small number of large eggs, have evolved in most organisms. This is because middle-size gametes do not increase individual fitness (Maynard-Smith 1978). Gonochorism or dioecy, in which an individual can function as only one of the two sexes, i.e., either male or female, throughout its life, is common in animals, but rare in plants.

Hermaphroditism is a phenomenon in which an individual can function as both sexes at the same time (simultaneous hermaphroditism or synchronous hermaphroditism) or at different stages of its life history (sequential hermaphroditism or sex change) (Avise 2011; Leonard 2019). Simultaneous hermaphroditism is common in plants such as among bisexual flowers but is rare in animals that can move when in search of mates. Sequential hermaphroditism is known in some plants and invertebrates, but in only 1% of vertebrate species, almost all of which are fishes (Avise 2011; Ashman et al. 2014). Sequential hermaphroditism can further be classified into three types, i.e., protandry (male-to-female sex change), protogyny (female-to-male sex change), and bidirectional sex change (or reversed sex change) (Sadovy de Mitcheson and Liu 2008; Kuwamura et al. 2020; Table 1.1). In most cases of bidirectional sex change, the reversed sex change occurs in primarily protogynous species.

Functional hermaphroditism has been studied extensively in fishes. Kuwamura et al. (2020) provided a list of 461 fish species in which functional hermaphroditism had been reported. Subsequently, 21 species were added (and one species deleted), and the current species list is shown in Table 1.2 and Chap. 6. These fishes belong to 41 families of 17 teleost orders. Protogyny is the most frequently observed type (314 species of 20 families), and the other types are much less common, with protandry seen in 62 species of 14 families, simultaneous hermaphroditism seen in 57 species of 13 families, and bidirectional sex change seen in 69 species of seven families (Table 1.3). Both protogyny and bidirectional sex change have been reported in 21 species (Table 1.2), in which the reversed sex change occurs in

Table 1.1 Types of functional hermaphroditism in fishes

Simultaneous hermaphroditism (synchronous hermaphroditism)
Sequential hermaphroditism
Protandry (male-to-female sex change)
Protogyny (female-to-male sex change)
Bidirectional sex change (reversed sex change in protogynous species: female to male to female)

Table 1.2 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 (modified from Table 1 of Kuwamura et al. 2020)

Order Family	Species	Sexual pattern	Mating system
Anguilliformes			
Muraenidae	*Gymnothorax griseus*	SH	
Muraenidae	*Gymnothorax pictus*	SH	
Muraenidae	*Gymnothorax thyrsoideus*	SH	
Muraenidae	*Rhinomuraena quaesita*	PA	
Clupeiformes			
Clupeidae	*Tenualosa macrura*	PA	
Clupeidae	*Tenualosa toli*	PA	
Cypriniformes			
Cobitidae	*Cobitis taenia*	PA, G	
Stomiiformes			
Gonostomatidae	*Cyclothone atraria*	PA	
Gonostomatidae	*Cyclothone microdon*	PA	
Gonostomatidae	*Gonostoma elongatum*	PA	
Gonostomatidae	*Sigmops bathyphilum*	PA	
Gonostomatidae	*Sigmops gracile*	PA	
Aulopiformes			
Ipnopidae	*Bathymicrops brevianalis*	SH	
Ipnopidae	*Bathymicrops regis*	SH	
Ipnopidae	*Bathypterois grallator*	SH	
Ipnopidae	*Bathypterois mediterraneus*	SH	
Ipnopidae	*Bathypterois quadrifilis*	SH, G	
Ipnopidae	*Bathypterois viridensis*	SH	
Ipnopidae	*Bathytyphlops marionae*	SH	
Ipnopidae	*Ipnops agassizii*	SH	
Ipnopidae	*Ipnops meadi*	SH	
Giganturidae	*Gigantura chuni*	SH	
Giganturidae	*Gigantura indica*	SH, G	
Bathysauridae	*Bathysaurus ferox*	SH	
Bathysauridae	*Bathysaurus mollis*	SH	
Chlorophthalmidae	*Chlorophthalmus agassizi*	SH	
Chlorophthalmidae	*Chlorophthalmus brasiliensis*	SH	
Chlorophthalmidae	*Parasudis truculenta*	SH	
Notosudidae	*Ahliesaurus brevis*	SH	
Scopelarchidae	*Benthalbella infans*	SH	
Scopelarchidae	*Scopelarchus guentheri*	SH	
Paralepididae	*Arctozenus risso*	SH	
Paralepididae	*Lestidium pseudosphyraenoides*	SH	

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Alepisauridae	*Omosudis lowii*	SH	
Gobiiformes			
Gobiidae	*Coryphopterus alloides*	PG	
Gobiidae	*Coryphopterus dicrus*	PG	
Gobiidae	*Coryphopterus eidolon*	PG	
Gobiidae	*Coryphopterus glaucofraenum*	PG	MTV polygamy
Gobiidae	*Coryphopterus hyalinus*	PG	
Gobiidae	*Coryphopterus lipernes*	PG	
Gobiidae	*Coryphopterus personatus*	PG	
Gobiidae	*Coryphopterus thrix*	PG	
Gobiidae	*Coryphopterus urospilus*	PG	
Gobiidae	*Eviota epiphanes*	PG, BS	
Gobiidae	*Fusigobius neophytus*	PG	MTV polygamy
Gobiidae	*Gobiodon erythrospilus*	BS	SA monogamy
Gobiidae	*Gobiodon histrio*	PG, BS	SA monogamy
Gobiidae	*Gobiodon micropus*	BS	SA monogamy
Gobiidae	*Gobiodon oculolinealus*	BS	SA monogamy
Gobiidae	*Gobiodon okinawae*	PG	SA monogamy
Gobiidae	*Gobiodon quinquestrigatus*	PG, BS	SA monogamy
Gobiidae	*Lythrypnus dalli*	PG, BS	MTV polygamy
Gobiidae	*Lythrypnus nesiotes*	PG	
Gobiidae	*Lythrypnus phorellus*	PG	
Gobiidae	*Lythrypnus pulchellus*	BS	
Gobiidae	*Lythrypnus spilus*	PG	
Gobiidae	*Lythrypnus zebra*	BS	MTV polygamy
Gobiidae	*Paragobiodon echinocephalus*	PG, BS	SA monogamy
Gobiidae	*Paragobiodon xanthosomus*	PG	SA monogamy
Gobiidae	*Priolepis akihitoi*	BS	SA monogamy
Gobiidae	*Priolepis borea*	BS	
Gobiidae	*Priolepis cincta*	BS	SA monogamy
Gobiidae	*Priolepis eugenius*	PG, BS	
Gobiidae	*Priolepis fallacincta*	BS	
Gobiidae	*Priolepis hipoliti*	PG, BS	
Gobiidae	*Priolepis inhaca*	BS	
Gobiidae	*Priolepis latifascima*	BS	
Gobiidae	*Priolepis semidoliata*	BS	SA monogamy
Gobiidae	*Rhinogobiops nicholsii*	PG	
Gobiidae	*Trimma annosum*	BS	
Gobiidae	*Trimma benjamini*	BS	

