Tetsuo Kuwamura · Kota Sawada ·
Tomoki Sunobe · Yoichi Sakai ·
Tatsuru Kadota *Editors*

Hermaphroditism and Mating Systems in Fish

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ISBN 978-981-19-6094-9 ISBN 978-981-19-6095-6 (eBook)
https://doi.org/10.1007/978-981-19-6095-6

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Preface

This book focuses on the behavioral ecology of functional hermaphroditism in fishes. Behavioral ecology, which examines the survival value of behavior and individual fitness based on the theory of natural selection, was established in the 1970s (Wilson 1975; Dawkins 1976; Krebs and Davies 1978, 1981). At around the same time, the evolution of hermaphroditism based on individual fitness was first explained by Michael T. Ghiselin (1969). Soon after, Robert R. Warner (1975) developed a simple mathematical model of life history strategy in relation to mating systems, which could predict the type of sex change (male-to-female or female-to-male) by the type of mating system of a species. Field research on fish behavioral ecology also started in the 1970s; e.g., D. Ross Robertson (1972) first confirmed social control of sex change by male-removal experiments in a haremic coral reef fish. Thereafter, many field studies focused on the mating systems of hermaphroditic fishes have been conducted primarily on coral reefs (Nakazono and Kuwamura 1987; Munday et al. 2006; Kuwamura et al. 2020).

Chapter 1 (by Tetsuo Kuwamura) of this book introduces the types and frequencies of hermaphroditism in fishes, phylogeny of hermaphroditic fishes and their habitats, theories of the evolution of hermaphroditism, types of mating systems, and examples of social control of sex change. Chapter 2 (by Kota Sawada) describes simultaneous hermaphroditism in fishes and their mating systems. Chapter 3 (by Tomoki Sunobe) introduces protandrous species that conduct male-to-female sex change and their mating systems. In Chapter 4 (by Yoichi Sakai), protogynous fishes that conduct female-to-male sex change and their mating systems are explained. Lastly, Chapter 5 (by Tatsuru Kadota) introduces species with bidirectional sex change (or reversed sex change in protogynous species) and their mating systems.

At the end of this book, we add Chapter 6, which provides a database of functionally hermaphroditic fish species and their references. Kuwamura et al. (2020) reported 461 species of functionally hermaphroditic fishes. This book adds 21 species and deletes one species.

Nagoya, Aichi, Japan

Tetsuo Kuwamura
On behalf of the authors and editors

References

Dawkins R (1976) The selfish gene. Oxford University Press

Ghiselin MT (1969) The evolution of hermaphroditism among animals. Q Rev Biol 44:189–208

Krebs JR, Davies NB (eds) (1978) Behavioural ecology. Blackwell

Krebs JR, Davies NB (1981) An introduction to behavioural ecology. Blackwell

Kuwamura T, Sunobe T, Sakai Y, Kadota T, Sawada K (2020) Hermaphroditism in fishes: an annotated list of species, phylogeny, and mating system. Ichthyol Res 67:341–360

Munday PL, Buston PM, Warner RR (2006) Diversity and flexibility of sex-change strategies in animals. Trends Ecol Evol 21:89–95

Nakazono A, Kuwamura T (eds) (1987) Sex change in fishes. Tokai University Press, Tokyo

Robertson DR (1972) Social control of sex reversal in a coral-reef fish. Science 177: 1007–1009

Warner RR (1975) The adaptive significance of sequential hermaphroditism in animals. Am Nat 109:61–82

Wilson EO (1975) Sociobiology: the new synthesis. Belknap Press of Harvard University Press

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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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T. Kuwamura et al. (eds.), *Hermaphroditism and Mating Systems in Fish*,
https://doi.org/10.1007/978-981-19-6095-6_1

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

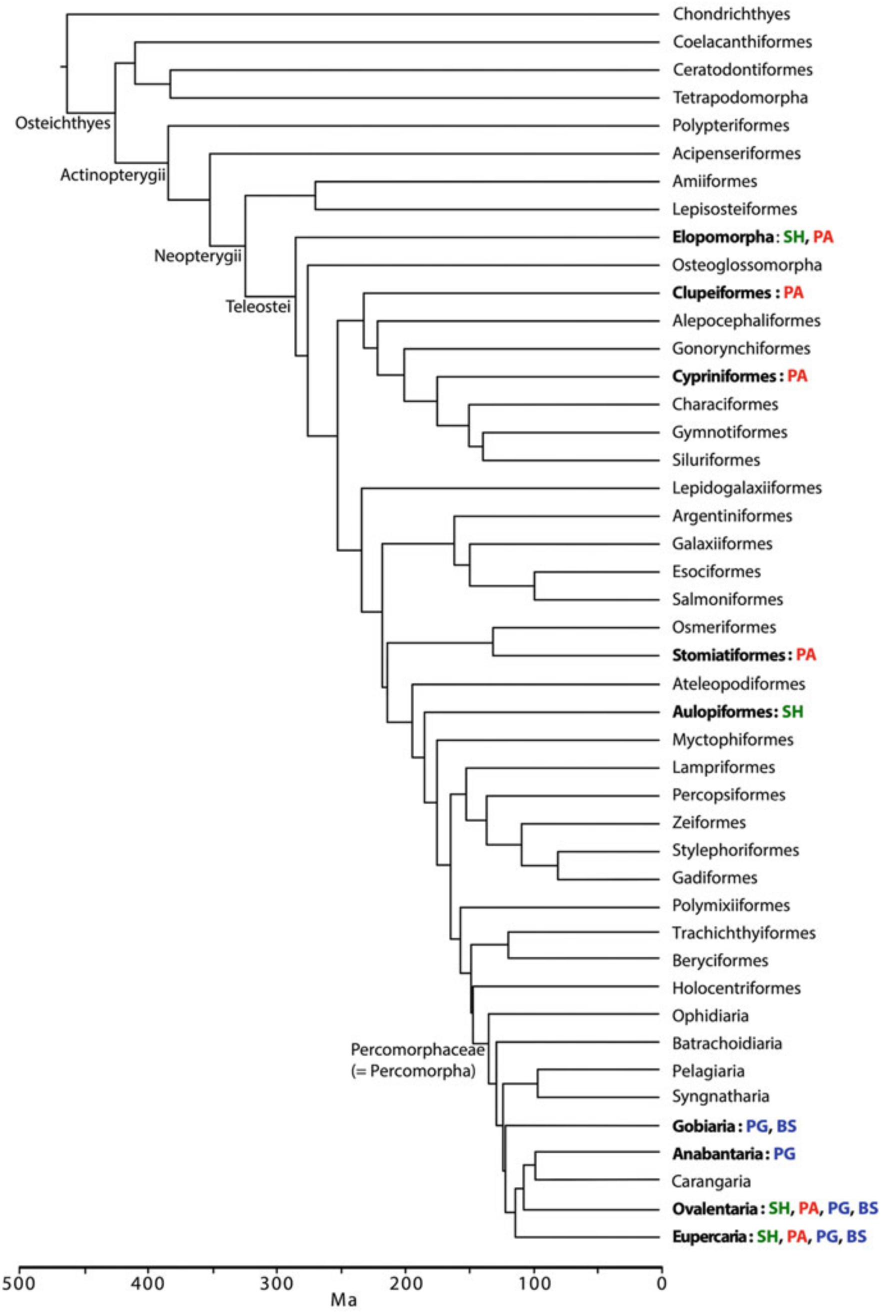

Fig. 1.1 Phylogeny of fishes and occurrence of hermaphroditism. The phylogenetic tree was processed from Betancur-R et al. (2017). *SH* simultaneous hermaphroditism, *PA* protandry, *PG* protogyny, *BS* bidirectional sex change or reversed sex change in protogynous species (reproduced from Kuwamura et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

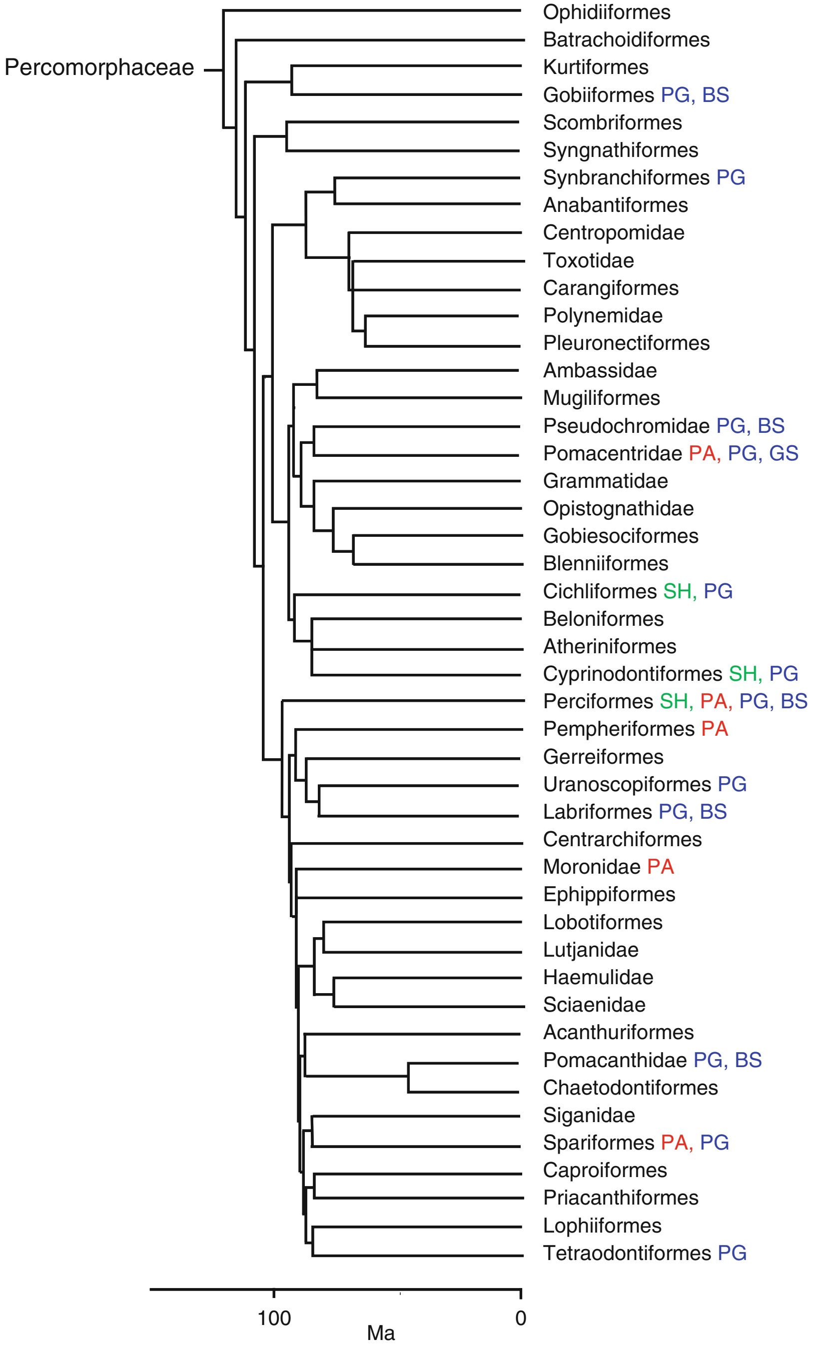

Fig. 1.2 Distribution of hermaphroditism within Percomorphaceae. The phyletic tree was processed from Hughes et al. (2018). *SH* simultaneous hermaphroditism, *PA* protandry, *PG* protogyny, *BS* bidirectional sex change or reversed sex change in protogynous species. The following families given in Tables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

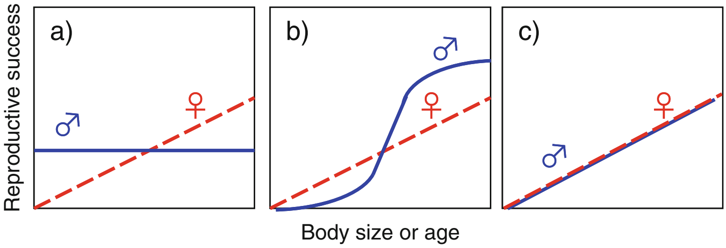

Fig. 1.3 Size-advantage model predicting evolution of sex change in relation to the type of mating system. (**a**) Protandry in species with random mating, (**b**) protogyny in species with polygyny, (**c**) gonochorism in species with size-assortative mating (modified from Warner 1984)

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

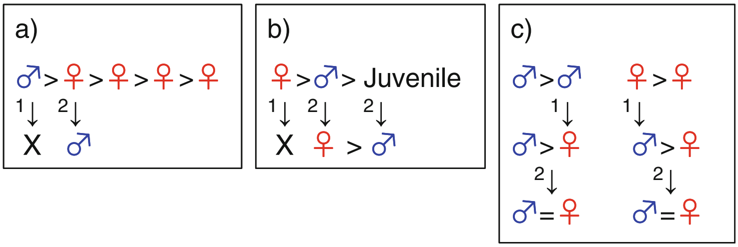

Fig. 1.4 Three types of social control of sex change. (**a**) protogyny in a harem (e.g., *Labroides dimidiatus*): (1) death of the male; (2) sex change of the largest female. (**b**) Protandry in a monogamous pair (e.g., *Amphiprion bicinctus*): (1) death of the female; (2) sex change of the male and 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.

Acknowledgments I thank Tatsuru Kadota, Yoichi Sakai, Kota Sawada, and Tomoki Sunobe for helpful comments to improve the manuscript. I also thank Enago (www.enago.jp) for the English language review.