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Gobiidae	*Trimma caesiura*	BS	
Gobiidae	*Trimma cana*	BS	
Gobiidae	*Trimma caudomaculatum*	BS	MTV polygamy
Gobiidae	*Trimma emeryi*	BS	Harem
Gobiidae	*Trimma fangi*	BS	
Gobiidae	*Trimma flammeum*	BS	
Gobiidae	*Trimma flavatram*	BS	
Gobiidae	*Trimma fucatum*	BS	
Gobiidae	*Trimma gigantum*	BS	
Gobiidae	*Trimma grammistes*	BS	Harem
Gobiidae	*Trimma hayashii*	BS	Harem
Gobiidae	*Trimma kudoi*	BS	
Gobiidae	*Trimma lantana*	BS	
Gobiidae	*Trimma macrophthalma*	BS	
Gobiidae	*Trimma maiandros*	BS	
Gobiidae	*Trimma marinae*	BS	
Gobiidae	*Trimma milta*	BS	
Gobiidae	*Trimma nasa*	BS	
Gobiidae	*Trimma naudei*	BS	
Gobiidae	*Trimma necopinum*	BS	
Gobiidae	*Trimma okinawae*	PG, BS	Harem
Gobiidae	*Trimma preclarum*	BS	
Gobiidae	*Trimma rubromaculatum*	BS	
Gobiidae	*Trimma sheppardi*	BS	
Gobiidae	*Trimma stobbsi*	BS	
Gobiidae	*Trimma striatum*	BS	
Gobiidae	*Trimma tauroculum*	BS	
Gobiidae	*Trimma taylori*	BS	
Gobiidae	*Trimma unisquamis*	BS	
Gobiidae	*Trimma yanagitai*	BS	
Uncertain in Ovalentaria			
Pomacentridae	*Amphiprion akallopisos*	PA	NSA monogamy
Pomacentridae	*Amphiprion bicinctus*	PA	NSA monogamy
Pomacentridae	*Amphiprion clarkii*	PA	NSA monogamy
Pomacentridae	*Amphiprion frenatus*	PA	NSA monogamy
Pomacentridae	*Amphiprion melanopus*	PA	NSA monogamy
Pomacentridae	*Amphiprion ocellaris*	PA	NSA monogamy
Pomacentridae	*Amphiprion percula*	PA	NSA monogamy
Pomacentridae	*Amphiprion perideraion*	PA	NSA monogamy
Pomacentridae	*Amphiprion polymnus*	PA	NSA monogamy
Pomacentridae	*Amphiprion sandaracinos*	PA	NSA monogamy

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Pomacentridae	*Dascyllus aruanus*	PG, BS, G	Harem, MTV polygamy
Pomacentridae	*Dascyllus carneus*	PG	Harem, MTV polygamy
Pomacentridae	*Dascyllus flavicaudus*	PG, G	Harem, MTV polygamy
Pomacentridae	*Dascyllus marginatus*	PG	Harem, MTV polygamy
Pomacentridae	*Dascyllus melanurus*	PG, G	Harem, MTV polygamy
Pomacentridae	*Dascyllus reticulatus*	PG, BS, G	Harem, MTV polygamy
Pseudochromidae	*Anisochromis straussi*	PG	
Pseudochromidae	*Ogilbyina queenslandiae*	PG	
Pseudochromidae	*Pseudochromis aldabraensis*	BS	
Pseudochromidae	*Pseudochromis cyanotaenia*	BS	
Pseudochromidae	*Pseudochromis flavivertex*	BS	
Pseudochromidae	*Pictichromis porphyrea*	BS	
Cichliformes			
Cichlidae	*Metriaclima* cf. *livingstoni*	PG	MTV polygamy
Cichlidae	*Satanoperca jurupari*	SH	
Cyprinodontiformes			
Rivulidae	*Kryptolebias hermaphroditus*	SH, G	
Rivulidae	*Kryptolebias marmoratus*	SH, G	
Rivulidae	*Kryptolebias ocellatus*	SH, G	
Poeciliidae	*Xiphophorus helleri*	PG, G	
Synbranchiformes			
Synbranchidae	*Monopterus albus*	PG	MTV polygamy
Synbranchidae	*Monopterus boueti*	PG	
Synbranchidae	*Ophisternon bengalense*	PG	
Synbranchidae	*Synbranchus marmoratus*	PG	
Trachiniformes			
Pinguipedidae	*Parapercis clathrata*	PG	
Pinguipedidae	*Parapercis colias*	PG	
Pinguipedidae	*Parapercis cylindrica*	PG	Harem
Pinguipedidae	*Parapercis hexophtalma*	PG	Harem
Pinguipedidae	*Parapercis nebulosa*	PG	
Pinguipedidae	*Parapercis snyderi*	PG	Harem
Pinguipedidae	*Parapercis xanthozona*	PG	
Trichonotidae	*Trichonotus filamentosus*	PG	
Creediidae	*Crystallodytes cookei*	PA	
Creediidae	*Limnichthys fasciatus*	PA	
Creediidae	*Limnichthys nitidus*	PA	
Labriformes			
Labridae	*Achoerodus gouldii*	PG	

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Labridae	*Achoerodus viridis*	PG	
Labridae	*Anampses geographicus*	PG	
Labridae	*Bodianus axillaris*	PG	
Labridae	*Bodianus diplotaenia*	PG	MTV polygamy
Labridae	*Bodianus eclancheri*	PG	GSP
Labridae	*Bodianus frenchii*	PG	
Labridae	*Bodianus mesothorax*	PG	SPA
Labridae	*Bodianus rufus*	PG	Harem
Labridae	*Cheilinus chlorurus*	PG	
Labridae	*Cheilinus fasciatus*	PG	Harem
Labridae	*Cheilinus trilobatus*	PG	Harem, MTV polygamy
Labridae	*Cheilinus undulatus*	PG	MTV polygamy
Labridae	*Choerodon azurio*	PG	
Labridae	*Choerodon cauteroma*	PG	
Labridae	*Choerodon cyanodus*	PG	
Labridae	*Choerodon fasciatus*	PG	
Labridae	*Choerodon graphicus*	PG	
Labridae	*Choerodon rubescens*	PG	
Labridae	*Choerodon schoenleinii*	PG	
Labridae	*Choerodon venustus*	PG	
Labridae	*Cirrhilabrus temmincki*	PG	MTV polygamy
Labridae	*Clepticus parrae*	PG	SPA
Labridae	*Coris auricularis*	PG	
Labridae	*Coris dorsomacula*	PG	Harem
Labridae	*Coris gaimard*	PG	MTV polygamy
Labridae	*Coris julis*	PG	MTV polygamy
Labridae	*Coris variegata*	PG	
Labridae	*Decodon melasma*	PG	
Labridae	*Epibulus insidiator*	PG	Harem, MTV polygamy
Labridae	*Gomphosus varius*	PG	MTV polygamy
Labridae	*Halichoeres bivittatus*	PG	MTV polygamy, GSP
Labridae	*Halichoeres garnoti*	PG	MTV polygamy
Labridae	*Halichoeres maculipinna*	PG	MTV polygamy
Labridae	*Halichoeres margaritaceus*	PG	Harem
Labridae	*Halichoeres marginatus*	PG	MTV polygamy, GSP
Labridae	*Halichoeres melanochir*	PG	MTV polygamy
Labridae	*Halichoeres melanurus*	PG	MTV polygamy
Labridae	*Halichoeres miniatus*	PG	Harem
Labridae	*Halichoeres nebulosus*	PG	
Labridae	*Halichoeres pictus*	PG	
Labridae	*Halichoeres poeyi*	PG	