References

Adolfi MC, Nakajima RT, Nóbrega RH, Schartl M (2019) Intersex, hermaphroditism, and gonadal plasticity in vertebrates: evolution of the Müllerian duct and Amh/Amhr2 signaling. Annu Rev Anim Biosci 7:149–172

Ashman TL, Bachtrog D, Blackmon H, Goldberg EE, Hahn MW et al (2014) Tree of sex: a database of sexual systems. Sci Data 1:140015

Avise J (2011) Hermaphroditism: a primer on the biology, ecology, and evolution of dual sexuality. Columbia University Press, New York

Barlow GW (1984) Patterns of monogamy among teleost fishes. Arch FischWiss 35:75–123

Betancur-R R, Wiley EO, Arratia G, Acero A, Bailly N et al (2017) Phylogenetic classification of bonyfishes. BMC Evol Biol 17:162

Casas L, Saborido-Rey F (2021) Environmental cues and mechanisms underpinning sex change in fish. Sex Dev 15:108–121

Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton

Erisman BE, Petersen CW, Hastings PA, Warner RR (2013) Phylogenetic perspectives on the evolution of functional hermaphroditism in teleost fishes. Integr Comp Biol 53:736–754

Fricke H, Fricke S (1977) Monogamy and sex change by aggressive dominance in coral reef fish. Nature 266:830–832

Ghiselin MT (1969) The evolution of hermaphroditism among animals. Q Rev Biol 44:189–208

Ghiselin MT (1974) The economy of nature and the evolution of sex. University of California Press, Berkeley, California

Gorbman A (1990) Sex differentiation in the hagfish *Eptatretus stouti*. Gen Comp Endocrinol 77: 309–332

Grafe TU, Linsenmair KE (1989) Protogynous sex change in the reed frog *Hyperolius viridiflavus*. Copeia 1989:1024–1029

Hamilton WD, Axelrod R, Tanese R (1990) Sexual reproduction as an adaptation to resist parasites (a review). Proc Natl Acad Sci U S A 87:3566–3573

Hayes TB (1998) Sex determination and primary sex differentiation in amphibians: genetic and developmental mechanisms. J Exp Zool 281:373–399

Heath DJ (1977) Simultaneous hermaphroditism; cost and benefit. J Theor Biol 64:363–373

Hughes LC, Ortí G, Huang Y, Sun Y, Baldwin CC et al (2018) Comprehensive phylogeny of ray-finned fishes (Actinopterygii) based on transcriptomic and genomic data. Proc Natl Acad Sci U S A 115:6249–6254

Iwasa Y (1991) Sex change evolution and cost of reproduction. Behav Ecol 2:56–68

Kazancıoğlu E, Alonzo SH (2010) A comparative analysis of sex change in Labridae supports the size advantage hypothesis. Evolution 64:2254–2264

Kuwamura T, Kadota T, Suzuki S (2014) Testing the low-density hypothesis for reversed sex change in polygynous fish: experiments in *Labroides dimidiatus*. Sci Rep 4:4369

Kuwamura T, Nakashima Y, Yogo Y (1994) Sex change in either direction by growth-rate advantage in the monogamous coral goby, *Paragobiodon echinocephalus*. Behav Ecol 5:434–438

Kuwamura T, Sunobe T, Sakai Y, Kadota T, Sawada K (2020) Hermaphroditism in fishes: an annotated list of species, phylogeny, and mating system. Ichthyol Res 67:341–360

Kuwamura T, Suzuki S, Kadota T (2011) Reversed sex change by widowed males in polygynous and protogynous fishes: female removal experiments in the field. Naturwissenschaften 98:1041–1048

Lehtonen J, Jennions MD, Kokko H (2012) The many costs of sex. Trends Ecol Evol 27:172–178

Leonard JL (2019) Transitions between sexual systems: understanding the mechanisms of, and pathways between, dioecy, hermaphroditism and other sexual systems. Springer, Berlin

Mank JE, Promislow DE, Avise JC (2006) Evolution of alternative sex-determining mechanisms in teleost fishes. Biol J Linn Soc 87:83–93

Maynard-Smith J (1978) The evolution of sex. Cambridge University Press, Cambridge

Munday PL, Buston PM, Warner RR (2006) Diversity and flexibility of sex-change strategies in animals. Trends Ecol Evol 21:89–95

Munday PL, Kuwamura T, Kroon FJ (2010) Bidirectional sex change in marine fishes. In: Cole KS (ed) Reproduction and sexuality in marine fishes: patterns and processes. University of California Press, Berkeley, California, pp 241–271

Muñoz RC, Warner RR (2003) A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size-fecundity skew. Am Nat 161:749–761

Muñoz RC, Warner RR (2004) Testing a new version of the size-advantage hypothesis for sex change: sperm competition and size-skew effects in the bucktooth parrotfish, *Sparisoma radians*. Behav Ecol 15:129–136

Nakashima Y, Kuwamura T, Yogo Y (1995) Why be a both-ways sex changer? Ethology 101:301–307

Nakashima Y, Sakai Y, Karino K, Kuwamura T (2000) Female-female spawning and sex change in a haremic coral-reef fish, *Labroides dimidiatus*. Zool Sci 17:967–970

Nakazono A, Kuwamura T (1987) Sex change in fishes. Tokai University Press, Tokyo

Nelson JS, Grande TC, Wilson MVH (2016) Fishes of the world, 5th edn. John Wiley & Sons, New Jersey

Pla S (2019) Evolutionary transitions, environmental correlates and life-history traits associated with the distribution of the different forms of hermaphroditism in fish. PhD. thesis. Universitat Autònoma de Barcelona, Spain

Pla S, Maynou F, Piferrer F (2021) Hermaphroditism in fish: incidence, distribution and associations with abiotic environmental factors. Rev Fish Biol Fisheries 31:935–955

Robertson DR (1972) Social control of sex reversal in a coral-reef fish. Science 177:1007–1009

Sadovy de Mitcheson Y, Liu M (2008) Functional hermaphroditism in teleosts. Fish Fish (Oxf) 9:1–43

Schärer L (2009) Tests of sex allocation theory in simultaneously hermaphroditic animals. Evolution 63:1377–1405

Sunobe T, Iwata S, Shi C, Kuwamura T (2022) Monogamy and protandry caused by exclusion of the same sex and random pairing in anemonefishes: a simulation model and aquarium experiments. J Ethol 40:265–272

Sunobe T, Sado T, Hagiwara K, Manabe H, Suzuki T et al (2017) Evolution of bidirectional sex change and gonochorism in fishes of the gobiid genera *Trimma*, *Priolepis*, and *Trimmatom*. Sci Nat 104:15

Todd EV, Ortega-Recalde O, Liu H et al (2019) Stress, novel sex genes, and epigenetic reprogramming orchestrate socially controlled sex change. Sci Adv 5:eaaw7006

Tomlinson J (1966) The advantages of hermaphroditism and parthenogenesis. J Theor Biol 11:54–58

Warner RR (1975) The adaptive significance of sequential hermaphroditism in animals. Am Nat 109:61–82

Warner RR (1978) The evolution of hermaphroditism and unisexuality in aquatic and terrestrial vertebrates. In: Reese ES, Lighter FJ (eds) Contrasts in behavior. Wiley, New York, pp 77–101

Warner RR (1984) Mating behavior and hermaphroditism in coral reef fishes. Am Sci 72:128–136

Warner RR (1988) Sex change and the size-advantage model. Trends Ecol Evol 3:133–136

Chapter 2
Simultaneous Hermaphroditism in Fishes

Kota Sawada

Abstract Simultaneous hermaphrodites have both male and female sexual functions at the same time. In this chapter, I briefly summarize the theories on the adaptive significance of simultaneous hermaphroditism and provide a detailed review of each teleost taxon having this sexual strategy, including Aulopiformes, *Kryptolebias* killifishes, Serranidae, and other understudied taxa. In Aulopiformes, simultaneous hermaphroditism is associated with deep-sea habitats and is most likely an adaptation to limited mating opportunities. *Kryptolebias* offer a unique case of mixed mating, including self-fertilizing hermaphrodites and males. Simultaneously hermaphroditic species of Serranidae exhibit diverse sexual and mating systems, including egg trading and harems. The lack of information on other taxa hampers any substantial discussion; however, some taxa offer important clues for understanding the evolution of hermaphroditism. Finally, I conclude with remarks on the apparent lack of evolutionary lability of simultaneous hermaphroditism and potential comparative approaches to this issue.

Keywords Androdioecy · Egg trading · Self-fertilization · Simultaneous hermaphroditism

2.1 What Is Simultaneous Hermaphroditism?

Simultaneous hermaphrodites have both male and female sexual functions at the same time, in contrast to sequential hermaphrodites, which have only one sexual function at a time (Ghiselin 1969; Smith 1975; Charnov 1982; Leonard 2018). Owing to the simultaneous coexistence of male and female functions, some can reproduce via self-fertilization, whereas others reproduce via outcrossing obligately or facultatively (mixed mating; Jarne and Charlesworth 1993). Although this sexual system is observed in a wide range of plants and invertebrates, it is rather rare in

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T. Kuwamura et al. (eds.), *Hermaphroditism and Mating Systems in Fish*,
https://doi.org/10.1007/978-981-19-6095-6_2

fishes and has only been reported in Muraenidae, Cichlidae, Rivulidae, Polynemidae, and several families of Aulopiformes (Kuwamura et al. 2020). Some fishes morphologically have male and female gonads at the same time, but only one of them is functional at a time (e.g. St. Mary 1993, 1994; see Chap. 5). Because this book focuses on functional sexuality, I do not categorize them as simultaneous hermaphrodites.

Simultaneous hermaphrodites sometimes coexist with other sexual expressions within a species or population (Weeks 2012), forming androdioecy (simultaneous hermaphrodites and males) or gynodioecy (hermaphrodites and females). Androdioecy has evolved several times in various invertebrate taxa (Weeks et al. 2006a), such as barnacles (Sawada et al. 2015; Yusa 2018), and is also found in teleost fishes (discussed later). In contrast, gynodioecy is much rarer among animals in general (Weeks 2012) and is absent among teleosts. The only known example of this system in vertebrates is the Atlantic hagfish *Myxine glutinosa* (see Powell et al. 2004; Weeks 2012). Trioecy (the coexistence of males, females, and hermaphrodites) has been reported in a few species of Polynemidae (Nayak 1959; Kagwade 1967), although the details are not known.

As several androdioecious species are discussed in this chapter, it is worth clarifying the definition of the term "androdioecy." In this chapter, androdioecy is defined as a sexual system in which simultaneous hermaphrodites and males coexist. Note that this definition includes systems in which males and simultaneous hermaphrodites are at different stages of a life history trajectory, caused by ontogenetic transitions from simultaneous hermaphrodites to males, or vice versa. As will be discussed later, the former transition has been observed in a few teleost taxa. The latter is relatively common in invertebrates and is often categorized as protandric simultaneous hermaphroditism. Some authors, including myself, have defined androdioecy to exclude such cases and have applied the term only when there are distinct life history trajectories corresponding to males and simultaneous hermaphrodites (Pannell 2002; Yusa et al. 2013; Sawada et al. 2015; Pla et al. 2021). Although I acknowledge the usefulness of this narrower definition in other contexts, in this chapter, I adopt the broader definition to maintain consistency with the relevant literature (e.g. Weeks 2012; Erisman et al. 2013; Leonard 2018) and to avoid confusion regarding killifishes in which both primary and secondary (derived from hermaphrodites) males can be induced (see Sect. 2.4).

The occurrence of simultaneous hermaphroditism among teleost fishes is summarized in Table 2.1 (extracted and modified from Chap. 6). Functional simultaneous hermaphroditism has been confirmed in 57 species of teleosts; however, inconclusive evidence has been obtained for several other species. Note that I dismissed a considerable number of species listed as simultaneous hermaphrodites by Pla et al. (2021) because their references include literature that mentions sexuality (often for larger taxa rather than each species) but provides no species-level evidence (several species of Aulopiformes; Smith 1975; Sulak 1995; Ota et al. 2000; Davis and Fielitz 2010), a species catalogue without any description of the focal species (*Serranus notospilus*; Longley and Hildebrand 1941), a paper that only described an immature specimen of the focal species (*Parasudis truculenta*; Mead 1960), a

Table 2.1 List of simultaneous hermaphrodites in teleost fishes (extracted from Chap. 6)

Order-family	Species	Confirmed*	Androdioecy/ trioecy**	Mating system	Habitat	Refs.	Remarks
Anguilliformes							
Muraenidae	*Gymnothorax griseus*	Y	N		Coral reef	Fishelson (1992)	
	Gymnothorax pictus	Y	N		Coral reef	Fishelson (1992)	
	Gymnothorax thyrsaoideus	Y	N		Coral reef	Fishelson (1992)	
Aulopiformes							
Ipnopidae	*Bathymicrops brevianalis*	Y	N		Deep sea	Nielsen (1966)	
	Bathymicrops regis	Y	N		Deep sea	Nielsen (1966)	
	Bathypterois grallator	Y	N		Deep sea	Mead (1960)	
	Bathypterois mediterraneus	Y	N		Deep sea	Fishelson and Galil (2001); Porcu et al. (2010)	
	Bathypterois quadrifilis	Y	N		Deep sea	Mead (1960)	
	Bathypterois viridensis	Y	N		Deep sea	Mead (1960)	
	Bathytyphlops marionae	Y	N		Deep sea	Nielsen (1966)	
	Bathytyphlops sewelli	N	N		Deep sea	Merrett et al. (1973)	[a]
	Ipnops agassizii	Y	N		Deep sea	Nielsen (1966)	
	Ipnops meadi	Y	N		Deep sea	Nielsen (1966)	

(continued)

Table 2.1 (continued)

Order-family	Species	Confirmed*	Androdioecy/ trioecy**	Mating system	Habitat	Refs.	Remarks
Giganturidae	*Gigantura chuni*	Y	N	Pair-bonding?	Deep sea	Johnson and Bertelsen (1991); Kupchik et al. (2018)	
	Gigantura indica	Y	N	Pair-bonding?	Deep sea	Johnson and Bertelsen (1991); Kupchik et al. (2018)	[b]
Bathysauridae	*Bathysaurus ferox*	Y	N		Deep sea	Sulak et al. 1985	
	Bathysaurus mollis	Y	N		Deep sea	Sulak et al. 1985	
Chlorophthalmidae	*Chlorophthalmus agassizi*	Y	N		Deep sea	Follesa et al. (2004); Anastasopoulou et al. (2006); Cabiddu et al. (2010)	
	Chlorophthalmus brasiliensis	Y	N		Deep sea	Mead (1960)	
	Parasudis truculenta	Y	N		Deep sea	Mead (1960)	
Notosudidae	*Ahliesaurus brevis*	Y	N		Deep sea	Bertelsen et al. (1976)	
Scopelarchidae	*Benthalbella infans*	Y	N		Deep sea	Merrett et al. (1973)	
	Scopelarchus guentheri	Y	N		Deep sea	Merrett et al. (1973)	
Paralepididae	*Arctozenus risso*	Y	N		Deep sea	Devine and Guelpen (2021)	
	Lestidium pseudosphyraenoides	Y	N		Deep sea	Mead (1960)	
Alepisauridae	*Alepisaurus brevirostris*	N	N		Deep sea	Gibbs (1960)	[c]
	Alepisaurus ferox	N	N		Deep sea	Gibbs (1960)	[c]
	Omosudis lowii	Y	N		Deep sea	Merrett et al. (1973); Smith and Atz (1973)	

Ovalentaria *incertae sedis*							
Pseudochromidae	*Pseudoplesiops howensis*	N	N		Coral reef	Cole and Gill (2000)	
Cichliformes							
Cichlidae	*Satanoperca jurupari*	Y	N	Internal self-fertilization, biparental mouthbrooder	Estuarine	Reid and Atz (1958); Matos et al. (2002)	[d]
Cyprinodontiformes							
Rivulidae	*Kryptolebias hermaphroditus*	Y	A?	Internal self-fertilization	Freshwater/brackish	Tatarenkov et al. (2009); Costa et al (2010); Berbel-Filho et al. (2016)	
	Kryptolebias marmoratus	Y	A	Internal self-fertilization, external outcrossing	Freshwater/brackish	Harrington Jr (1961, 1963, 1971); Soto et al. (1992); Sakakura and Noakes (2000); Sakakura et al. (2006); Furness et al. (2015)	
	Kryptolebias ocellatus	Y	A	Predominantly outcrossing	Freshwater	Tatarenkov et al. (2009); Costa et al. (2010); Berbel-Filho et al. (2020)	
Perciformes							
Polynemidae	*Filimanus heptadactyla*	Y	T		Tropical sea	Nayak (1959); Kagwade (1967)	
	Polydactylus microstomus	Y	T		Tropical sea	Dorairaj 1973	

(continued)

Table 2.1 (continued)

Order-family	Species	Confirmed*	Androdioecy/ trioecy**	Mating system	Habitat	Refs.	Remarks
Serranidae	*Bullisichthys caribbaeus*	Y	N		Coral reef	Smith and Erdman (1973)	
	Diplectrum bivittatum	Y	N		Temperate sea	Touart and Bortone (1980)	
	Diplectrum formosum	Y	N		Temperate sea	Bortone (1971)	
	Diplectrum macropoma	Y	N		Temperate sea	Bortone (1977a)	
	Diplectrum pacificum	Y	N		Tropical sea	Bortone (1977b)	
	Diplectrum rostrum	Y	N		Tropical sea	Bortone (1974)	
	Hypoplectrus aberrans	Y	N	Reciprocal pair spawning	Coral reef	Fischer (1981)	
	Hypoplectrus chlorurus	Y	N	Reciprocal pair spawning	Coral reef	Barlow (1975)	
	Hypoplectrus nigricans	Y	N	Reciprocal pair spawning, serial monogamy	Coral reef	Fischer (1980); Petersen (1991)	
	Hypoplectrus puella	Y	N	Repeated pair spawning	Coral reef	Barlow (1975); Fischer (1981)	
	Hypoplectrus unicolor	Y	N	Reciprocal pair spawning	Coral reef	Barlow (1975); Fischer (1981)	
	Serraniculus pumilio	Y	N		Tropical sea	Hastings (1973)	

	Serranus annularis	Y	N		Tropical sea	Bullock and Smith (1991)	
	Serranus atricauda	Y	N		Temperate sea	García-Díaz et al. (2002)	
	Serranus auriga	Y	N		Temperate sea	Militelli and Rodrigues (2011)	
	Serranus baldwini	Y	A	Harem	Tropical sea	Fischer and Petersen (1986); Petersen and Fischer (1986)	
	Serranus cabrilla	Y	N		Temperate sea	García-Díaz et al. (1997)	
	Serranus hepatus	Y	N		Temperate sea	Bruslé (1983)	
	Serranus phoebe	Y	N		Tropical sea	Smith (1959)	
	Serranus psittacinus	Y	A	Harem, monogamy, complex harem	Tropical sea	Hastings and Petersen (1986); Petersen (1987; 1990a, 1990b)	
	Serranus scriba	Y	N		Temperate sea	Zorica et al. (2005); Tuset et al. (2005)	
	Serranus subligarius	Y	N	Reciprocal pair spawning, promiscuous	Temperate sea	Hastings and Bortone (1980); Oliver (1997)	
	Serranus tabacarius	Y	N	Reciprocal pair spawning, promiscuous	Coral reef	Petersen 1995	
	Serranus tigrinus	Y	N	Monogamy, pair spawning	Coral reef	Pressley (1981); Petersen (1991)	

(continued)

Table 2.1 (continued)

Order-family	Species	Confirmed*	Androdioecy/ trioecy**	Mating system	Habitat	Refs.	Remarks
	Serranus tortugarum	Y	N	Reciprocal pair spawning, serial monogamy, monogamy	Coral reef	Fischer (1984b); Fischer and Hardison (1987); Petersen (1991); Hart (2016)	
	Pseudogramma gregoryi	Y	N		Coral reef	Smith and Atz (1969)	

Order and family names are arranged following Nelson et al. (2016), and genus and species in alphabetical order within each family and genus, respectively.

? indicates that it is suggested but not confirmed

**Y* yes, *N* no, ***N* neither and rodioecy nor trioecy, *A* androdioecy, *T* trioecy

[a] Male function not confirmed

[b] Clarke and Wagner (1976) described males and one matured female for *Bathyleptus lisae*, a synonym of *Gigantura indica*

[c] Poor fixation of gonad

[d] Reid and Atz (1958) described mating behavior by males and females

review discussing functionally sequential hermaphrodites (*Priolepis* spp.; Cole 2010), or a completely irrelevant paper on a different taxon (*Stemonosudis macrura*; Leem et al. 1998).

In this chapter, I first briefly summarize the evolutionary theory of simultaneous hermaphroditism. Then, I provide reviews of three taxa (deep-sea aulopiforms, *Kryptolebias* killifishes, and serranids) that are relatively well studied in relation to the evolutionary conditions of simultaneous hermaphroditism. I conclude with a perspective on the evolutionary patterns of this sexual strategy.

2.2 Evolutionary Theory for Simultaneous Hermaphroditism

Two hypotheses have been widely recognized as explanations for the adaptive significance of simultaneous hermaphroditism in animals (Sawada and Yamaguchi 2020). The "low-density" hypothesis argues that simultaneous hermaphroditism is favored under conditions of limited mating opportunity because of low population density or limited mate-search ability (Tomlinson 1966; Ghiselin 1969; Smith 1975). When finding a mate is extremely difficult, hermaphrodites are more advantageous than gonochorists because (1) they can reproduce via self-fertilization without any mating encounter or (2) they can outcross with every conspecific adult they encounter, in contrast to gonochorists, who need to find an opposite-sex adult to reproduce. This hypothesis is often mentioned as an explanation for simultaneous hermaphroditism in deep-sea fishes (Ghiselin 1969; Merrett 1994).

Another hypothesis is called the "diminishing return hypothesis" (Charnov et al. 1976; Charnov 1982), which argues that diminishing fitness returns on investment in one sexual function favors simultaneous hermaphroditism (Fig. 2.1). For example, if reproductive success as a female is limited by brooding space, investing all available resources in female function should be wasteful; thus, it is adaptive to allocate some resources to male function (Heath 1979; Charnov 1982). The reproductive success of a male is limited by local sperm competition (Schärer 2009). If the mating group size is limited, e.g., by low population density or mobility, and thus sperm competition is weak, excess investment in male function (sperm production) is wasteful because it causes competition among sibling sperm over a limited number of eggs produced by individuals in the same group. As a result, allocating resources to both sexual functions (i.e., simultaneous hermaphroditism) is the optimal strategy. Local egg competition may also favor simultaneous hermaphroditism when sibling eggs compete, for example, over sperm or brooding spaces (Charnov 1982; Henshaw et al. 2014b). Diminishing fitness return can be caused by other peculiar mechanisms such as egg trading (see Sect. 2.5).

Although both hypotheses predict the evolution of simultaneous hermaphroditism under low mate availability or population density, the detailed prediction differs qualitatively (Charnov et al. 1976; Sawada and Yamaguchi 2020). For example, the

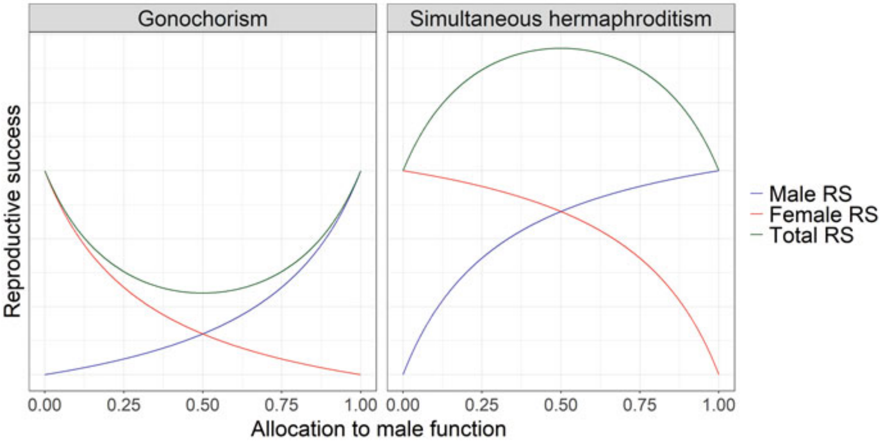

Fig. 2.1 A schematic drawing of evolutionary conditions favoring gonochorism and simultaneous hermaphroditism under diminishing return hypothesis (Charnov et al. 1976; Charnov 1982). The horizontal axis represents the proportion of reproductive resources allocated to male function. The vertical axis represents reproductive success (RS) as a male (blue), as a female (red), and in total (green). If the fitness return on each sexual function is increasing (left), total reproductive success is optimized by allocating all resources to male or female function (i.e., gonochoristic males or females). In contrast, if the fitness return is diminishing (right), intermediate allocation (i.e., simultaneous hermaphroditism) is optimal

low-density hypothesis does not predict hermaphroditism when individuals easily find a limited number of mates, but find it difficult to obtain additional mates, in contrast to the diminishing return hypothesis. Such a situation is likely to occur in sessile and aggregative organisms (Sawada and Yamaguchi 2020).

2.3 Deep-Sea Aulopiforms

It is often mentioned that simultaneous hermaphroditism is common among deep-sea fishes (Warner 1984; Herring 2001). More than one-third of fish species confirmed to be simultaneous hermaphrodites are deep-sea dwellers (Table 2.1). This proportion is remarkably high, given the scarcity and difficulty of studies on deep-sea species (cf. only six species, out of approximately 400 species for which sequential hermaphroditism is confirmed, live in deep sea; Kuwamura et al. 2020). However, this does not imply that simultaneous hermaphroditism has frequently evolved in the deep sea because these species represent a single origin of hermaphroditism in the order Aulopiformes.

Among the three extant suborders of the order Aulopiformes (Nelson et al. 2016), only Alepisauroidei (Fig. 2.2) is hermaphroditic, and others (Aulopoidei and Paraulopoidei) are gonochoristic (Smith 1975; Davis and Fielitz 2010). Although direct evidence of functional simultaneous hermaphroditism has been obtained from

Fig. 2.2 Greeneye *Chlorophthalmus borealis*. Although this species is not listed in Table 2.1 due to the lack of matured specimens collected, all species in the suborder Alepisauroidei are presumed to be simultaneous hermaphrodites. (Photos taken by the author at Aquamarine Fukushima, Fukushima, Japan, and used under the permission from Aquamarine Fukushima)

only 21 species in eight families (Ipnopidae, Giganturidae, Bathysauridae, Chlorophthalmidae, Notosudidae, Scopelarchidae, Paralepididae, and Alepisauridae) of Alepisauroidei (Kuwamura et al. 2020), weak evidence is available for several other species of Alepisauroidei (Gibbs 1960; Merrett 1980; Iwami and Takahashi 1992), including Evermannellidae (Merrett et al. 1973). It is widely accepted that all species in this suborder are simultaneous hermaphrodites (Johnson 1982; Davis and Fielitz 2010). There is no evidence of self-fertilization in these fishes (Davis and Fielitz 2010) although it might be possible morphologically (Mead et al. 1964; Cabiddu et al. 2010).

Phylogenetic studies have suggested that hermaphroditism evolved only once in the common ancestor of Alepisauroidei (Baldwin and Johnson 1996) during the Early Cretaceous, from gonochoristic ancestors (Davis and Fielitz 2010). This is the oldest known origin of hermaphroditism in vertebrates (Davis and Fielitz 2010).

In the deep sea, population density is generally low because of low productivity (Herring 2001), although there are some exceptions, such as greeneyes (Chlorophthalmidae), which are often abundant on continental shelves (Mead et al. 1964) or live in large shoals (Anastasopoulou et al. 2006). In low-density populations, finding mates is likely to be difficult. Thus, simultaneous hermaphroditism in deep-sea aulopiforms is regarded as evidence for the low-density hypothesis (Mead et al. 1964; Ghiselin 1969; Warner 1984). The lack of hermaphroditism in shallow-water aulopiforms (Aulopoidei) supports this hypothesis (Erisman et al. 2013). In addition, under conditions of limited mating opportunities owing to low density, weak sperm competition also favors hermaphroditism because of diminishing returns on investment in male function (Charnov et al. 1976). It is possible that group living is disadvantageous in the deep sea because of low food availability, preventing the opportunity for multiple matings, even if finding a mate is possible. In summary, it is plausible that hermaphroditism in this taxon is an adaptation to deep-sea environments, although the detailed selective pressure is unclear.

A major bottleneck in understanding the evolution of hermaphroditism in deep-sea fishes is the difficulty in directly observing mating behavior. However, some information can be obtained from behavioral observations and other indirect evidence. Kupchik et al. (2018) suggested pair-bonding in telescopefishes *Gigantura indica* and *G. chuni*, based on video observations using remotely operated vehicles and an excess of even-numbered catch (i.e., records of even-numbered catch were more frequent than expected from random occurrence). They also mentioned a similar unpublished observation of barracudinas (Paralepididae). Given the presumed difficulty of mate acquisition outside a pair, it is plausible that these species reproduce via monogamous mating between hermaphrodites, although no direct evidence is available. Another in situ observation of deep-sea aulopiforms is available for the Japanese greeneyes *Chlorophthalmus albatrossis* or *C. borealis* (Yamauchi 2008; Fig. 2.2), although this may not be informative about their mating system because unfortunately, no mature individuals were found in these species (Hirakawa et al. 2008).

Comparative approaches will help us to understand the evolution of simultaneous hermaphroditism in the deep sea. First, we can compare hermaphroditic and gonochoristic lineages within Aulopiformes (Erisman et al. 2013). Unfortunately, the phylogenetic distribution of sexuality within Aulopiformes cannot be subjected to statistical comparative analyses because of the single evolutionary transition of sexuality (Davis and Fielitz 2010). Nevertheless, comparisons between hermaphroditic and gonochoristic suborders will be useful in gaining insight. Maile et al. (2020) estimated that the common ancestor of Aulopiformes was deep-benthic and that Aulopoidei secondarily invaded shallow seas, whereas Paraulopoidei and Alepisauroidei remained in deep seas.

Among the Aulopoidei, information on mating systems is available for two lizardfish species, *Synodus dermatogenys* and *S. ulae*. The sand lizardfish *S. dermatogenys* forms lek-like aggregations outside their feeding sites and exhibits group spawning at high density and pair spawning at low density (Donaldson 1990). Pair spawning and frequent courtship/aggressive behavior have been observed in the red lizardfish, *S. ulae* (Zaiser and Moyer 1981). Although no information is available on the mating systems in Paraulopoidei, it is interesting to note that many species are sexually dimorphic in fin coloration and/or elongation (Sato and Nakabo 2003), suggesting some sort of sexual selection. It is also worth noting that they are gonochoristic despite often being distributed in the deep seas (Sato and Nakabo 2003). As sexual selection should be weak in situations assumed by the low-density hypothesis (Sekizawa et al. 2019), mating systems may differ greatly between Paraulopoidei and Alepisauroidei, even though their depth ranges overlap.

Another comparison can be made between hermaphroditic aulopiforms and other deep-sea fishes with different adaptations to deep-sea environments (Cocker 1978). For example, male dwarfism and male-female association, which are adopted by some anglerfishes and various invertebrates, also provide a way to assure reproduction under low density (Ghiselin 1969; Pietsch 1976, 2005) or low food availability (Yamaguchi et al. 2012). Sexually dimorphic bioluminescence can increase the efficiency of mate searches (Herring 2007). Sexual dimorphism in traits related to sound communication (otoliths and swimbladders) in deep-sea cusk eels may also help fish to locate potential partners (Schwarzhans 1994; Haedrich 1996). The evolutionary conditions for these different strategies to ensure reproduction in the deep seas have not been fully explored.

2.4 Self-Fertilization and Androdioecy in Killifishes

Mangrove rivulus (*Kryptolebias marmoratus*; Fig. 2.3) and a few other *Kryptolebias* species are simultaneous hermaphrodites and the only known teleosts that routinely engage in self-fertilization (Avise and Tatarenkov 2012). Additionally, males are known at least in some species, i.e., they are androdioecious. I first discuss the sexual system of *K. marmoratus*, the most extensively studied species in this genus, and then discuss other hermaphroditic species.

Kryptolebias marmoratus lives within mangroves over a wide range of neotropical coastlines of the western Atlantic, Caribbean Sea, and Gulf of Mexico (Taylor 2000, 2012). This species is found in unique microhabitats including intermittently dry pools and crab burrows and feeds on aquatic and terrestrial invertebrates (Taylor 2012). Most individuals are simultaneous hermaphrodites (Fig. 2.3a), can reproduce via internal self-fertilization (Harrington Jr 1961), and never outcross with other hermaphrodites (Furness et al. 2015) as far as known. Although Cole and Noakes (1997) suggested the existence of a female phase because ovarian tissues mature

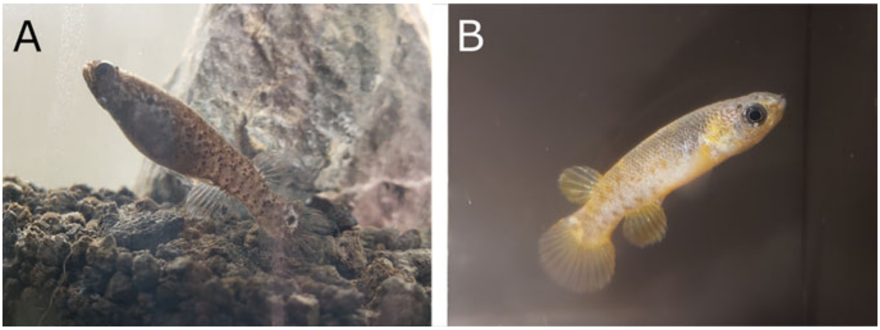

Fig. 2.3 Mangrove rivulus *Kryptolebias marmoratus*, an androdioecious species (Table 2.1) including simultaneous hermaphrodites (**a**) and males (**b**), the latter can be distinguished by orange coloration. (Photos provided by Brooke Fitzwater and Ryan Earley of The University of Alabama)

earlier than testicular tissues do (i.e., protogynous simultaneous hermaphroditism), this phase is unlikely to be functional (Gresham et al. 2020). Testicular tissues occupy only a small portion of the ovotestis (Soto et al. 1992), likely because of internal self-fertilization and lack of sperm competition.