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Labridae	*Halichoeres radiatus*	PG	
Labridae	*Halichoeres scapularis*	PG	
Labridae	*Halichoeres semicinctus*	PG	MTV polygamy, GSP
Labridae	*Halichoeres tenuispinnis*	PG	MTV polygamy
Labridae	*Halichoeres trimaculatus*	PG, BS	MTV polygamy, GSP
Labridae	*Hemigymnus fasciatus*	PG	
Labridae	*Hemigymnus melapterus*	PG	
Labridae	*Hologymnosus annulatus*	PG	
Labridae	*Iniistius dea*	PG	
Labridae	*Iniistius geisha*	PG	
Labridae	*Iniistius pentadactylus*	PG	Harem
Labridae	*Labrichthys unilineatus*	PG	Harem
Labridae	*Labroides dimidiatus*	PG, BS	Harem
Labridae	*Labrus bergylta*	PG	
Labridae	*Labrus merula*	PG	
Labridae	*Labrus mixtus*	PG	
Labridae	*Labrus viridis*	PG	
Labridae	*Lachnolaimus maximus*	PG	Harem
Labridae	*Macropharyngodon moyeri*	PG	Harem
Labridae	*Notolabrus celidotus*	PG	MTV polygamy
Labridae	*Notolabrus gymnogenis*	PG	
Labridae	*Notolabrus parilus*	PG	
Labridae	*Notolabrus tetricus*	PG	MTV polygamy
Labridae	*Ophthalmolepis lineolatus*	PG	
Labridae	*Oxycheilinus digramma*	PG	
Labridae	*Parajulis poecilepterus*	PG	GSP
Labridae	*Pictilabrus laticlavius*	PG	MTV polygamy
Labridae	*Pseudocheilinops ataenia*	PG	
Labridae	*Pseudocheilinus evanidus*	PG	
Labridae	*Pseudocheilinus hexataenia*	PG	Harem
Labridae	*Pseudolabrus guentheri*	PG	
Labridae	*Pseudolabrus rubicundus*	PG	MTV polygamy
Labridae	*Pseudolabrus sieboldi*	PG	MTV polygamy
Labridae	*Pteragogus aurigarius*	PG	MTV polygamy
Labridae	*Semicossyphus darwini*	PG	
Labridae	*Semicossyphus pulcher*	PG	MTV polygamy
Labridae	*Semicossyphus reticulatus*	PG	
Labridae	*Stethojulis balteata*	PG	
Labridae	*Stethojulis interrupta*	PG	MTV polygamy
Labridae	*Stethojulis strigiventer*	PG	
Labridae	*Stethojulis trilineata*	PG	MTV polygamy

(continued)

Table 1.2 (continued)

Order / Family	Species	Sexual pattern	Mating system
Labridae	*Suezichthys ornatus*	PG	MTV polygamy
Labridae	*Symphodus melanocercus*	PG	MTV polygamy
Labridae	*Symphodus tinca*	PG, G	MTV polygamy
Labridae	*Thalassoma bifasciatum*	PG	MTV polygamy, GSP
Labridae	*Thalassoma cupido*	PG	MTV polygamy, GSP
Labridae	*Thalassoma duperrey*	PG	MTV polygamy, GSP
Labridae	*Thalassoma hardwicke*	PG	MTV polygamy, GSP
Labridae	*Thalassoma jansenii*	PG	MTV polygamy, GSP
Labridae	*Thalassoma lucasanum*	PG	MTV polygamy, GSP
Labridae	*Thalassoma lunare*	PG	MTV polygamy, GSP
Labridae	*Thalassoma lutescens*	PG	MTV polygamy, GSP
Labridae	*Thalassoma pavo*	PG	MTV polygamy, GSP
Labridae	*Thalassoma purpureum*	PG	
Labridae	*Thalassoma quinquevittatum*	PG	MTV polygamy, GSP
Labridae	*Xyrichtys martinicensis*	PG	Harem
Labridae	*Xyrichtys novacula*	PG	Harem
Odacidae	*Odax pullus*	PG	
Scaridae	*Calotomus carolinus*	PG	MTV polygamy
Scaridae	*Calotomus japonicus*	PG	MTV polygamy
Scaridae	*Calotomus spinidens*	PG	MTV polygamy
Scaridae	*Cetoscarus bicolor*	PG	
Scaridae	*Chlorurus sordidus*	PG	MTV polygamy
Scaridae	*Chlorurus spilurus*	PG	
Scaridae	*Cryptotomus roseus*	PG	MTV polygamy
Scaridae	*Hipposcarus harid*	PG	
Scaridae	*Hipposcarus longiceps*	PG	
Scaridae	*Scarus ferrugineus*	PG	
Scaridae	*Scarus festivus*	PG	
Scaridae	*Scarus forsteni*	PG	MTV polygamy
Scaridae	*Scarus frenatus*	PG	Harem
Scaridae	*Scarus ghobban*	PG	
Scaridae	*Scarus globiceps*	PG	MTV polygamy, GSP
Scaridae	*Scarus iseri*	PG	Harem, GSP
Scaridae	*Scarus niger*	PG	MTV polygamy, GSP
Scaridae	*Scarus oviceps*	PG	MTV polygamy
Scaridae	*Scarus psittacus*	PG	MTV polygamy
Scaridae	*Scarus rivulatus*	PG	MTV polygamy
Scaridae	*Scarus rubroviolaceus*	PG	
Scaridae	*Scarus russelii*	PG	
Scaridae	*Scarus scaber*	PG	
Scaridae	*Scarus schlegeli*	PG	MTV polygamy

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Scaridae	*Scarus spinus*	PG	
Scaridae	*Scarus taeniopterus*	PG	
Scaridae	*Scarus tricolor*	PG	
Scaridae	*Scarus vetula*	PG	Harem, MTV polygamy
Scaridae	*Scarus viridifucatus*	PG	
Scaridae	*Sparisoma atomarium*	PG	Harem
Scaridae	*Sparisoma aurofrenatum*	PG	Harem
Scaridae	*Sparisoma chrysopterum*	PG	MTV polygamy
Scaridae	*Sparisoma cretense*	PG, G	Harem
Scaridae	*Sparisoma radians*	PG	Harem, MTV polygamy, GSP
Scaridae	*Sparisoma rubripinne*	PG	MTV polygamy, GSP
Scaridae	*Sparisoma viride*	PG	MTV polygamy
Perciformes			
Centropomidae	*Centropomus parallelus*	PA, G	
Centropomidae	*Centropomus undecimalis*	PA	
Latidae	*Lates calcarifer*	PA	
Polynemidae	*Eleutheronema tetradactylum*	PA, G	
Polynemidae	*Filimanus heptadactyla*	SH, G	
Polynemidae	*Galeoides decadactylus*	PA, G	
Polynemidae	*Polydactylus macrochir*	PA	
Polynemidae	*Polydactylus microstomus*	SH, G	
Polynemidae	*Polydactylus quadrifilis*	PA, G	
Terapontidae	*Bidyanus bidyanus*	PA	
Terapontidae	*Mesopristes cancellatus*	PA	
Serranidae (Epinephelinae)	*Cephalopholis argus*	PG	Harem
Serranidae (Epinephelinae)	*Cephalopholis boenak*	PG, BS	Harem
Serranidae (Epinephelinae)	*Cephalopholis cruentata*	PG	Harem
Serranidae (Epinephelinae)	*Cephalopholis cyanostigma*	PG	Harem
Serranidae (Epinephelinae)	*Cephalopholis fulva*	PG	Harem
Serranidae (Epinephelinae)	*Cephalopholis hemistiktos*	PG	Harem
Serranidae (Epinephelinae)	*Cephalopholis miniata*	PG	Harem
Serranidae (Epinephelinae)	*Cephalopholis panamensis*	PG	Harem
	Cephalopholis taeniops	PG	

(continued)

Table 1.2 (continued)

Order / Family	Species	Sexual pattern	Mating system
Serranidae (Epinephelinae)			
Serranidae (Epinephelinae)	*Cephalopholis urodeta*	PG	
Serranidae (Epinephelinae)	*Epinephelus adscensionis*	PG	Harem
Serranidae (Epinephelinae)	*Epinephelus aeneus*	PG	
Serranidae (Epinephelinae)	*Epinephelus akaara*	PG, BS	
Serranidae (Epinephelinae)	*Epinephelus andersoni*	PG	
Serranidae (Epinephelinae)	*Epinephelus areolatus*	PG	
Serranidae (Epinephelinae)	*Epinephelus bruneus*	PG, BS	
Serranidae (Epinephelinae)	*Epinephelus chlorostigma*	PG	
Serranidae (Epinephelinae)	*Epinephelus coioides*	PG, BS	
Serranidae (Epinephelinae)	*Epinephelus diacanthus*	PG	
Serranidae (Epinephelinae)	*Epinephelus drummondhayi*	PG	
Serranidae (Epinephelinae)	*Epinephelus fasciatus*	PG	
Serranidae (Epinephelinae)	*Epinephelus fuscoguttatus*	PG	SPA
Serranidae (Epinephelinae)	*Epinephelus guttatus*	PG	SPA
Serranidae (Epinephelinae)	*Epinephelus labriformis*	PG	
Serranidae (Epinephelinae)	*Epinephelus malabaricus*	PG	
Serranidae (Epinephelinae)	*Epinephelus marginatus*	PG	MTV polygamy
Serranidae (Epinephelinae)	*Epinephelus merra*	PG	SPA
Serranidae (Epinephelinae)	*Epinephelus morio*	PG	
Serranidae (Epinephelinae)	*Epinephelus ongus*	PG	SPA
Serranidae (Epinephelinae)	*Epinephelus rivulatus*	PG	
	Epinephelus striatus	PG, G	GSP