The males (Fig. 2.3b) of *K. marmoratus* are derived from two developmental pathways. Under laboratory conditions, the development of primary males is induced by rearing embryos at low temperatures such as 18–20 °C (Harrington Jr 1967). However, the temperature range is lower than the temperature that this species experiences in its natural habitat and is so low that hermaphrodites usually do not oviposit (Turner et al. 2006), suggesting that these primary males are absent or rare in nature (Earley et al. 2012). Secondary males, derived from simultaneous hermaphrodites via the loss of female function, are likely to be ecologically relevant (Earley et al. 2012). The transition from hermaphrodites to males is induced by environmental conditions, such as high temperature and short daytime (Earley et al. 2012), but is also observed in common laboratory conditions (Gresham et al. 2020). The frequency of transition is also genetically controlled, as suggested by the different frequencies of secondary males among different lineages, even under the same rearing conditions (Turner et al. 2006; Gresham et al. 2020). Turner et al. (2006) hypothesized that this variation depends on the degree of heterozygosity. Both primary and secondary males can be distinguished from hermaphrodites by the presence of orange pigmentation (Fig. 2.3b), although a small proportion of males lack this coloration (cryptic male, Marson et al. 2018).

Kryptolebias marmoratus exhibits mixed mating, that is, both self-fertilization and outcrossing (Mackiewicz et al. 2006c). Although hermaphrodites usually lay fertilized eggs via internal self-fertilization, a small number of unfertilized eggs are also released, offering males the opportunity for siring. The occurrence of outcrossing between hermaphrodites and males has been demonstrated under laboratory conditions using microsatellite DNA (Mackiewicz et al. 2006a), and population genetic studies have supported that outcrossing also occurs in the field (Lubinski et al. 1995; Mackiewicz et al. 2006b, c). According to Kristensen (1970), hermaphrodites oviposit a small number of unfertilized eggs on substrata and males simultaneously fertilize them. Taylor (2012) noted an unpublished observation of “many of the classic killifish courtship/spawning behaviors: recurved bodies coupling closely and vibrating” between a male and a hermaphrodite.

To understand the reproductive strategies of *K. marmoratus*, three questions need to be addressed: why is simultaneous hermaphroditism with selfing adaptive, why do hermaphrodites occasionally outcross with males, and why do they lose female function to change into males? The answer to the first question is likely the low-density hypothesis (Ghiselin 1969). *Kryptolebias marmoratus* possesses a set of traits that facilitate frequent colonization (Avise and Tatarenkov 2012). For example, they can survive and migrate out of water (“emersion”) and exhibit various morphological and physiological adaptation for emersion, which is triggered by water quality (hydrogen sulfide concentration) and intraspecific aggression (Taylor 2012). Just after colonization of a novel habitat, population density is extremely low and mating opportunities are highly limited. As a result, simultaneous hermaphroditism with selfing should be adaptive to assure reproduction. Frequent colonization of novel habitats is suggested to be an evolutionary driver of selfing hermaphroditism in other animals, such as tadpole shrimps (Baker 1955; Mathers et al. 2013). Avise and Tatarenkov (2012) tested an alternative hypothesis that selfing is advantageous because it preserves locally adapted sets of alleles, but found no support for the hypothesis because locally common multilocus genotypes predicted from the hypothesis were not detected.

Why do hermaphrodites occasionally outcross with males? Hermaphrodites prefer to associate with males compared to other hermaphrodites (Martin 2007; Ellison et al. 2013), suggesting that outcrossing is beneficial, at least under some conditions. One possible benefit is avoidance of inbreeding depression. The male preference for genetically dissimilar hermaphrodites supports this hypothesis (Ellison et al. 2013). The lack of such a preference in hermaphrodites may be explained by the rarity of males (Ellison et al. 2013). Ellison et al. (2011) demonstrated that individuals with higher genome-wide heterozygosity (i.e., derived from outcrossing) are less susceptible to parasites than those with lower heterozygosity (i.e., derived from selfing), offering a possible mechanism of inbreeding depression in this species. It is worth noting that this mechanism can explain why inbreeding depression has not been lost despite frequent selfing. If inbreeding depression is caused by recessive deleterious alleles, it will be purged by frequent inbreeding, including selfing. In contrast, if parasite resistance depends on genome-wide heterozygosity itself, inbreeding depression persists because inbreeding always increases homozygosity. Hermaphrodites have the “best of both worlds” (Ellison et al. 2011), by assuring mating under low density after colonization via selfing and increasing parasite resistance under high density (a high risk situation of parasite infection, see Arneberg et al. 1998).

By transitioning to males, hermaphrodites lose all reproductive success via female function. Therefore, there should be an advantage that complements this loss of fitness. One possibility is that males can mate with multiple hermaphrodites and, as a result, achieve high siring success in total. However, no data are available to test this hypothesis in the field, likely because of the difficulty in observing this fish in its muddy habitat. Gresham et al. (2020) proposed another hypothesis: loss of female function leads to a high survival rate, especially under stressful conditions. They demonstrated that individuals who changed sex to male had a higher survival rate under harsh conditions (high salinity and low water availability) than those who retained both sexual functions. Note that mating and survival advantages are not mutually exclusive and may work together to determine the costs and benefits of being male.

In summary, *K. marmoratus* takes advantage of selfing to ensure reproduction under low population density, likely after colonization. In addition, some hermaphrodites lose female function and become males, thereby increasing their survival under stressful conditions. Outcrossing between males and hermaphrodites increases heterozygosity and parasite resistance of their offspring. However, this scenario is still hypothetical and likely to be oversimplified. For example, Gresham et al. (2021) reported outbreeding depression for several fitness components. How multiple factors (inbreeding depression, outbreeding depression, and reproductive assurance) interact to produce the net fitness payoffs of selfing remains unresolved and may vary depending on environmental conditions such as population density, environmental stress, and parasites.

The reproductive biology of *K. marmoratus* exhibits considerable geographical variation throughout its range. The frequency of males varies from almost absent to approximately 20% (Turner et al. 1992; Mackiewicz et al. 2006b; Marson et al. 2018) and the frequency of outcrossing varies accordingly (Tatarenkov et al. 2015). Individuals from the population with the highest male frequency (Twin Cays, Belize) showed a higher propensity to produce secondary males than those from other populations, even in the "common garden" (i.e., rearing in the same condition) experiment (Turner et al. 2006). Yamaguchi and Iwasa (2021) theoretically analyzed the coupled evolution of male frequency and selfing propensity in androdioecious species, especially *K. marmoratus* as a model, and predicted that either populations with selfing-oriented hermaphrodites and no males or populations with outcross-oriented hermaphrodites and highly frequent males ($>$20%) are evolutionarily stable, depending on the extent of inbreeding depression and mating opportunities. It would be interesting to examine whether geographic variation in male production in *K. marmoratus* reflects the alternative stable states predicted by Yamaguchi and Iwasa (2021). It is worth noting that populations with low male frequency ($<$20%) cannot be stable as isolated populations in their models, and migration from male-abundant populations to male-absent populations will help explain the low frequency of males commonly observed in the field (Yamaguchi and Iwasa 2021).

According to the nomenclature of Costa (2011), *Kryptolebias* includes two other hermaphroditic species, *K. ocellatus* and *K. hermaphroditus*. Interestingly, these three hermaphroditic species have different mating patterns, although they are closely related (Costa et al. 2010; note that *K. caudomarginatus* and *K. ocellatus* in Costa et al. 2010 correspond to *K. ocellatus* and *K. hermaphroditus* in Costa 2011, respectively). Until recently, *K. hermaphroditus* was regarded as a purely hermaphroditic species (Costa 2011), despite a few unsubstantiated records of males (Costa 2006) and histological observations (atretic follicles in hermaphrodite gonads) suggesting the possibility of transition into secondary males (Costa et al. 2010). Berbel-Filho et al. (2016) reported only one male individual, based on external morphology (i.e., not histologically examined to maintain the integrity of the unique specimen). Tatarenkov et al. (2011) found only one heterozygous individual, and as a result, the estimated selfing rate was very high. These findings suggest that although *K. hermaphroditus* is androdioecious, males and outcrossings are rare in this species. In contrast, population genetic studies on *K. ocellatus* have indicated that outcrossing is predominant in this species (Tatarenkov et al. 2009; Berbel-Filho et al. 2020). In addition, males are likely to be more frequent in this species than in the other two species because equal numbers of males and hermaphrodites were collected during a field survey (Costa 2006; Costa et al. 2010). Even the functionality of hermaphroditism in this species is doubted (Tatarenkov et al. 2009), although its gonadal structure is similar to that of other hermaphroditic species (Costa 2006). Whether the species is functionally gonochoristic or retains the ability to self-fertilize as a last resort to assure reproduction when no males are available is unclear.

If the former is true, then the species should be removed from the list of functional hermaphrodites. Either way, it is clear that *K. ocellatus* is predominantly outcrossing.

Among the three hermaphroditic species of *Kryptolebias*, the two species in which males and outcrossings are rare (*K. marmoratus* and *K. hermaphroditus*) are most closely related and *K. ocellatus* is located at the basal position (Tatarenkov et al. 2009; Costa et al. 2010). As a result, simultaneous hermaphroditism (at least morphologically) was estimated to have evolved once at the common ancestor of these species, and then the reduction in males and outcrossings occurred at the common ancestor of *K. marmoratus* and *K. hermaphroditus* (Costa et al. 2010). According to this reconstruction, hermaphroditism in *K. ocellatus* cannot be regarded as a vestigial trait inherited from a functionally hermaphroditic ancestor. A phylogenetic analysis within *K. marmoratus* suggests that the Belize population, in which males and outcrossings are more frequent than that in other populations (Tatarenkov et al. 2015), is not basal and located within the clade of other populations with few or no males and outcrossings (Weibel et al. 1999). This implies that males and outcrossings, once reduced in the ancestral species of *K. marmoratus* and *K. hermaphroditus*, secondarily increased in this population. Both between-species variation within the genus and within-species geographic variation of sexual and mating systems offer opportunities to understand the evolution of sexual systems in *Kryptolebias*.

2.5 Hermaphroditism and Egg Trading in Serranids

The third well-studied group of simultaneous hermaphrodites in fishes is the dwarf seabass from the family Serranidae (Fig. 2.4). Self-fertilization is thought to be absent in this family under natural conditions (Fischer 1981; Petersen 2006; Avise and Mank 2009) despite the gametes being self-compatible under laboratory

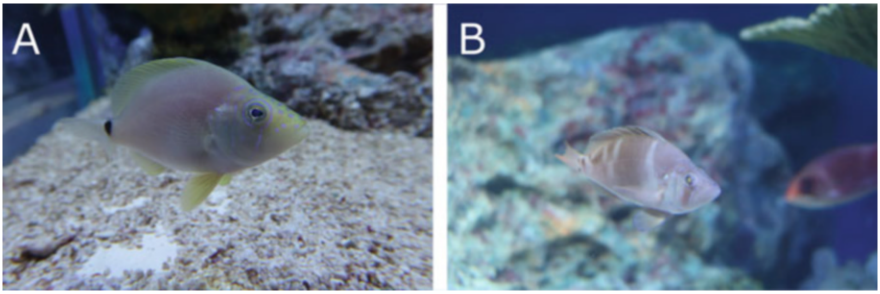

Fig. 2.4 Simultaneously hermaphroditic serranid species, butter hamlet *Hypoplectrus unicolor* (**a**) and barred hamlet *H. puella* (**b**). Both species mate with egg trading (Table 2.1). (Photos taken by the author at Sunshine Aquarium, Tokyo, Japan, and used under the permission from Sunshine Aquarium)

conditions (Clark 1959; Fischer 1981). In this family, all species in the "*Serranus* clade" (Erisman and Hastings 2011), that is, the genera *Diplectrum*, *Hypoplectrus*, *Serranus*, and *Serraniculus*, exhibit simultaneous hermaphroditism as far as known, representing a single origin of this sexual system (Erisman and Hastings 2011; Erisman et al. 2013). A special type of androdioecy, in which larger individuals lose female function and become males, has evolved from pure simultaneous hermaphroditism and is represented by two *Serranus* species, *S. psittacinus*, and *S. baldwini* (Petersen 2006; Weeks 2012). In addition, simultaneous hermaphroditism is reported in the pugnose bass *Bullisichthys caribbaeus* (Smith and Erdman 1973) and the reef bass *Pseudogramma gregoryi* (Smith and Atz 1969). Although the former is classified under the subfamily Serraninae, its phylogenetic position is unknown; hence, its relationship with the *Serranus* clade remains unclear. The latter is the only simultaneously hermaphroditic species in the subfamily Epinephelinae and is estimated to represent another evolutionary transition to simultaneous hermaphroditism (Smith and Atz 1969; Erisman et al. 2009). Unfortunately, the mating behavior of these two species is not yet known (Erisman et al. 2009; Erisman and Hastings 2011). Therefore, I focused on the *Serranus* clade, especially the genera *Hypoplectrus* (Fig. 2.4) and *Serranus*, which includes species that have been extensively studied both empirically and theoretically.

Unlike deep-sea aulopiforms and highly colonizing rivulus, mating opportunities are apparently not scarce in the *Serranus* clade, which lives in shallow coral reefs, usually at a high density (Fischer 1980). Therefore, the low-density hypothesis (Ghiselin 1969) cannot explain simultaneous hermaphroditism in this clade (Warner 1984). To explain this using the hypothesis of Charnov et al. (1976), there should be some factors that cause diminishing fitness returns on investment in one sexual function, especially in the male function, because in general, it is easier for males to achieve additional reproductive success by investing more in mate acquisition. The harlequin bass *Serranus tigrinus* forms long-term, size-assortative pairs that jointly defend territories (used for both feeding and spawning) and mates within pairs, although sometimes a solitary fish participates in a spawning event that results in group spawning (Pressley 1981). During a spawning bout, each member of a pair does not always spawn in both sexual roles; that is, sometimes one member plays only the male role, and the other plays only the female role (Pressley 1981), indicating a lack of egg trading (see below), at least within a day. In this species, the need for long-term pair-bonding for territory defense, and probably the limitation of time available for spawning (spawning only occurs in the late dusk), may inhibit mate acquisition outside the pair (Fischer 1984a; Warner 1984). Consequently, pure males cannot achieve a high mating success to complement the loss of female function. In addition, because hermaphrodites allocate a large fraction of reproductive resources to female function owing to the lack of sperm competition in monogamous systems, it is difficult for pure females to achieve sufficient fecundity to complement the loss of male function (Fischer 1980; Henshaw et al. 2015). Although this hypothesis is plausible, it cannot explain why many other fishes with similar mating systems (monogamy, joint territory defense, and short spawning time) are not simultaneous hermaphrodites (Warner 1984).

Egg trading, another possible mechanism that restricts male mating success, has been observed in all *Hypoplectrus* species whose mating has been studied and in three *Serranus* species (Barlow 1975; Fischer 1984a; Fischer and Petersen 1987; Petersen 2006). In egg trading, individuals spawn in pairs, divide their clutches into multiple parcels, and typically take turns playing male and female roles with their partners multiple times in one spawning bout (Fischer 1980, 1984a; Hart et al. 2016). If the partner does not reciprocate by releasing eggs, the next spawning is delayed (Fischer 1980; Petersen 1995). Egg trading has also been observed in the hermaphroditic polychaete *Ophryotrocha diadema* (Picchi and Lorenzi 2018). Through egg trading, individuals avoid being cheated by individuals who only play the male role, which is more favorable than a female role because of cheaper physiological costs (Leonard 1993). This behavior has been studied both as a rare example of direct reciprocity in animals (Friedman and Hammerstein 1991; Henshaw et al. 2014a; Peña et al. 2020) and as a potential mechanism for stabilizing simultaneous hermaphroditism (Fischer and Petersen 1987; Fischer 1988; Petersen 2006; Henshaw et al. 2015). Under the prevalence of egg trading, fitness returns to male investment should diminish, because individuals cannot sire partners' eggs without offering their own eggs. Theoretical studies (Fischer 1984b; Henshaw et al. 2015) have shown that egg trading stabilizes simultaneous hermaphroditism under relatively high mating opportunities, which otherwise enable the invasion of cheaters (i.e., individuals who do not pay the cost of the female role).

The mating systems of egg-trading species are considerably diverse. For example, the black hamlet *Hypoplectrus nigricans* and the chalk bass *Serranus tortugarum* are serially monogamous; that is, a hermaphrodite typically mates with a single partner per day and with the same partner on successive days (Fischer and Petersen 1987; Hart et al. 2016). In contrast, hermaphrodites in the tobbacofish *Serranus tabacarius* mate with 3.2 partners per day on average, although they often mate with the same partner several times (Petersen 1995). The belted sandfish *Serranus subligarius* also mates with multiple neighboring individuals (Oliver 1997). In addition, the frequency of streaking varies depending on species (Petersen 2006) and density (Oliver 1997; Hart et al. 2010). However, the effects of mating system diversity on the evolutionary stability of egg trading and simultaneous hermaphroditism are not fully understood.

Contrary to the prediction of ideal egg trading, hermaphrodites in these species often play male and female roles asymmetrically, particularly in relation to body size (Petersen 2006). In general, larger hermaphrodites play a male role more frequently (Fischer 1980; Petersen 1995; Oliver 1997). Again, the effect of such asymmetry on mating roles is not yet understood (Petersen 2006). In the chalk bass, fecundity correlates strongly between partners partly owing to, but stronger than predicted by, size-assortative mating (Hart et al. 2016). This resource matching may stabilize reciprocity even under variations in body size among individuals. Petersen (2006) also noted that sperm competition caused by streaking, combined with the increased fecundity of large hermaphrodites, may disfavor a pure male tactic by large individuals in the same manner as a protogynous fish, in which the largest females do not change sex (Muñoz and Warner 2003). However, it should be noted that intense sperm competition may not necessarily disfavor increased male allocation. On the contrary, increased streaking and extra-pair mating under high population density leads to increased male allocation in the chalk bass (Hart et al. 2010), as predicted by the theory of sex allocation under local mate competition (Charnov 1982; Schärer 2009).

The most extreme case of male-biased sex roles by larger individuals occurs in two haremic *Serranus* species, the lantern bass *S. baldwini* (Petersen and Fischer 1986) and the barred serrano *S. psittacinus* (Hastings and Petersen 1986; Petersen and Fischer 1996). These species are closely related, suggesting a single origin for androdioecy in these taxa (Erisman and Hastings 2011). Egg parceling does not occur in these species (Fischer and Petersen 1987). In the lantern bass, large individuals lose female function, become secondary males, and defend the harems of several smaller hermaphrodites. This transition to males is similar to protogynous sex change explained by the size-advantage hypothesis (Fischer and Petersen 1987); that is, individuals change sex to male when they are large enough to monopolize mating with multiple females (or female-role hermaphrodites). Males reduce general activity and increase aggression toward conspecifics during the reproductive period, likely to prevent hermaphrodite-hermaphrodite mating, suggesting that they reallocate resources from female to male function (Petersen and Fischer 1986). Hermaphrodites spawn daily in the female role with the harem males but rarely spawn in the male role. It is not clear why smaller individuals have a male function, despite rarely utilizing it (Petersen and Fischer 1986). Petersen and Fischer (1986) proposed multiple hypotheses, including (1) simultaneous hermaphroditism enables faster transition to males, with a shorter delay than a protogynous sex change, and (2) simultaneous hermaphroditism is adaptive in habitats other than the study area. If (1) is the primary adaptive significance of simultaneous hermaphroditism, lantern bass would be functionally close to protogyny. Reducing the temporal cost of sex change through bisexual gonadal structure has been observed in some gobies that conduct bidirectional sex change (Yamaguchi and Iwasa 2017). Variation in mating systems, predicted by (2), has been reported in barred serrano (Petersen 1990a).

The barred serrano *S. psittacinus* exhibits plastic mating systems that depend on the population density (Petersen 1990a, 2006). First, under moderate density, a social group is a harem, similar to the lantern bass. Harem males successfully monopolized the male role within the harem, and mating between hermaphrodites was rarely observed. Small hermaphrodites may spawn in the male role via streaking, although this is infrequent (6.6% of spawning events). Sometimes, a hermaphrodite, rather than a male, dominates the harem. The dominant hermaphrodites were smaller than the harem males and spawned in the female role with males in the adjacent harems. Second, under low density, they reproduce monogamously within isolated pairs (Petersen 1990a). Each member of a pair spawns daily in both the male and female roles. This monogamous mating system is similar to that of the harlequin bass *S. tigrinus*, although in the harlequin bass, both members do not necessarily play both sexual roles per day (Pressley 1981). Finally, under high density, a unique system called a "complex harem" is formed (Petersen 1990a). Within complex harems, mate monopolization by dominant males is incomplete. Some hermaphrodites are "subdominant" and mate with the dominant males in the female role. However, they dominate a "sub-harem" consisting of other hermaphrodites and mate with the members of the sub-harem in the male role. Members of a sub-harem mate almost exclusively with a subdominant.

Harems and complex harems in barred serrano represent an example of a contrasting structure of hermaphroditic society, as compared to sequential hermaphrodites who adopt dichotomous tactics (males or females) in terms of sexuality (Wong et al. 2012; Sawada et al. 2017) depending on social conditions. To understand this unique system, we must explain why male function is maintained by nondominants and why dominant males tolerate subdominants (Iwasa and Yamaguchi 2022).

Plasticity in mating systems may help to understand why hermaphrodites maintain male function rather than being pure females. The male function of subordinates in harems and of hermaphrodites other than subdominants in complex harems still contributes little to reproductive success and is wasteful, at least in the short term. However, hermaphrodites may achieve male reproductive success when they become a pair member in isolated pairs or a subdominant in complex harems, in addition to rare streaking. Given that gonadal allocation to male function is small (Petersen 1990b), opportunities to effectively utilize male function could favor the retention of male function among hermaphrodites (Petersen 1990a).

Why do dominant males tolerate the existence of subdominants who take over their mating success? The key to the answer is that subdominants provide eggs to be sired by the dominant males (Petersen 1990a). As a result of mating with subdominants, the reproductive success of dominant males positively correlates with social group size (Petersen 1990a), despite the incomplete monopolization of mating opportunities in large groups (i.e., complex harems). Therefore, dominant males achieve higher mating success by accepting subdominants than by evicting them to monopolize mating. The application of the reproductive skew theory (Nonacs and Hager 2011) will be useful in facilitating our understanding of the evolutionary stability of this unique mating system.

The evolutionary conditions for androdioecy and pure simultaneous hermaphroditism in the *Serranus* clade are unclear. By applying the classical mating system theory (Emlen and Oring 1977), Petersen and Fischer (1986) hypothesized that high density and/or predictability of resources (food) enables mate monopolization by large individuals, leading to haremic systems with androdioecy. The effect of density is also supported by the within-species density dependence of mating systems in the barred serrano (Petersen 1990b, 2006). However, there were no consistent differences in the range of population density between androdioecious and other species of *Serranus* and *Hypoplectrus*, suggesting that density is not the sole factor (Petersen 2006).

In summary, mating systems in hermaphroditic serranids are diverse, and unlike aulopiforms and killifishes, they are not characterized by limited mating opportunities owing to colonization or depth. The evolutionary stability of simultaneous hermaphroditism (including androdioecy) can be explained by monogamous mating (harlequin bass), egg trading (several *Serranus* and *Hypoplectrus* species), and plastic mating systems (barred serrano and possibly, lantern bass). However, why simultaneous hermaphroditism, an uncommon sexual strategy among teleosts, has evolved in this clade is not known (Warner 1984). Egg trading is a specialized behavioral trait that makes sense only in simultaneous hermaphrodites and has arguably evolved after the evolution of this form of sexuality. Monogamy and plastic systems, including harems, are common mating systems among gonochoristic and sequentially hermaphroditic fishes. Although Warner (1984) speculated that their ancestors lived in the deep sea, no evidence has been provided. It would be interesting to reconstruct the ecology of the ancestral species when simultaneous hermaphroditism evolved.

2.6 Other Taxa

In addition to the three taxa I have reviewed so far (Aulopiformes, *Kryptolebias*, and Serranidae), there are three taxa in which simultaneous hermaphroditism has been confirmed, and one species in which simultaneous hermaphroditism has been suggested but not confirmed (Table 2.1). Simultaneous hermaphroditism is confirmed or suggested by the histological analysis of gonads, but little is known about other aspects of mating in three species of moray eels *Gymnothorax* spp. (Fishelson 1992) and Lord Howe dottyback *Pseudoplesiops howensis* (Cole and Gill 2000). The demon eartheater *Satanoperca jurupari* was described as a simultaneous hermaphrodite with internal self-fertilization by Matos et al. (2002) based on histological analysis, although spawning behavior involving external fertilization by males and females has been reported for this species (Reid and Atz 1958).

Two species of threadfins (family Polynemidae), the smallmouth threadfin *Polydactylus microstomus* and the seven-finger threadfin *Filimanus heptadactyla* have been reported to exhibit trioecy (Nayak 1959; Kagwade 1967; Dorairaj 1973), an extremely rare sexual system among animals (Leonard 2018). The frequency of hermaphrodites is 35% in *P. microstomus* (Dorairaj 1973) and approximately 10% or 17% in *F. heptadactyla* (Nayak 1959; Kagwade 1967). Hermaphrodites are much more frequent in these species than in many other trioecious animals, in which hermaphrodites are exceedingly rare (Weeks 2012). Although hermaphroditic individuals were reported as transitional state during protandrous sex change among several threadfin species (Motomura 2004), rather than functional simultaneous hermaphrodites, hermaphroditic individuals in the seven-finger threadfin are supposed to be functional in both sexes, based on observations of developed and spent stages of ovotestis (Nayak 1959; Kagwade 1967). Detailed studies on the mating systems of trioecious threadfins are required to elucidate the evolution of complex sexual systems.

2.7 Future Research Directions

This review indicated that simultaneous hermaphroditism in teleost fishes evolved under different selective backgrounds. Each of the well-studied taxa exhibits mating systems that are predicted to make this strategy evolutionarily stable, such as limited mating opportunities owing to depth or colonization, egg-trading, and flexible haremic systems, although some aspects of the explanations are still more or less hypothetical. However, it is difficult to attain a unified view of the evolution of simultaneous hermaphroditism in teleost fishes, which is comparable to the size-advantage hypothesis for sequential hermaphroditism. In addition, it is difficult to understand why simultaneous hermaphroditism has not evolved in many other taxa, even though similar mating systems (except for egg trading and reciprocal mating, which make sense only in hermaphrodites) are also observed in gonochoristic or sequentially hermaphroditic taxa (Warner 1984).

The apparent lack of evolutionary lability is one of the problems in applying the evolutionary ecological approach to simultaneous hermaphroditism in fishes. It is important to note that the evolution from simultaneous hermaphroditism to gonochorism or sequential hermaphroditism has never been confirmed, even in the well-studied taxa including species-rich Alepisauroidei (Davis and Fielitz 2010) and in the *Serranus* clade in which mating systems are highly diverse (Erisman and Hastings 2011), apart from the evolution of androdioecy. In other words, once simultaneous hermaphroditism has evolved, it is rarely lost. Hermaphroditism has not been lost even in some androdioecious species, in which the male function of hermaphrodites is estimated to be used only infrequently, such as the lantern bass *S. baldwini* and killifish *K. ocellatus*.

If we assume that simultaneous hermaphroditism is evolutionarily stable under such wide ecological conditions that no reverse evolution occurs, the limited number of evolutionary transitions to simultaneous hermaphroditism cannot be explained. Similar evolutionary patterns have been observed in several invertebrate taxa, including broken-back shrimp (Baeza 2013) and clam shrimp (Weeks et al. 2006b). In a broader context, among animals, many higher taxa exclusively (almost) exhibit one type of sexual system. This pattern is called "Williams' paradox" by Leonard (1990, 2013). Although the taxonomic levels are much lower, the abovementioned evolutionary patterns can be regarded as examples of this paradox.

Comparing the evolutionary patterns of simultaneous hermaphroditism in fishes against those of other taxa or traits with different levels of evolutionary lability will be useful. For example, evolution from androdioecy to gonochorism occurred repeatedly in thoracican barnacles (Yusa et al. 2012; Lin et al. 2015). In some taxa where sequential hermaphroditism is common, the evolutionary loss of hermaphroditism is not rare and is often associated with the evolution of mating systems (Erisman et al. 2009, 2013; Kazancıoğlu and Alonzo 2010; Sunobe et al. 2017).

In conclusion, this chapter illuminates that simultaneous hermaphroditism, at least in well-studied taxa, can be understood from the perspective of evolutionary ecology, particularly in relation to mating systems. However, we are yet to understand the evolutionary patterns of this sexual strategy in teleost fishes or animals in general. In addition to the accumulation of knowledge on each hermaphroditic species, comparative analyses to elucidate the determinants of evolutionary lability could help us answer this question.

2.8 Conclusions

In this chapter, the following topics related to simultaneous hermaphroditism in fishes were introduced

1. Simultaneous hermaphroditism is rare in fishes and has been reported in 57 species of Muraenidae, Cichlidae, Rivulidae, Polynemidae, and several families of Aulopiformes.
2. Two hypotheses, reproductive assurance under low density and diminishing fitness returns on investment in one sexual function, are widely recognized as explanations for the adaptive significance of simultaneous hermaphroditism.
3. To the best of our knowledge, all species in the suborder Alepisauroidei (order Aulopiformes) are simultaneous hermaphrodites, which is likely an adaptation to deep seas where population density is usually low.
4. Mangrove rivulus has a mixed mating system in which hermaphrodites self-fertilize but occasionally outcross with males. This system can be explained by a combination of reproductive assurance, survival advantage of males, and inbreeding depression.
5. Simultaneously hermaphroditic species in Serranidae exhibit diverse mating systems that are not characterized by limited mating opportunities. In two species, large hermaphrodites become males, and monopolizing harems consist of hermaphrodites. Although the mechanisms stabilizing hermaphroditism, such as egg trading, have been well studied, why hermaphroditism has originated in this clade remains unclear.
6. Little is known about the sexual and mating systems of other teleost taxa that exhibit simultaneous hermaphroditism.
7. The apparent lack of evolutionary lability is a problem when applying the evolutionary ecological approach to simultaneous hermaphroditism in fishes. A comparison of evolutionary patterns with other taxa or traits with different levels of evolutionary lability would be useful.

Acknowledgements I thank Tetsuo Kuwamura, Tatsuru Kadota, Yoichi Sakai, and Tomoki Sunobe for helpful comments to improve the manuscript. I also thank Ryan Earley and Brooke Fitzwater for providing photos of *Kryptolebias*, Aquamarine Fukushima and Sunshine Aquarium, for permitting the use of photos, and Editage (www.editage.com) for English language review.