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Serranidae (Epinephelinae)			
Serranidae (Epinephelinae)	*Epinephelus tauvina*	PG	
Serranidae (Epinephelinae)	*Hyporthodus flavolimbatus*	PG	
Serranidae (Epinephelinae)	*Hyporthodus niveatus*	PG	
Serranidae (Epinephelinae)	*Hyporthodus quernus*	PG	
Serranidae (Epinephelinae)	*Mycteroperca bonaci*	PG	
Serranidae (Epinephelinae)	*Mycteroperca interstitialis*	PG	
Serranidae (Epinephelinae)	*Mycteroperca microlepis*	PG	SPA
Serranidae (Epinephelinae)	*Mycteroperca olfax*	PG	SPA
Serranidae (Epinephelinae)	*Mycteroperca phenax*	PG	SPA
Serranidae (Epinephelinae)	*Mycteroperca rubra*	PG	SPA
Serranidae (Epinephelinae)	*Mycteroperca venenosa*	PG	GSP
Serranidae (Epinephelinae)	*Plectropomus laevis*	PG	
Serranidae (Epinephelinae)	*Plectropomus leopardus*	PG	SPA
Serranidae (Epinephelinae)	*Plectropomus maculatus*	PG	
Serranidae (Serraninae)	*Bullisichthys caribbaeus*	SH	
Serranidae (Serraninae)	*Centropristis striata*	PG	
Serranidae (Serraninae)	*Centropristis ocyurus*	PG	
Serranidae (Serraninae)	*Chelidoperca hirundinacea*	PG	
Serranidae (Serraninae)	*Diplectrum bivittatum*	SH	
Serranidae (Serraninae)	*Diplectrum formosum*	SH	
Serranidae (Serraninae)	*Diplectrum macropoma*	SH	

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Serranidae (Serraninae)	*Diplectrum pacificum*	SH	
Serranidae (Serraninae)	*Diplectrum rostrum*	SH	
Serranidae (Serraninae)	*Hypoplectrus aberrans*	SH	SA monogamy
Serranidae (Serraninae)	*Hypoplectrus chlorurus*	SH	SA monogamy
Serranidae (Serraninae)	*Hypoplectrus nigricans*	SH	SA monogamy
Serranidae (Serraninae)	*Hypoplectrus puella*	SH	SA monogamy
Serranidae (Serraninae)	*Hypoplectrus unicolor*	SH	SA monogamy
Serranidae (Serraninae)	*Paralabrax maculatofasciatus*	PG, G	
Serranidae (Serraninae)	*Serraniculus pumilio*	SH	
Serranidae (Serraninae)	*Serranus annularis*	SH	
Serranidae (Serraninae)	*Serranus atricauda*	SH	
Serranidae (Serraninae)	*Serranus auriga*	SH	
Serranidae (Serraninae)	*Serranus baldwini*	SH	Harem
Serranidae (Serraninae)	*Serranus cabrilla*	SH	
Serranidae (Serraninae)	*Serranus hepatus*	SH	
Serranidae (Serraninae)	*Serranus phoebe*	SH	
Serranidae (Serraninae)	*Serranus psittacinus*	SH	Harem
Serranidae (Serraninae)	*Serranus scriba*	SH	
Serranidae (Serraninae)	*Serranus subligarius*	SH	SA monogamy
Serranidae (Serraninae)	*Serranus tabacarius*	SH	SA monogamy
Serranidae (Serraninae)	*Serranus tigrinus*	SH	SA monogamy
Serranidae (Serraninae)	*Serranus tortugarum*	SH	SA monogamy
Serranidae (Grammistini)	*Pseudogramma gregoryi*	SH	

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Serranidae (Grammistini)	*Rypticus saponaceus*	PG	
Serranidae (Grammistini)	*Rypticus subbifrenatus*	PG	
Serranidae (Anthiinae)	*Anthias anthias*	PG	
Serranidae (Anthiinae)	*Anthias nicholsi*	PG	
Serranidae (Anthiinae)	*Anthias noeli*	PG	
Serranidae (Anthiinae)	*Baldwinella vivanus*	PG	
Serranidae (Anthiinae)	*Hemanthias leptus*	PG	
Serranidae (Anthiinae)	*Hemanthias peruanus*	PG	
Serranidae (Anthiinae)	*Hypoplectrodes huntii*	PG	
Serranidae (Anthiinae)	*Hypoplectrodes maccullochi*	PG	
Serranidae (Anthiinae)	*Pronotogrammus martinicensis*	PG	
Serranidae (Anthiinae)	*Pseudanthias conspicuus*	PG	
Serranidae (Anthiinae)	*Pseudanthias elongatus*	PG	
Serranidae (Anthiinae)	*Pseudanthias pleurotaenia*	PG	
Serranidae (Anthiinae)	*Pseudanthias rubrizonatus*	PG	
Serranidae (Anthiinae)	*Pseudanthias squamipinnis*	PG	MTV polygamy
Serranidae (Anthiinae)	*Sacura margaritacea*	PG	
Pomacanthidae	*Apolemichthys trimaculatus*	PG	
Pomacanthidae	*Centropyge acanthops*	PG, BS	
Pomacanthidae	*Centropyge bicolor*	PG	Harem
Pomacanthidae	*Centropyge ferrugata*	PG, BS	Harem
Pomacanthidae	*Centropyge fisheri*	PG, BS	
Pomacanthidae	*Centropyge flavissimus*	BS	Harem
Pomacanthidae	*Centropyge heraldi*	PG	Harem
Pomacanthidae	*Centropyge interruptus*	PG	Harem
Pomacanthidae	*Centropyge multispinus*	PG	
Pomacanthidae	*Centropyge potteri*	PG	Harem
Pomacanthidae	*Centropyge tibicen*	PG	Harem
Pomacanthidae	*Centropyge vrolicki*	PG	Harem
Pomacanthidae	*Chaetodontoplus septentrionalis*	PG	Harem
Pomacanthidae	*Genicanthus bellus*	PG	
Pomacanthidae	*Genicanthus caudovittatus*	PG	Harem
Pomacanthidae	*Genicanthus lamarck*	PG	Harem
Pomacanthidae	*Genicanthus melanospilos*	PG	Harem