References

Anastasopoulou A, Yiannopoulos C, Megalofonou P, Papaconstantinou C (2006) Distribution and population structure of the *Chlorophthalmus agassizi* (Bonaparte, 1840) on an unexploited fishing ground in the Greek Ionian Sea. J Appl Ichthyol 22:521–529

Arneberg P, Skorping A, Grenfell B, Read AF (1998) Host densities as determinants of abundance in parasite communities. Proc R Soc B 265:1283–1289

Avise JC, Mank JE (2009) Evolutionary perspectives on hermaphroditism in fishes. Sex Dev 3: 152–163

Avise JC, Tatarenkov A (2012) Allard's argument versus Baker's contention for the adaptive significance of selfing in a hermaphroditic fish. Proc Natl Acad Sci U S A 109:18862–18867

Baeza JA (2013) Molecular phylogeny of broken-back shrimps (genus *Lysmata* and allies): a test of the 'Tomlinson–Ghiselin' hypothesis explaining the evolution of hermaphroditism. Mol Phylogenet Evol 69:46–62

Baker HG (1955) Self-compatibility and establishment after "long-distance" dispersal. Evolution 9: 347–349

Baldwin CC, Johnson GD (1996) Interrelationships of Aulopiformes. In: Stiassny MLJ, Parenti LR, Johnson GD (eds) Interrelationships of fishes. Academic Press, San Diego, pp 355–404

Barlow GW (1975) On the sociobiology of some hermaphroditic serranid fishes, the hamlets, in Puerto Rico. Mar Biol 33:295–300

Berbel-Filho WM, Espírito-Santo HMV, Lima SMQ (2016) First record of a male of *Kryptolebias hermaphroditus* Costa, 2011 (Cyprinodontiformes: Cynolebiidae). Neotrop Ichthyol 14: e160024

Berbel-Filho WM, Tatarenkov A, Espírito-Santo HMV, Lira MG, Garcia de Leaniz C, Lima SMQ, Consuegra S (2020) More than meets the eye: syntopic and morphologically similar mangrove killifish species show different mating systems and patterns of genetic structure along the Brazilian coast. Heredity 125:340–352

Bertelsen E, Krefft G, Marshall NB (1976) The fishes of the family Notosudidae. Dana Rep 86:1–114

Bortone SA (1971) Studies on the biology of the sand perch, *Diplectrum formosum* (Linnaeus), (Perciformes: Serranidae). Florida Dept Nat Res Tech Ser 65:1–27

Bortone SA (1974) *Diplectrum rostrum*, a hermaphroditic new species (Pisces: Serranidae) from the eastern Pacific coast. Copeia 1974:61–65

Bortone SA (1977a) Revision of the sea basses of the genus *Diplectrum* (Pisces: Serranidae). US Dept Commer, NOAA Tech Rep NMFS Circ 404:1–49

Bortone SA (1977b) Gonad morphology of the hermaphroditic fish *Diplectrum pacificum* (Serranidae). Copeia 25:448–453

Duslé S (1983) Contribution to the sexuality of a hermaphroditic teleost, *Serranus hepatus* L. J Fish Biol 22:283–292

Bullock LH, Smith GB (1991) Seabasses (Pisces: Serranidae). Mem Hourglass Cruises 8:1–206

Cabiddu S, Follesa MC, Porcu C, Cau A (2010) Gonad development and reproduction in the monoecious species *Chlorophthalmus agassizi* (Actinopterygii: Aulopiformes: Chlorophthalmidae) from the Sardinian waters (Central-Western Mediterranean). Acta Ichthyol Piscat 40:167–177

Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton

Charnov EL, Bull JJ, Maynard Smith J (1976) Why be an hermaphrodite? Nature 263:125–126

Clark E (1959) Functional hermaphroditism and self-fertilization in a serranid fish. Science 129: 215–216

Clarke TA, Wagner PJ (1976) Vertical distribution and other aspects of the ecology of certain mesopelagic fishes taken near Hawaii. Fish Bull 74:635–645

Cocker J (1978) Adaptations of deep sea fishes. Environ Biol Fishes 3:389–399

Cole KS (2010) Gonad morphology in hermaphroditic gobies. In: Cole KS (ed) Reproduction and sexuality in marine fishes: patterns and processes. University of California Press, Berkeley, pp 117–164

Cole KS, Gill AC (2000) Specialization of the urinary bladder in two pseudoplesiopines (Teleostei: Pseudochromidae). Copeia 2000:1083–1089

Cole KS, Noakes DLG (1997) Gonadal development and sexual allocation in mangrove killifish, *Rivulus marmoratus* (Pisces: Atherinomorpha). Copeia 1997:596–600

Costa WJEM (2006) Redescription of *Kryptolebias ocellatus* (Hensel) and *K. caudomarginatus* (Seegers) (Teleostei: Cyprinodontiformes: Rivulidae), two killifishes from mangroves of South-Eastern Brazil. J Ichthyol Aquat Biol 11:5–12

Costa WJEM (2011) Identity of *Rivulus ocellatus* and a new name for a hermaphroditic species of *Kryptolebias* from South-Eastern Brazil (Cyprinodontiformes: Rivulidae). Ichthyol Explor Freshwaters 22:185–192

Costa WJEM, Lima SMQ, Bartolette R (2010) Androdioecy in *Kryptolebias* killifish and the evolution of self-fertilizing hermaphroditism. Biol Bull 99:344–349

Davis MP, Fielitz C (2010) Estimating divergence times of lizardfishes and their allies (Euteleostei: Aulopiformes) and the timing of deep-sea adaptations. Mol Phylogenet Evol 57:1194–1208

Devine B, Guelpen LV (2021) Loss of gill rakers and teeth in adult specimens of barracudina *Arctozenus risso* (Aulopiformes: Paralepididae) from the western North Atlantic. J Fish Biol 98: 329–332

Donaldson TJ (1990) Lek-like courtship by males, and multiple spawnings by females of *Synodus dermatogenys* (Synodontidae). Jpn J Ichthyol 37:292–301

Dorairaj K (1973) Hermaphroditism in the threadfin fish, *Polynemus microstoma* Bleeker. Indian J Fish 20:256–259

Earley RL, Hanninen AF, Fuller A, Garcia MJ, Lee EA (2012) Phenotypic plasticity and integration in the mangrove rivulus (*Kryptolebias marmoratus*): a prospectus. Integr Comp Biol 52:814–827

Ellison A, Cable J, Consuegra S (2011) Best of both worlds? Association between outcrossing and parasite loads in a selfing fish. Evolution 65:3021–3026

Ellison A, Jones J, Inchley C, Consuegra S (2013) Choosy males could help explain androdioecy in a selfing fish. Am Nat 181:855–862

Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223

Erisman BE, Hastings PA (2011) Evolutionary transitions in the sexual patterns of fishes: insights from a phylogenetic analysis of the seabasses (Teleostei: Serranidae). Copeia 2011:357–364

Erisman BE, Craig MT, Hastings PA (2009) A phylogenetic test of the size-advantage model: evolutionary changes in mating behavior influence the loss of sex change in a fish lineage. Am Nat 174:E83–E99

Erisman BE, Petersen CW, Hastings PA, Warner RR (2013) Phylogenetic perspectives on the evolution of functional hermaphroditism in teleost fishes. Integr Comp Biol 53:736–754

Fischer EA (1980) The relationship between mating system and simultaneous hermaphroditism in the coral reef fish, *Hypoplectrus nigricans* (Serranidae). Anim Behav 28:620–633

Fischer EA (1981) Sexual allocation in a simultaneously hermaphroditic coral reef fish. Am Nat 117:64–82

Fischer EA (1984a) Egg trading in the chalk bass, *Serranus tortugarum*, a simultaneous hermaphrodite. Z Tierpsychol 66:143–151

Fischer EA (1984b) Local mate competition and sex allocation in simultaneous hermaphrodites. Am Nat 124:590–596

Fischer EA (1988) Simultaneous hermaphroditism, tit-for-tat, and the evolutionary stability of social systems. Ethol Sociobiol 9:119–136

Fischer EA, Hardison PD (1987) The timing of spawning and egg production as constraints on male mating success in a simultaneously hermaphroditic fish. Environ Biol Fishes 20:301–310

Fischer EA, Petersen CW (1986) Social behavior of males and simultaneous hermaphrodites in the lantern bass. Ethology 73:235–246

Fischer EA, Petersen CW (1987) The evolution of sexual patterns in the seabasses. Bioscience 37: 482–489

Fishelson L (1992) Comparative gonad morphology and sexuality of the Muraenidae (Pisces, Teleostei). Copeia 1992:197–209

Fishelson L, Galil BS (2001) Gonad structure and reproductive cycle in the deep-sea hermaphrodite tripodfish, *Bathypterois mediterraneus* (Chlorophthalmidae, Teleostei). Copeia 2001:556–560

Follesa MC, Cabiddu S, Davini MA, Porcu C, Cau A (2004) Reproductive biology of *Chlorophthalmus agassizi* in the Central-Western Mediterranean. Rapp Comm Int Mer Médit 37:356

Friedman JW, Hammerstein P (1991) To trade, or not to trade; that is the question. In: Selten R (ed) Game equilibrium models I: evolution and game dynamics. Springer, Berlin, pp 257–275

Furness AI, Tatarenkov A, Avise JC (2015) A genetic test for whether pairs of hermaphrodites can cross-fertilize in a selfing killifish. J Hered 106:749–752

García-Díaz MM, Lorente MJ, González JA, Tuset VM (2002) Morphology of the ovotestis of *Serranus atricauda* (Teleostei, Serranidae). Aquat Sci 64:87–96

García-Díaz MM, Tuset VM, González JA, Socorro J (1997) Sex and reproductive aspects in *Serranus cabrilla* (Osteichthyes: Serranidae): macroscopic and histological approaches. Mar Biol 127:379–386

Ghiselin MT (1969) The evolution of hermaphroditism among animals. Q Rev Biol 44:189–208

Gibbs RH (1960) *Alepisaurus brevirostris*, a new species of lancetfish from the western North Atlantic. Breviora 123:1–14

Gresham JD, Marson KM, Tatarenkov A, Earley RL (2020) Sex change as a survival strategy. Evol Ecol 34:27–40

Gresham JD, Lewis KA, Summers SP, Gresham PE, Earley RL (2021) Outbreeding depression as a selective force on mixed mating in the mangrove rivulus fish, *Kryptolebias marmoratus*. bioRxiv 2021:432322. https://doi.org/10.1101/2021.02.22.432322

Haedrich RL (1996) Deep-water fishes: evolution and adaptation in the Earth's largest living spaces. J Fish Biol 49:40–53

Harrington RW Jr (1961) Oviparous hermaphroditic fish with internal self-fertilization. Science 134:1749–1750

Harrington RW Jr (1963) Twenty-four-hour rhythms of internal self-fertilization and of oviposition by hermaphrodites of *Rivulus marmoratus*. Physiol Zool 36:325–341

Harrington RW Jr (1967) Environmentally controlled induction of primary male gonochorists from eggs of the self-fertilizing hermaphroditic fish, *Rivulus marmoratus* Poey. Biol Bull 132:174–199

Harrington RW Jr (1971) How ecological and genetic factors interact to determine when self-fertilizing hermaphrodites of *Rivulus marmoratus* change into functional secondary males, with a reappraisal of the modes of intersexuality among fishes. Copeia 1971:389–432

Hart MK (2016) Phenotypic plasticity in sex allocation and body size leads to trade-offs between male function and growth in a simultaneously hermaphroditic fish. Evol Ecol 30:173–190

Hart MK, Kratter AW, Svoboda AM, Lawrence CL, Sargent RC, Crowley PH (2010) Sex allocation in a group-living simultaneous hermaphrodite: effects of density at two different spatial scales. Evol Ecol Res 12:189–202

Hart MK, Kratter AW, Crowley PH (2016) Partner fidelity and reciprocal investments in the mating system of a simultaneous hermaphrodite. Behav Ecol 27:1471–1479

Hastings RW (1973) Biology of the pygmy sea bass, *Serraniculus pumilio* (Pisces: Serranidae). Fish Bull 1:235–242

Hastings PA, Bortone SA (1980) Observations on the life history of the belted sandfish, *Serranus subligarius* (Serranidae). Environ Biol Fishes 5:365–374

Hastings P, Petersen C (1986) A novel sexual pattern in serranid fishes: simultaneous hermaphrodites and secondary males in *Serranus fasciatus*. Environ Biol Fishes 15:59–68

Heath DJ (1979) Brooding and the evolution of hermaphroditism. J Theor Biol 81:151–155

Henshaw JM, Jennions MD, Kokko H (2014a) The economics of egg trading: mating rate, sperm competition and positive frequency-dependence. Dyn Games Appl 4(4):379–390

Henshaw JM, Marshall DJ, Jennions MD, Kokko H (2014b) Local gamete competition explains sex allocation and fertilization strategies in the sea. Am Nat 184:E32–E49

Henshaw JM, Kokko H, Jennions MD (2015) Direct reciprocity stabilizes simultaneous hermaphroditism at high mating rates: a model of sex allocation with egg trading. Evolution 69:2129–2139

Herring P (2001) The biology of the deep ocean. Oxford University Press, Oxford

Herring PJ (2007) Review. Sex with the lights on? A review of bioluminescent sexual dimorphism in the sea. J Mar Biol Assoc UK 87:829–842

Hirakawa N, Suzuki N, Narimatsu Y (2008) Recruitment mechanisms of *Chlorophthalmus albatrossis* in the Pacific Ocean coast of Japan. Aquabiology 30:740–748

Iwami T, Takahashi M (1992) Notes on some fishes associated with the Antarctic krill. III. *Anotopterus pharao* ZUGMAYER (family Anotopteridae). Proc NIPR Symp Polar Biol 5: 90–97

Iwasa Y, Yamaguchi S (2022) On the role of eviction in group living sex changers. Behav Ecol Sociobiol 76:49

Jarne P, Charlesworth D (1993) The evolution of the selfing rate in functionally hermaphrodite plants and animals. Annu Rev Ecol Syst 24:441–466

Johnson RK (1982) Fishes of the families Evermannellidae and Scopelarchidae: systematics, morphology, interrelationships, and zoogeography. Fieldiana Zool New Series 12:1–252

Johnson RK, Bertelsen E (1991) The fishes of the family Giganturidae: systematics, development, distribution and aspects of biology. Dana Rep 91:1–45

Kagwade PV (1967) Hermaphroditism in a teleost, *Polynemus heptadactylus* Cuv. and Val. Indian J Fish 14:187–197

Kazancıoğlu E, Alonzo SH (2010) A comparative analysis of sex change in Labridae supports the size advantage hypothesis. Evolution 64:2254–2264

Kristensen I (1970) Competition in three cyprinodont fish species in the Netherlands Antilles. Stud Fauna Curaçao Carib Isl 119:82–101

Kupchik MJ, Benfield MC, Sutton TT (2018) The first in situ encounter of *Gigantura chuni* (Giganturidae: Giganturoidei: Aulopiformes: Cyclosquamata: Teleostei), with a preliminary investigation of pair-bonding. Copeia 106:641–645

Kuwamura T, Sunobe T, Sakai Y, Kadota T, Sawada K (2020) Hermaphroditism in fishes: an annotated list of species, phylogeny, and mating system. Ichthyol Res 67:341–360

Leem JB, Sakamoto K, Tsuruda Y, Nakazono A (1998) Sexual pattern of the labrid fishes collected from Kuchinoerabu-jima, Kagoshima, Japan. J Fac Agric Kyushu Univ 43:409–419