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Pomacanthidae	*Genicanthus personatus*	PG	Harem
Pomacanthidae	*Genicanthus semifasciatus*	PG	Harem
Pomacanthidae	*Genicanthus watanabei*	PG	
Pomacanthidae	*Holacanthus passer*	PG, G	Harem
Pomacanthidae	*Holacanthus tricolor*	PG	Harem
Pomacanthidae	*Pomacanthus zonipectus*	PG	
Malacanthidae	*Malacanthus plumieri*	PG	Harem
Cirrhitidae	*Amblycirrhitus pinos*	PG	
Cirrhitidae	*Cirrhitichthys aprinus*	PG	Harem
Cirrhitidae	*Cirrhitichthys aureus*	PG, BS	
Cirrhitidae	*Cirrhitichthys falco*	PG, BS	Harem
Cirrhitidae	*Cirrhitichthys oxycephalus*	PG	Harem
Cirrhitidae	*Neocirrhites armatus*	PG	Harem
Eleginopsidae	*Eleginops maclovinus*	PA	
Scorpaeniformes			
Platycephalidae	*Cociella crocodila*	PA	
Platycephalidae	*Inegocia japonica*	PA	Random mating
Platycephalidae	*Kumococius rodericensis*	PA	
Platycephalidae	*Onigocia macrolepis*	PA	
Platycephalidae	*Platycephalus* sp.	PA	Random mating
Platycephalidae	*Suggrundus meerdervoorti*	PA	
Platycephalidae	*Thysanophrys celebica*	PA	Random mating
Scorpaenidae	*Caracanthus unipinna*	PG	Harem
Moroniformes			
Moronidae	*Morone saxatilis*	PA	
Spariformes			
Nemipteridae	*Scolopsis monogramma*	PG	
Nemipteridae	*Scolopsis taenioptera*	PG	
Lethrinidae	*Lethrinus atkinsoni*	PG	
Lethrinidae	*Lethrinus genivittatus*	PG	
Lethrinidae	*Lethrinus harak*	PG	
Lethrinidae	*Lethrinus lentjan*	PG	
Lethrinidae	*Lethrinus miniatus*	PG	
Lethrinidae	*Lethrinus nebulosus*	PG, G	MTV polygamy, GSP
Lethrinidae	*Lethrinus olivaceus*	PG	SPA
Lethrinidae	*Lethrinus ornatus*	PG	
Lethrinidae	*Lethrinus ravus*	PG	
Lethrinidae	*Lethrinus rubrioperculatus*	PG	
Lethrinidae	*Lethrinus variegatus*	PG	
Sparidae	*Acanthopagrus australis*	PA	
Sparidae	*Acanthopagrus berda*	PA	SPA

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Sparidae	*Acanthopagrus bifasciatus*	PA, G	
Sparidae	*Acanthopagrus latus*	PA	
Sparidae	*Acanthopagrus morrisoni*	PA	
Sparidae	*Acanthopagrus pacificus*	PA	
Sparidae	*Acanthopagrus schlegelii*	PA	
Sparidae	*Argyrops spinifer*	PG, G	
Sparidae	*Boops boops*	PG, G	
Sparidae	*Calamus leucosteus*	PG	
Sparidae	*Calamus proridens*	PG	
Sparidae	*Chrysoblephus cristiceps*	PG	
Sparidae	*Chrysoblephus puniceus*	PG	
Sparidae	*Chrysoblephus laticeps*	PG	
Sparidae	*Dentex gibbosus*	PG	
Sparidae	*Dentex tumifrons*	PG	
Sparidae	*Diplodus annularis*	PA, G	
Sparidae	*Diplodus argenteus*	PA, G	
Sparidae	*Diplodus cadenati*	PA, G	
Sparidae	*Diplodus capensis*	PA, G	
Sparidae	*Diplodus kotschyi*	PA, G	
Sparidae	*Diplodus puntazzo*	PA, G	
Sparidae	*Diplodus sargus*	PA, G	
Sparidae	*Diplodus vulgaris*	PA, G	
Sparidae	*Lithognathus mormyrus*	PA, G	
Sparidae	*Pachymetopon aeneum*	PG	
Sparidae	*Pagellus acarne*	PA, G	
Sparidae	*Pagellus bellottii*	PG, G	
Sparidae	*Pagellus bogaraveo*	PA, G	
Sparidae	*Pagellus erythrinus*	PG	
Sparidae	*Pagrus auriga*	PG	
Sparidae	*Pagrus caeruleostictus*	PG	
Sparidae	*Pagrus ehrenbergii*	PG, G	
Sparidae	*Pagrus major*	PG, G	
Sparidae	*Pagrus pagrus*	PG	
Sparidae	*Rhabdosargus sarba*	PA, G	
Sparidae	*Sarpa salpa*	PA, G	SPA
Sparidae	*Sparidentex hasta*	PA	
Sparidae	*Sparus aurata*	PA	GSP
Sparidae	*Spicara chryselis*	PG	
Sparidae	*Spicara smaris*	PG	
Sparidae	*Spicara maena*	PG	
Sparidae	*Spondyliosoma cantharus*	PG	MTV polygamy

(continued)

Table 1.2 (continued)

Order Family	Species	Sexual pattern	Mating system
Sparidae	*Spondyliosoma emarginatum*	PG	MTV polygamy
Tetraodontiformes			
Balistidae	*Sufflamen chrysopterus*	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 sytem, two or more types are shown. Detailed data of each species and references are given in Chap. 6; 26 species for which functional hermaphroditism is suggested by weak evidence (with a question mark in Chap. 6) are not included in this table

protogynous species. Pla et al. (2021) provided a list of 370 species of hermaphroditic fishes from 34 families in eight orders based on the dataset of Pla (2019). Since there are differences in the citation and interpretation of original papers, this book follows Kuwamura et al. (2020).

Hermaphroditism in teleost fishes is evolutionarily labile, since interspecific variation in the type of hermaphroditism is common even within a single family. Three types of hermaphroditism, i.e., protandry, protogyny, and bidirectional sex change, have been reported in Pomacentridae and simultaneous hermaphroditism, protogyny, and bidirectional sex change in Serranidae (Table 1.3). Simultaneous hermaphroditism and protandry have been reported in Muraenidae and Polynemidae; simultaneous hermaphroditism and protogyny in Cichlidae; protandry and protogyny in Sparidae; and protogyny and bidirectional sex change in Gobiidae, Pseudochromidae, Labridae, Pomacanthidae, and Cirrhitidae (Table 1.3). Gonochoristic species are also found in these families, and phylogenetic studies have suggested that different types of hermaphroditism have appeared in different lineages repeatedly (see Mank et al. 2006).

1.2 Phylogeny of Hermaphroditic Fishes and Their Habitat

Recent phylogenetic trees indicate that hermaphrodites are found only among Teleostei fishes (Kuwamura et al. 2020: Fig. 1.1). Simultaneous hermaphroditism and protandry have evolved several times in not closely related lineages of Teleostei, whereas protogyny and bidirectional sex change have evolved only in Percomorphaceae. Simultaneous hermaphroditism has been reported in four major lineages: Elopomorpha (1 family), Aulopiformes (8), Ovalentaria (2), and Eupercaria (2), and protandry in six major lineages: Elopomorpha (1), Clupeiformes (1), Cypriniformes (1), Stomiatiformes (1), Ovalentaria (1), and Eupercaria

Table 1.3 Frequency of hermaphroditic fish species in each family. Order and family names are arranged following Nelson et al. (2016). Summed up from Table 1.2 (modified from Table 2 of Kuwamura et al. 2020)

Order	Family	Number of hermaphroditic species						Total number of species	Habitat[b]
		SH	PA	PG	BS	Total	%[a]		
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	2	0	0	0	2	100.0	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	2	0	0	0	2	7.4	27	M
	Alepisauridae	1	0	0	0	1	11.1	9	M
Gobiiformes	Gobiidae	0	0	24	51	67	4.9	1359	M(&F)
Uncertain in Ovalentaria	Pomacentridae	0	10	6	2	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	99	2	99	19.1	519	M
	Odacidae	0	0	1	0	1	8.3	12	M

	Scaridae	0	0	36	0	36	36.4	99	M
Perciformes	Centropomidae	0	2	0	0	2	16.7	12	M&F
	Latidae	0	1	0	0	1	7.7	13	M&F
	Polynemidae	2	4	0	0	6	14.3	42	M
	Terapontidae	0	2	0	0	2	3.8	52	(M&)F
	Serranidae	26	0	66	4	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
Spariformes	Nemipteridae	0	0	2	0	2	3.0	67	M
	Lethrinidae	0	0	11	0	11	28.9	38	M
	Sparidae	0	22	22	0	44	8.7	507	M
Tetraodontiformes	Balistidae	0	0	1	0	1	2.4	42	M
Total number of species		57	62	314	69	481			