Leonard JL (1990) The hermaphrodite's dilemma. J Theor Biol 147:361–371

Leonard J (1993) Sexual conflict in simultaneous hermaphrodites: evidence from serranid fishes. Environ Biol Fishes 36:135–148

Leonard JL (2013) Williams' paradox and the role of phenotypic plasticity in sexual systems. Integr Comp Biol 53:671–688

Leonard JL (2018) The evolution of sexual systems in animals. In: Leonard JL (ed) Transitions between sexual systems: understanding the mechanisms of, and pathways between, dioecy, hermaphroditism and other sexual systems. Springer International Publishing, Cham, pp 1–58

Lin H-C, Høeg JT, Yusa Y, Chan BKK (2015) The origins and evolution of dwarf males and habitat use in thoracican barnacles. Mol Phylogenet Evol 91:1–11

Longley WH, Hildebrand SF (1941) Systematic catalogue of the fishes of Tortugas, Florida with observations on color, habits, and local distribution. Pap Tortugas Lab 34:1–331

Lubinski BA, Davis WP, Taylor DS, Turner BJ (1995) Outcrossing in a natural population of a self-fertilizing hermaphroditic fish. J Hered 86:469–473

Mackiewicz M, Tatarenkov A, Perry A, Martin JR, Elder JF Jr, Bechler DL, Avise JC (2006a) Microsatellite documentation of male-mediated outcrossing between inbred laboratory strains of the self-fertilizing mangrove killifish (*Kryptolebias marmoratus*). J Hered 97:508–513

Mackiewicz M, Tatarenkov A, Taylor DS, Turner BJ, Avise JC (2006b) Extensive outcrossing and androdioecy in a vertebrate species that otherwise reproduces as a self-fertilizing hermaphrodite. Proc Natl Acad Sci U S A 103:9924–9928

Mackiewicz M, Tatarenkov A, Turner BJ, Avise JC (2006c) A mixed-mating strategy in a hermaphroditic vertebrate. Proc R Soc B 273:2449–2452

Maile AJ, May ZA, DeArmon ES, Martin RP, Davis MP (2020) Marine habitat transitions and body-shape evolution in lizardfishes and their allies (Aulopiformes). Copeia 108:820–832

Marson KM, Taylor DS, Earley RL (2018) Cryptic male phenotypes in the mangrove rivulus fish, *Kryptolebias marmoratus*. Biol Bull 236:13–28

Martin SB (2007) Association behaviour of the self-fertilizing *Kryptolebias marmoratus* (Poey): the influence of microhabitat use on the potential for a complex mating system. J Fish Biol 71: 1383–1392

Mathers TC, Hammond RL, Jenner RA, Zierold T, Hänfling B, Gómez A (2013) High lability of sexual system over 250 million years of evolution in morphologically conservative tadpole shrimps. BMC Evol Biol 13:30

Matos E, Santos MNS, Azevedo C (2002) Biflagellate spermatozoon structure of the hermaphrodite fish *Satanoperca jurupari* (Heckel, 1840) (Teleostei, Cichlidae) from the Amazon River. Braz J Biol 62:847–852

Mead GW (1960) Hermaphroditism in archibenthic and pelagic fishes of the order Iniomi. Deep-Sea Res 6:234–235

Mead GW, Bertelsen E, Cohen DM (1964) Reproduction among deep-sea fishes. Deep-Sea Res Oceanogr Abstr 11:569–596

Merrett NR (1980) *Bathytyphlops sewelli* (Pisces: Chlorophthalmidae) a senior synonym of *B. azorensis*, from the eastern North Atlantic with notes on its biology. Zool J Linn Soc 68: 99–109

Merrett NR (1994) Reproduction in the North Atlantic oceanic ichthyofauna and the relationship between fecundity and species' sizes. Environ Biol Fishes 41:207–245

Merrett NR, Badcock J, Herring PJ (1973) The status of *Benthalbella infans* (Pisces: Myctophoidei), its development, bioluminescence, general biology and distribution in the eastern North Atlantic. J Zool 170:1–48

Militelli MI, Rodrigues KA (2011) Morphology of the ovotestis of a hermaphroditic teleost, *Serranus auriga* (Osteichthyes: Serranidae). Pan-Am J Aquat Sci 6:320–324

Motomura H (2004) Threadfins of the world (family Polynemidae). An annotated and illustrated catalogue of Polynemid species known to date. FAO, Rome

Muñoz RC, Warner RR (2003) A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size-fecundity skew. Am Nat 161:749–761

Nayak PD (1959) Occurrence of hermaphroditism in *Polynemus heptadactylus* Cuv. & Val. J Mar Biol Assoc India 1:257–258

Nielsen JG (1966) Synopsis of the Ipnopidae (Pisces, Iniomi) with description of two new abyssal species. Galathea Rep 8:49–75

Nelson JS, Grande TC, Wilson MVH (2016) Fishes of the world, 5th edn. Wiley, New Jersy

Nonacs P, Hager R (2011) The past, present and future of reproductive skew theory and experiments. Biol Rev 86:271–298

Oliver AS (1997) Size and density dependent mating tactics in the simultaneously hermaphroditic seabass *Serranus subligarius* (Cope, 1870). Behaviour 134:563–594

Ota K, Kobayashi T, Ueno K, Gojobori T (2000) Evolution of heteromorphic sex chromosomes in the order Aulopiformes. Gene 259:25–30

Pannell JR (2002) What is functional androdioecy? Funct Ecol 16:862–865

Peña J, Nöldeke G, Puebla O (2020) The evolution of egg trading in simultaneous hermaphrodites. Am Nat 195:524–533

Petersen CW (1987) Reproductive behaviour and gender allocation in *Serranus fasciatus*, a hermaphroditic reef fish. Anim Behav 35:1601–1614

Petersen CW (1990a) The relationships among population density, individual size, mating tactics, and reproductive success in a hermaphroditic fish, *Serranus fasciatus*. Behaviour 113:57–80

Petersen CW (1990b) Variation in reproductive success and gonadal allocation in the simultaneous hermaphrodite, *Serranus fasciatus*. Oecologia 83:62–67

Petersen CW (1991) Sex allocation in hermaphroditic sea basses. Am Nat 138:650–667

Petersen CW (1995) Reproductive behavior, egg trading, and correlates of male mating success in the simultaneous hermaphrodite, *Serranus tabacarius*. Environ Biol Fish 43:351–361

Petersen CW (2006) Sexual selection and reproductive success in hermaphroditic seabasses. Integr Comp Biol 46:439–448

Petersen CW, Fischer EA (1986) Mating system of the hermaphroditic coral-reef fish, *Serranus baldwini*. Behav Ecol Sociobiol 19:171–178

Petersen CW, Fischer EA (1996) Intraspecific variation in sex allocation in a simultaneous hermaphrodite: the effect of individual size. Evolution 50:636–645

Picchi L, Lorenzi MC (2018) Polychaete worms on the brink between hermaphroditism and separate sexes. In: Leonard JL (ed) Transitions between sexual systems: understanding the mechanisms of, and pathways between, dioecy, hermaphroditism and other sexual systems. Springer International Publishing, Cham, pp 123–163

Pietsch TW (1976) Dimorphism, parasitism and sex: reproductive strategies among deepsea ceratioid anglerfishes. Copeia 1976:781–793

Pietsch TW (2005) Dimorphism, parasitism, and sex revisited: modes of reproduction among deep-sea ceratioid anglerfishes (Teleostei: Lophiiformes). Ichthyol Res 52:207–236

Pla S, Maynou F, Piferrer F (2021) Hermaphroditism in fish: incidence, distribution and associations with abiotic environmental factors. Rev Fish Biol Fish 31(4):935–955

Porcu C, Follesa MC, Grazioli E, Deiana AM, Cau A (2010) Reproductive biology of a bathyal hermaphrodite fish, *Bathypterois mediterraneus* (Osteichthyes: Ipnopidae) from the south-eastern Sardinian Sea (Central-Western Mediterranean). J Mar Biol Assoc UK 90:719–728

Powell ML, Kavanaugh SI, Sower SA (2004) Seasonal concentrations of reproductive steroids in the gonads of the Atlantic hagfish, *Myxine glutinosa*. J Exp Zool A Comp Exp Biol 301:352–360

Pressley PH (1981) Pair formation and joint territoriality in a simultaneous hermaphrodite: the coral reef fish *Serranus tigrinus*. Z Tierpsychol 56:33–46

Reid MJ, Atz JW (1958) Oral incubation in the cichlid fish *Geophagus jurupari* Heckel. Zool Sci Contrib NY Zool Soc 43:77–88

Sakakura Y, Noakes DLG (2000) Age, growth, and sexual development in the self-fertilizing hermaphroditic fish *Rivulus marmoratus*. Environ Biol Fishes 59:309–317

Sakakura Y, Soyano K, Noakes DLG, Hagiwara A (2006) Gonadal morphology in the self-fertilizing mangrove killifish, *Kryptolebias marmoratus*. Ichthyol Res 53:427–430

Sato T, Nakabo T (2003) A revision of the *Paraulopus oblongus* group (Aulopiformes: Paraulopidae) with description of a new species. Ichthyol Res 50:164–177

Sawada K, Yamaguchi S (2020) An evolutionary ecological approach to sex allocation and sex determination in crustaceans. In: Cothran RD, Thiel M (eds) The natural history of the Crustacea: reproductive biology, vol 6. Oxford University Press, Oxford, pp 177–196

Sawada K, Yoshida R, Yasuda K, Yamaguchi S, Yusa Y (2015) Dwarf males in the epizoic barnacle *Octolasmis unguisiformis* and their implications for sexual system evolution. Invertebr Biol 134:162–167

Sawada K, Yamaguchi S, Iwasa Y (2017) Be a good loser: a theoretical model for subordinate decision-making on bi-directional sex change in haremic fishes. J Theor Biol 421:127–135

Schärer L (2009) Tests of sex allocation theory in simultaneously hermaphroditic animals. Evolution 63:1377–1405

Schwarzhans W (1994) Sexual and ontogenetic dimorphism in otoliths of the family Ophidiidae. Cybium 18:71–98

Sekizawa A, Goto SG, Nakashima Y (2019) A nudibranch removes rival sperm with a disposable spiny penis. J Ethol 37:21–29

Smith CL (1959) Hermaphroditism in some serranid fishes from Bermuda. Pap Michigan Acad Sci Arts Let 44:111–119

Smith CL (1975) The evolution of hermaphroditism in fishes. In: Reinboth PDR (ed) Intersexuality in the animal kingdom. Springer, Berlin, pp 295–310

Smith CL, Atz EH (1969) The sexual mechanism of the reef bass *Pseudogramma bermudensis* and its implications in the classification of the Pseudogrammidae (Pisces: Perciformes). Z Morph Tiere 65:315–326

Smith CL, Atz EH (1973) Hermaphroditism in the mesopelagic fishes *Omosudis lowei* and *Alepisaurus ferox*. Copeia 1973:41

Smith CL, Erdman DS (1973) Reproductive anatomy and color pattern of *Bullisichthys caribbaeus* (Pisces: Serranidae). Copeia 1973:149–151

Soto CG, Leatherland JF, Noakes DLG (1992) Gonadal histology in the self-fertilizing hermaphroditic fish *Rivulus marmoratus* (Pisces, Cyprinodontidae). Can J Zool 70:2338–2347

St. Mary CM (1993) Novel sexual patterns in two simultaneously hermaphroditic gobies, *Lythrypnus dalli* and *Lythrypnus zebra*. Copeia 1993:1062–1072

St. Mary CM (1994) Sex allocation in a simultaneous hermaphrodite, the blue-banded goby (*Lythrypnus dalli*): the effects of body size and behavioral gender and the consequences for reproduction. Behav Ecol 5:304–313

Sulak KJ (1995) Chlorophthalmidae: ojiverdes. In: Fischer W, Krupp F, Schneider W, Sommer C, Carpenter KE, Niem VH (eds) Pacífico centro-oriental volumen II. Vertebrados-Parte, vol 1. FAO, Rome, pp 1005–1006

Sulak KJ, Wenner CA, Sedberry GR, Guelpen LV (1985) The life history and systematics of deep-sea lizard fishes, genus *Bathysaurus* (Synodontidae). Can J Zool 63:623–642

Sunobe T, Sado T, Hagiwara K, Manabe H, Suzuki T, Kobayashi Y, Sakurai M, Dewa S, Matsuoka M, Shinomiya A, Fukuda K, Miya M (2017) Evolution of bidirectional sex change and gonochorism in fishes of the gobiid genera *Trimma*, *Priolepis*, and *Trimmatom*. Sci Nat 104: 15

Tatarenkov A, Lima SMQ, Taylor DS, Avise JC (2009) Long-term retention of self-fertilization in a fish clade. Proc Natl Acad Sci U S A 106:14456–14459

Tatarenkov A, Lima SMQ, Avise JC (2011) Extreme homogeneity and low genetic diversity in *Kryptolebias ocellatus* from South-Eastern Brazil suggest a recent foundation for this androdioecious fish population. J Fish Biol 79:2095–2105

Tatarenkov A, Earley RL, Perlman BM, Scott Taylor D, Turner BJ, Avise JC (2015) Genetic subdivision and variation in selfing rates among Central American populations of the mangrove rivulus, *Kryptolebias marmoratus*. J Hered 106:276–284

Taylor DS (2000) Biology and ecology of *Rivulus marmoratus*: new insights and a review. Florida Sci 63:242–255

Taylor DS (2012) Twenty-four years in the mud: what have we learned about the natural history and ecology of the mangrove rivulus, *Kryptolebias marmoratus*? Integr Comp Biol 52:724–736

Tomlinson J (1966) The advantages of hermaphroditism and parthenogenesis. J Theor Biol 11:54–58

Touart LW, Bortone SA (1980) The accessory reproductive structure in the simultaneous hermaphrodite *Diplectrum bivittatum*. J Fish Biol 16:397–403

Turner BJ, Davis WP, Taylor DS (1992) Abundant males in populations of a selfing hermaphrodite fish, *Rivulus marmoratus*, from some Belize cays. J Fish Biol 40:307–310

Turner BJ, Fisher MT, Taylor DS, Davis WP, Jarrett BL (2006) Evolution of ‘maleness’ and outcrossing in a population of the self-fertilizing killifish, *Kryptolebias marmoratus*. Evol Ecol Res 8:1475–1486

Tuset VM, García-Díaz MM, González JA, Lorente MJ, Lozano IJ (2005) Reproduction and growth of the painted comber *Serranus scriba* (Serranidae) of the Marine Reserve of Lanzarote Island (Central-Eastern Atlantic). Estuar Coast Shelf Sci 64:335–346

Warner RR (1984) Mating behavior and hermaphroditism in coral reef fishes. Am Sci 72:128–136

Weeks SC (2012) The role of androdioecy and gynodioecy in mediating evolutionary transitions between dioecy and hermaphroditism in the Animalia. Evolution 66:3670–3686

Weeks SC, Benvenuto C, Reed SK (2006a) When males and hermaphrodites coexist: a review of androdioecy in animals. Integr Comp Biol 46:449–464

Weeks SC, Sanderson TF, Reed SK, Zofkova M, Knott B, Balaraman U, Pereira G, Senyo DM, Hoeh WR (2006b) Ancient androdioecy in the freshwater crustacean *Eulimnadia*. Proc R Soc B 273:725–734

Weibel AC, Dowling TE, Turner BJ (1999) Evidence that an outcrossing population is a derived lineage in a hermaphroditic fish (*Rivulus marmoratus*). Evolution 53:1217–1225

Wong MYL, Fauvelot C, Planes S, Buston PM (2012) Discrete and continuous reproductive tactics in a hermaphroditic society. Anim Behav 84:897–906

Yamaguchi S, Iwasa Y (2017) Advantage for the sex changer who retains the gonad of the nonfunctional sex. Behav Ecol Sociobiol 71:39