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

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

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

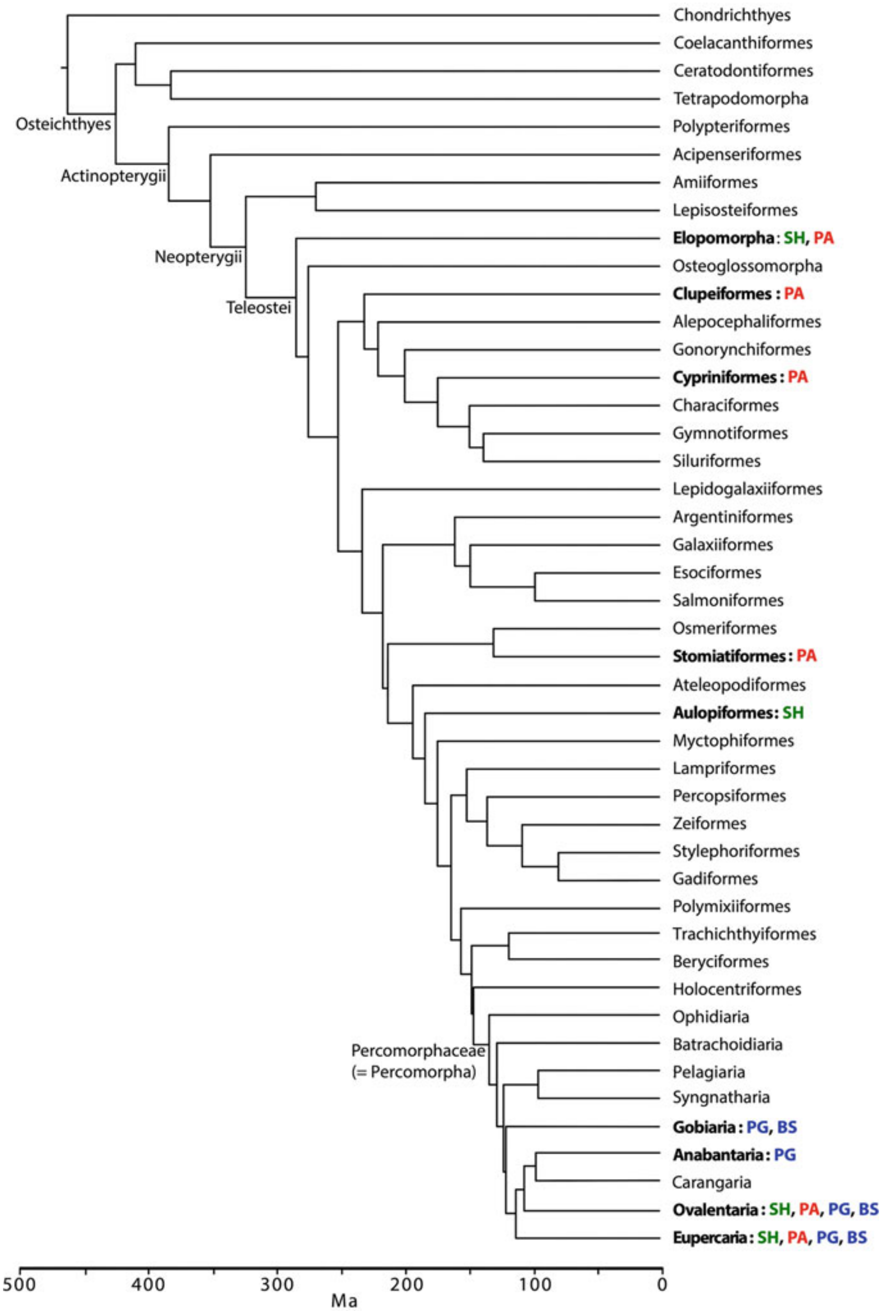

Fig. 1.1 Phylogeny of fishes and occurrence of hermaphroditism. The phylogenetic tree was processed from Betancur-R et al. (2017). *SH* simultaneous hermaphroditism, *PA* protandry, *PG* protogyny, *BS* bidirectional sex change or reversed sex change in protogynous species (reproduced from Kuwamura et al. 2020)

(9) (Fig. 1.1; Table 1.3). Protogyny has evolved in four major lineages: Gobiaria (1 family), Anabantaria (1), Ovalentaria (4), and Eupercaria of Percomorphaceae (14), and bidirectional sex change in three of them Gobiaria (1), Ovalentaria (2), and Eupercaria (4) (Fig. 1.1; Table 1.3).

Within the Percomorphaceae, protogyny and bidirectional sex change are widely distributed (Fig. 1.2). Protogyny has evolved in 12 (26%) of the 46 lineages of Percomorphaceae as shown in Fig. 1.2, and bidirectional sex change evolved in six of them (13%), whereas protandry evolved in five (11%) and simultaneous hermaphroditism in only three (7%). The abundance and wide distribution of protogyny in Percomorphaceae may be related to their mating systems which are associated with small social groups. These are seen especially in coral reef fishes, which will be described fully in Chap. 4. The predominance of protogyny in hermaphroditic fish contrasts markedly with the prevalence of simultaneous hermaphroditism observed in plant and invertebrate hermaphrodites (Avise 2011; Leonard 2019).

Functional hermaphroditism has not been confirmed in any vertebrates outside the infraclass Teleostei. It has been suggested in some hagfishes (Myxinoidea) through gonad histology (Gorbman 1990) but has never been confirmed (Adolfi et al. 2019). Protogynous sex change was suggested in a frog (Tetrapoda) by behavioral observations in captivity (Grafe and Linsenmair 1989) but has never been histologically confirmed (Hayes 1998; Leonard 2019). One of the factors hindering the evolution of functional hermaphroditism in major groups of vertebrates is thought to be the large anatomical differences between the sexes in these groups (Warner 1978). For example, sharks and rays (Chondrichthyes) have large copulatory organs, as do mammals and reptiles (Tetrapoda), and it would be very costly to maintain both types of organs simultaneously or to change from one type to the other.

In examining the habitats of extant hermaphroditic fishes, less than 3% (13 species) inhabit freshwater (Table 1.3). This is despite the fact that approximately 43% of all fish species inhabit freshwater (Nelson et al. 2016). Among freshwater species, simultaneous hermaphroditism is known in Cichlidae (1 species) and Rivulidae (3), protandry in Cobitidae (1) and Terapontidae (2), protogyny in Cichlidae (1), Poeciliidae (1), and Synbranchidae (4), and bidirectional sex change is unknown (Table 1.3). All these families, except for Cobitidae (Cypriniformes), belong to Percomorphaceae. The lack of hermaphroditism in freshwater fishes has been suggested to be due to anatomical sex differences (Warner 1978; Sadovy de Mitcheson and Liu 2008), mating systems (Kuwamura et al. 2020), or evolutionary history (Pla et al. 2021), but further research will be needed to explain this incongruity.

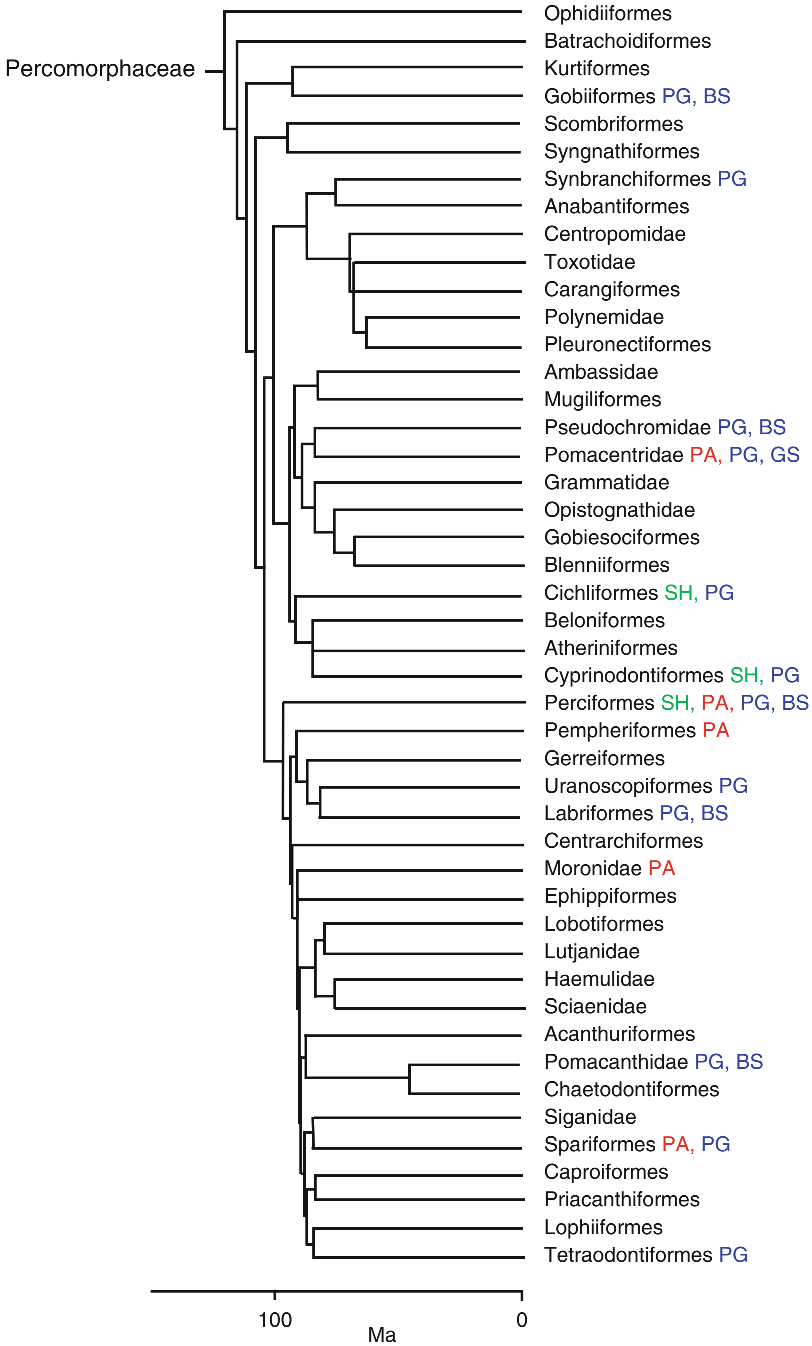

Fig. 1.2 Distribution of hermaphroditism within Percomorphaceae. The phyletic tree was processed from Hughes et al. (2018). *SH* simultaneous hermaphroditism, *PA* protandry, *PG* protogyny, *BS* bidirectional sex change or reversed sex change in protogynous species. The following families given in Tables 1.2 and 1.3 are classified to the orders in parentheses by

1.3 Theories for the Evolution of Hermaphroditism

The evolution of hermaphroditism among animals has been successfully explained by individual fitness, with two major hypotheses: the low-density model for simultaneous hermaphroditism and the size-advantage model for sequential hermaphroditism (Ghiselin 1969, 1974).

In low population density conditions, few mating opportunities are expected and mating success will be much higher in simultaneous hermaphrodites than in gonochorists if random mating occurs (Tomlinson 1966). This is despite the energy cost to hermaphrodites of maintaining two reproductive systems (Heath 1977). Self-fertilization further increases the benefits of simultaneous hermaphroditism in extreme low-population density environments with little opportunity to find conspecifics (Tomlinson 1966). Simultaneous hermaphroditism could also be favored if the investment in a sexual function shows diminishing fitness returns because of low mobility (Ghiselin 1969), restricted mating-group size (Charnov 1982), and/or local sperm competition (Schärer 2009), thus favoring reallocation of remaining reproductive resources to other sexual functions. A detailed explanation of this concept will be given in Chap. 2.

The size-advantage (SA) model predicts that the difference in the rate of increase in male and female fitness associated with body size (the SA) drives the evolution of sequential hermaphroditism or sex change (Ghiselin 1969, 1974). The occurrence and direction of sex change are determined by the mating system of each species, because the relation between reproductive success and body size of males depends on the mating system whereas reproductive success of females increases with growth irrespective of the mating system (Warner 1975, 1984: Fig. 1.3). For example, in species with random mating regardless of male body size (i.e., females do not have preference for larger males and accept smaller ones), male reproductive success is

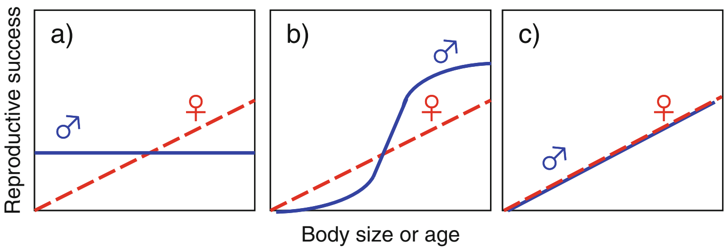

Fig. 1.3 Size-advantage model predicting evolution of sex change in relation to the type of mating system. (**a**) Protandry in species with random mating, (**b**) protogyny in species with polygyny, (**c**) gonochorism in species with size-assortative mating (modified from Warner 1984)

Fig. 1.2 (continued) Betancur-R et al. (2017), which are shown in this figure: Pinguipedidae (Uranoscopiformes), Trichonotidae (Gobiiformes), Creediidae (Pempheriformes), Platycephalidae (Perciformes), and Scorpaenidae (Perciformes) not related to body size. In these species, male-to-female sex change (protandry) will be favored because the reproductive success of small males is higher than that of females of the same size and vice versa in larger sizes (Fig. 1.3a). In contrast, in species with polygynous mating systems in which large males monopolize access to females, male reproductive success sharply increases with growth, and female-to-male sex change (protogyny) will be favored because large females can increase reproductive success by becoming male (Fig. 1.3b). 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 (Fig. 1.3c). Some mating systems with extensive sperm competition and size-fecundity skew will also reduce or eliminate the SA and result in a reduction or even an absence of sex change (Muñoz and Warner 2003, 2004).

Large volumes 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; Kuwamura et al. 2020). In contrast, bidirectional sex change has recently been seen 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 population density (Munday et al. 2010). This type of change has been suggested to derive from either protogynous ancestors (the low-density hypothesis for the evolution of reversed sex change in protogynous species: Kuwamura et al. 2011, 2014) or gonochoristic ones (Sunobe et al. 2017). Reversed sex change has not been reported at all from protandrous fish species (Kuwamura et al. 2020). In random mating, where the SA model predicts protandry, large females do not monopolize multiple mates, and smaller females have the opportunity to acquire mates without sex change (see Chap. 3), whereas in polygynous and protogynous species, small males have no opportunity to acquire females in the vicinity of larger males that monopolize access to females, thus necessitating reversed sex change (see Chaps. 4 and 5). In size-assortative monogamy (size-matched pairings: e.g., the coral goby *Paragobiodon echinocephalus*), where the SA model predicts gonochorism, both sexes seek large mates and undergo bidirectional sex change to avoid the risk of movement (see Chap. 5), whereas in non-size-assortative monogamy, females accept smaller males (e.g., the protandrous anemonefishes) and do not undergo reversed sex change as in random mating (see Chap. 3).

1.4 Mating System and Social Control of Sex Change

Since many studies, both empirical and theoretical, have suggested mating systems as one of the important drivers of the evolution of hermaphroditism, the relationship between mating systems and hermaphroditism will be the main focus of this book. In this book we follow the classification of fish mating systems into seven types by

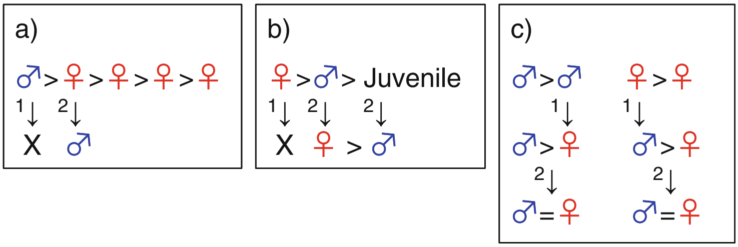

Fig. 1.4 Three types of social control of sex change. (**a**) protogyny in a harem (e.g., *Labroides dimidiatus*): (1) death of the male; (2) sex change of the largest female. (**b**) Protandry in a monogamous pair (e.g., *Amphiprion bicinctus*): (1) death of the female; (2) sex change of the male and maturation of the largest juvenile into a male. (**c**) Bidirectional sex change in a size-assortative monogamy (e.g., *Paragobiodon echinocephalus*): (1) sex change of the smaller male in a male-male pair and the larger female in a female-female pair; (2) growth-rate advantage in females

Kuwamura et al. (2020) and show the type of each hermaphroditic species in Table 1.2.

1. Random mating: Females mate with males regardless of the males' body size and without preference for larger males. Pair bonding (i.e., close and lasting association between a male and female) does not occur.
2. Non-size-assortative monogamy: Pair bonding of a male and a female occurs, in which females have no preference for male size and accept smaller males.
3. Size-assortative monogamy: Pair bonding of a male and a female occurs, in which both prefer larger mates, resulting in pairing of similar-sized mates.
4. Harem polygyny: A large male monopolizes a harem of females with territorial male-male competition.
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: This category is used 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 conditions (Barlow 1984), is not shown in Table 1.2.

The mating systems and types of hermaphroditism observed in each species fit the predictions of the SA model in most cases (Kuwamura et al. 2020), and detailed examples will be presented in the following chapters. In the remainder of this section, three typical cases are used to explain the relationship between the type of mating system, social control of sex change, and the SA model (Fig. 1.4).

Social control of sex change was first confirmed by male-removal experiments in the haremic protogynous wrasse *Labroides dimidiatus* on a coral reef (Robertson 1972). Only the largest female of a harem can change sex after male-removal, and smaller females are inhibited to change sex by the dominant fish (Fig. 1.4a). Within an hour after the removal of the male, the largest female started male courtship behavior and conducted pair spawning with a smaller female (Nakashima et al. 2000). Female-female spawning continued for a few weeks until the completion of gonadal change had occurred. The largest female can increase its fitness or reproductive success by changing sex to fertilize eggs of multiple females of its harem (Fig. 1.3b). Despite this benefit, it suffers the cost of sex change as it cannot reproduce during the sex change transition period. In general, an individual should change sex if it can increase its reproductive value (future expected reproduction) by doing so (Warner 1988; Munday et al. 2006). Reproductive values are often dependent on the local environment, local population demography, and the individual's own status, so labile sex change appears to be common.

In the protandrous anemonefish *Amphiprion bicinctus*, only the largest male can change sex after female removal from a monogamous pair, and the smaller fish will mature as males (Fricke and Fricke 1977: Fig. 1.4b). In monogamous pairs of anemonefish, the larger partner is female because it can produce more eggs than the smaller partner. Additionally, the female accepts a smaller male because even small males can guard eggs attached to the substrate adjacent to its host sea anemone whose tentacles often cover the egg clutch, thus protecting the eggs from predators. In such monogamous pairs in which the female is larger than the male, the rate of increase in male and female fitness with body size is similar to that seen in random mating fishes as shown in Fig. 1.3a (see Sunobe et al. 2022).

In contrast, monogamous pairs of the coral goby *P. echinocephalus* are size-assortative because females prefer large males that can guard a large clutch of eggs attached on the surface of coral branches (Kuwamura et al. 1994). Large pairs live in large coral heads, and small pairs in small corals. No SA in fecundity exists in such size-assortative pairs (Fig. 1.3c), but growth-rate advantage in females will favor protogyny (Iwasa 1991; Kuwamura et al. 1994). In newly formed pairs, the larger will become male: if two males meet, the smaller changes sex to female, and if two females meet, the larger changes sex to male (bidirectional sex change; Nakashima et al. 1995: Fig. 1.4c). The smaller female will grow faster than the male, which has less feeding time due to guarding the eggs, and therefore results in a size-assortative pair (Kuwamura et al. 1994). The reversed sex change (male-to-female) has also been reported in facultative monogamous pairs of the protogynous *L. dimidiatus* in low-density conditions, such as when females were removed from monogamous pairs. In this case, when two widowed males met, the smaller proceeded to change sex to female (Kuwamura et al. 2011, 2014).

The degree of social control depends on the type of mating system. This will be described in detail in the following chapters.

1.5 Physiological Mechanisms of Sex Change

The physiological mechanisms of sex change are not described in detail in this book, but are briefly summarized here. The mechanisms of socially cued sex change have been hypothesized as follows (e.g., in the bluehead wrasse *Thalassoma bifasciatum*, Todd et al. 2019). In the brain of the largest female of a social group, after the perception of a social cue (i.e., absence of a dominant male), cortisol increases *isotocin* expression to promote male-typical behaviors that rapidly establish social dominance. In the gonads, cortisol promotes transition from ovaries to testes via three pathways: (1) downregulates aromatase (*cyp19a1a*) expression to cease estrogen (17ß-estradiol: E2) production and to decline feminizing expression, causing ovarian atresia; (2) upregulates *amh* expression, which can suppress feminizing genes and promote oocyte apoptosis while promoting masculinizing expression and spermatogonial recruitment; and (3) upregulates androgenic genes *cyp11c1* and *hsd11b2* to increase androgen (11-ketotestosterone: 11-KT) production which supports testicular development. Epigenetic reprogramming, via changes in sexually dimorphic DNA methylation, rewrites cellular memory of sexual fate and canalizes sex-specific expression.

In addition to the hypothalamic-pituitary-interrenal axis mentioned above, the hypothalamic-pituitary-gonadal axis has been proposed as the major signaling pathway regulating sex change in hermaphroditic fish (Casas and Saborido-Rey 2021). The hypothalamus released gonadotropin-releasing hormones (GnRH) in the brain, stimulating the pituitary to synthetize and secrete the two gonadotropins (GtHs: luteinizing hormone and follicle stimulating hormone) into the blood system. Subsequently, GtHs regulate the production of sex hormones in the gonad via their receptors, either follicle cells in the ovaries, or Leydig cells in the testes. However, despite intense research, significant gaps remain in our knowledge of the perception of environmental cues and how they are mediated by the social context, the mechanisms underlying their integration and processing at the brain level, and the exact roles of well-known players at the gonadal level (Casas and Saborido-Rey 2021).

1.6 Conclusions

1. Functional hermaphroditism has been reported in 481 fish species belonging to 41 families of 17 teleost orders. Simultaneous hermaphroditism is known in 57 species belonging to 13 families, and among species exhibiting sequential hermaphroditism, protogyny is much more common (314 species of 20 families) than protandry (62 species of 14 families) and bidirectional sex change (69 species of 7 families).
2. Simultaneous hermaphroditism and protandry have evolved several times in not closely related lineages of Teleostei, whereas protogyny and bidirectional sex change have evolved widely and only in Percomorphaceae.

3. The evolution of hermaphroditism has been successfully explained by individual fitness, with two major hypotheses: the low-density model for simultaneous hermaphroditism and the size-advantage model for sequential hermaphroditism.
4. Mating system type is one of the important drivers of the evolution of hermaphroditism, and the relationship between mating systems and hermaphroditism will be focused on in the following chapters.
5. Sex change is socially controlled in many fishes, and its physiological mechanisms are briefly summarized.

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