Yamaguchi S, Iwasa Y (2021) Evolutionary game in an androdioecious population: coupling of outcrossing and male production. J Theor Biol 513:110594

Yamaguchi S, Charnov EL, Sawada K, Yusa Y (2012) Sexual systems and life history of barnacles: a theoretical perspective. Integr Comp Biol 52:356–365

Yamauchi S (2008) Breeding and exhibition of Greeneyes (*Chlorophothalmus* spp.). Aquabiology 30:770–775

Yusa Y (2018) Hermaphrodites, dwarf males, and females: evolutionary transitions of sexual systems in barnacles. In: Leonard JL (ed) Transitions between sexual systems: understanding the mechanisms of, and pathways between, dioecy, hermaphroditism and other sexual systems. Springer International Publishing, Cham, pp 221–245

Yusa Y, Yoshikawa M, Kitaura J, Kawane M, Ozaki Y, Yamato S, Høeg JT (2012) Adaptive evolution of sexual systems in pedunculate barnacles. Proc R Soc B 279:959–966

Yusa Y, Takemura M, Sawada K, Yamaguchi S (2013) Diverse, continuous, and plastic sexual systems in barnacles. Integr Comp Biol 53:701–712

Zaiser MJ, Moyer JT (1981) Notes on the reproductive behavior of the lizardfish *Synodus ulae* at Miyake-jima, Japan. Jpn J Ichthyol 28:95–98

Zorica B, Sinovčić G, Keč VČ (2005) Reproductive period and histological analysis of the painted comber, *Serranus scriba* (Linnaeus, 1758), in the Trogir Bay area (eastern mid-Adriatic). Acta Adriat 46:77–82

Chapter 3
Protandry in Fishes

Tomoki Sunobe

Abstract Protandry (male-to-female sex change) is known in 62 fish species among various higher taxa that are not closely related to each other phylogenetically. The size-advantage model predicts that protandry is favored under random mating. The mating systems of protandrous fishes have been reported only in the following species: 10 species of anemonefish (*Amphiprion*; Pomacentridae) are monogamous, with females larger than their partners, but it is suggested that pairing occurred randomly in gonochoristic ancestors; in three species of flatheads (Platycephalidae), mating occurs randomly, with individuals changing their partners after each spawning; in the seabream *Sparus aurata* (Sparidae), a female spawns with one of several males in a spawning aggregation, which is considered random mating as there seems to be no competition between the males. These cases suggest that protandry will evolve if pairing occurs randomly regardless of pair continuity. Partial protandry, in which protandrous and gonochoristic individuals coexist, is reported for 28 of these species. Gonochorism is predicted to evolve in the case of mating with equal reproductive success of females and males at each size according to the size-advantage model. Fishes exhibiting partial protandry are suggested to have the opportunity to spawn either by random mating or by the above mating.

Keywords Gonochorism · Group spawning · Mate choice · Monogamy · Population density · Random mating

3.1 Evolution of Protandry and Types of Sexual Patterns

Protandry (male-to-female sex change) is known among 62 fish species of 14 families (Table 3.1). These species belong to the Anguilliformes (1 species), Clupeiformes (2), Cypriniformes (1), Stomiiformes (5), and Percomorpha (Ovalentaria [10], Trachiniformes [3], Perciformes [10], Scorpaeniformes [7],

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T. Kuwamura et al. (eds.), *Hermaphroditism and Mating Systems in Fish*,
https://doi.org/10.1007/978-981-19-6095-6_3

Table 3.1 Species exhibiting protandrous sex change with type of sexual pattern, mating system, and habitat

		Type of sexual pattern	Mating system	Habitat	References
Anguilliformes					
Muraenidae	*Rhinomuaena quaesita*	I		Coral reef	Shen et al. (1979)
Clupeiformes					
Clupeidae	*Tenualosa macrura*	I		Tropical estuaries and coastal (Bengakalis, Sumatora)	Blaber et al. (1999)
		III		Tropical estuaries and coastal (Sarawak, Sumatora)	Blaber et al. (2005)
	T. toli	I		Tropical estuaries and coastal	Blaber et al. (1996)
Cypriniformes					
Cobitidae	*Cobitis taenia*	IV		Fresh water (Chisola River, Italy)	Lodi (1967)
		Gonochorism		Fresh water (Po River* and Timonchio River**, Italy)	Lodi (1980)*, Rasotto (1992)**
Stomiiformes					
Gonostomatidae	*Cyclothone atraria*	I		Deep sea	Miya and Nemoto (1985, 1987)
	C. microdon	I		Deep sea	Badcock and Merrett (1976)
	Gonostoma elongatum	III		Deep sea	Fisher (1983)
	Sigmops bathyphilus	III		Deep sea	Badcock (1986) identified as *Gonostoma bathyphilum*
	S. gracile	I		Deep sea	Kawaguchi and Marumo (1967)

Ovalentaria					
Pomacentridae	*Amphiprion akallopisos*	I	Monogamy	Coral reef	Fricke and Fricke (1977), Fricke (1979)
	A. bicinctus	I	Monogamy	Coral reef	Fricke and Fricke (1977), Fricke (1983)
	A. clarkii	I	Monogamy	Coral reef (low-density hosts)	Moyer and Nakazono (1978)
		IV	Monogamy	Temperate reef (high-density hosts)	Ochi (1989b), Hattori and Yanagisawa (1991)
	A. frenatus	I	Monogamy	Coral reef	Moyer and Nakazono (1978), Hattori (1991)
	A. melanopus	I	Monogamy	Coral reef	Godwin (1994a), Godwin (1994b), Ross (1978)
	A. ocellaris	I	Monogamy	Coral reef	Moyer and Nakazono (1978), Madhu et al. (2010)
	A. percula	I	Monogamy	Coral reef	Madhu and Madhu (2006)
	A. perideraion	I	Monogamy	Coral reef	Moyer and Nakazono (1978), Hattori (2000)
	A. polymnus	I	Monogamy	Coral reef	Moyer and Nakazono (1978), Rattanayuvakorn et al. (2006)
	A. sandaracinos	I	Monogamy	Coral reef	Moyer and Nakazono (1978)
Trachiniformes					
Creediidae	*Crystallodytes cookei*	I		Coral reef	Langston (2004)
	Limnichthys fasciatus	I		Temperate reef	Shitamitsu and Sunobe (2017)
	L. nitidus	I		Coral reef	Langston (2004), Shitamitsu and Sunobe (2017)
Perciformes					
Centropomidae	*Centropomus parallelus*	III		Tropical Sea and estuaries	Costa e Silva et al. (2021)
	C. undecimalis	I		Tropical Sea and estuaries	Taylor et al. (1998), Taylor et al. (2000), Young et al. (2020)
Latidae	*Lates calcarifer*	III		Tropical Sea and estuaries	Guiguen et al. (1994), Roberts et al. (2021)

(continued)

Table 3.1 (continued)

		Type of sexual pattern	Mating system	Habitat	References
Polynemidae	*Eleutheronema tetradactylum*	I		Tropical Sea	Shihab et al. (2017), Junnan et al. (2020)
	Galeoides decadactylus	III		Tropical Sea	Longhurst (1965)
	Polydactylus macrochir	I		Tropical Sea (1986a–1990)	Moore et al. (2017)
		II		Tropical Sea (2007–2009)	
	P. quadrifilis	II		Tropical Sea	Butler et al. (2018, 2021)
Terapontidae	*Bidyanus bidyanus*	II		Fresh water	Moiseeva et al. (2001)
	Mesopristes cancellatus	I		Fresh water	Barazona et al. (2015)
Eleginopsidae	*Eleginops maclovinus*	I		Temperate Sea	Calvo et al. (1992), Brickle et al. (2005), Licandeo et al. (2006)
Scorpaeniformes					
Platycephalidae	*Cociella crocodila*	I		Temperate Sea	Aoyama et al. (1963)
	Inegocia japonica	II (inferred)	Random mating	Temperate Sea	Shinomiya et al. (2003)
	Kumococcius rodericensis	I		Temperate Sea	Fujii (1971)
	Onigocia macrolepis	I		Temperate Sea	Fujii (1970)
	Platycephalus sp.2	IV	Random mating	Temperate Sea	Hara and Sunobe (2021)
	Suggrundus meerdervoortii	I		Temperate Sea	Shitamitsu and Sunobe (2018)
	Thysanophrys celebica	I	Random mating	Temperate Sea	Sunobe et al. (2016)
Moroniformes					
Moronidae	*Morone saxatulis*	I			Moser et al. (1983)

				Temperate Sea and fresh water	
Spariformes					
Sparidae	*Acanthopagrus australis*	IV		Tropical and temperate sea	Pollock (1985)
	A. berda	I*	Spawning aggregation (inferred) **	Tropical Sea	Anam et al. (2019)*, Garratt (1993)**
	A. bifasciatus	III		Tropical Sea	Etessami (1983)
	A. latus	I		Temperate Sea	Kinoshita (1939), Akazaki (1962)
	A. morrisoni	I		Subtropical and temperate sea	Hesp et al. (2004) identified as *A. latus*
	A. pacificus	II		Tropical Sea	Tobin et al. (1997) indentified as *A. berda*
	A. schlegelii	I		Tropical and temperate sea	Kinoshita (1936), Chang and Yueh (1990), Lee et al. (2001), Law and Sadovy de Mitheson (2017)
	Diplodus annularis	IV		Temperate Sea(Canary Islands)	Lissia-Frau et al. (1976), Pajuelo and Lorenzo (2001)
		Gonochorism		Temperate Sea(Central Mediterranean)	Chaouch et al. (2013)
	D. argenteus	IV		Tropical Sea	David et al. (2005)
	D. cadenati	IV		Temperate Sea	Pajuelo and Lorenzo (2004)
	D. capensis	IV	Spawning aggregation (inferred)	Temperate Sea (Tsitsikamma, South Africa)	Mann and Buxton (1998))
		Gonochorism		Temperate Sea(Angola)	Joubert (1981), Richardson et al. (2011)
	D. kotschyi	III		Temperate Sea(Kuwait)	Abou-Seedo et al. (1990)
	D. puntazzo	IV		Temperate Sea	Lissia-Frau et al. (1976), Pajuelo et al. (2008)
	D. sargus	III		Temperate Sea(Tunisia)	Mouine et al. (2007)

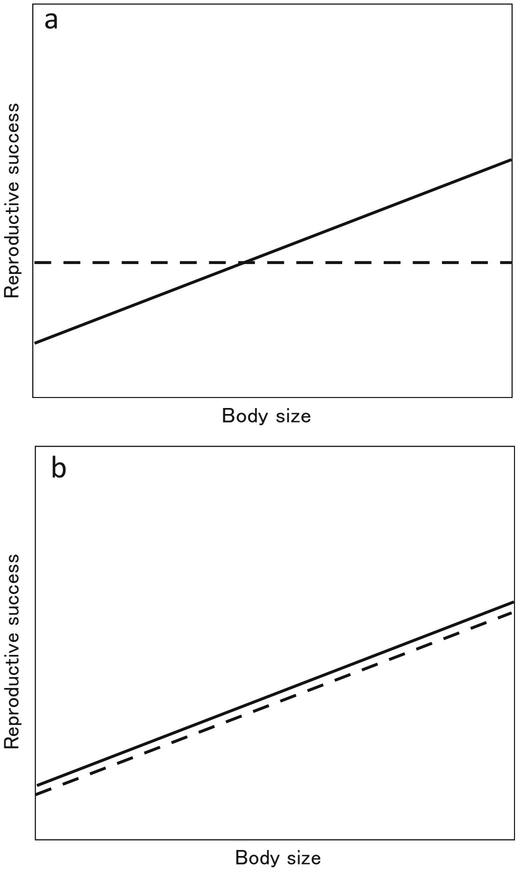
(continued)

Table 3.1 (continued)

		Type of sexual pattern	Mating system	Habitat	References
		IV		Temperate Sea	Lissia-Frau et al. (1976)
	D. vulgaris	IV		Temperate Sea	Gonçalves and Erzini (2000), Pajuelo et al. (2006)
	Lithognathus mormyrus	I		Temperate Sea	Lissia-Frau et al. (1976), Besseau and Brusl-é-Sicard (1995), Lorenzo et al. (2002)
	Pagellus acarne	IV		Temperate Sea	Lamrini 1986
	P. bogaraveo	III		Temperate Sea(Messina, Italy)	Micale et al. (2002)
		IV		Temperate Sea(Azores Islands)	Krug (1990, 1998)
	Rhabdosargus sarba	II*	Pair spawning**	Tropical Sea(Hong Kong* and Taiwan**)	Kinoshita (1939)*, Yeung and Chan (1987)*, Leu (1994)**
		Gonochorism		Temperate Sea(Australia)	Hesp and Potter (2003)
	Sarpa salpa	I		Temperate Sea	Lissia-Frau et al. (1976), van der Walt and Mann (1998)
	Sparidentex hasta	I		Tropical Sea	Abu-Hakima (1984), Lone and Al-Marzouk (2000)
	Sparus aurata	II	Pair and group spawning	Temperate Sea	Zohar et al. (1978), Bruslé-Sicard and Fourcault (1997), Ibarra-Zatarain and Duncan (2015)

For type of sexual pattern (I–IV), see Fig. 3.2

Fig. 3.1 Relationship between the reproductive success and body size of females (solid line) and males (broken line) in random mating (**a**), which favors protandry, and ERS mating (**b**), which favors gonochorism (modified from Warner 1975 and 1984)

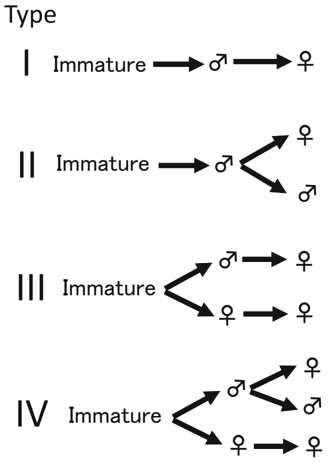


Moroniformes [1], and Spariformes [22]). These taxa are not closely related to each other phylogenetically, whereas all of the protogynous species belong to Percomorpha (Kuwamura et al. 2020), which indicates that the evolution of protandry occurred independently in each taxon.

The size-advantage model (SA model) predicts that protandry is favored under random mating (i.e., lack of female mate choice and/or monopolization of multiple females by large males) (Warner 1975, 1984; Fig. 3.1a). In this condition, male reproductive success is equal in all size classes, while that of females increases linearly with body size. Consequently, at small body sizes, the reproductive success of males is higher than that of females, and vice versa at large sizes. To maximize lifetime reproductive success, protandry should be favored.

For protogynous species (female-to-male sex change), many studies have been conducted on the relationship between the mating system and sex change to test the SA model (see Chap. 4). Notably, most protogynous fishes inhabit shallow rocky and coral reefs, where they are easily observed. For protandrous fishes, however, detailed studies on mating systems in the field are so far limited to 10 species of

Fig. 3.2 Schematic depiction of the four types of sexual patterns (I, II, III, and IV) in protandrous fishes



anemonefishes (*Amphiprion*; Pomacentridae) and three species of flatheads (Platycephalidae) (Kuwamura et al. 2020), undoubtedly because of the difficulties in accessing their habitats (deep-sea, turbid estuaries and/or offshore) and/or because of their nocturnal habits. Although various protandrous species are known among the seabreams (Sparidae; Kuwamura et al. 2020; Pla et al. 2020; Table 3.1), mating system has been described only in *Sparus aurata* through observations during artificial rearing (Ibarra-Zatarain and Duncan 2015), and spawning behavior of *Rhabdosargus sarba* in captivity was briefly reported (Leu 1994).

Protandrous species do not always show a simple sexual pattern of male-to-female sex change, but in some species, protandry and gonochorism coexist within a population, which is called "partial protandry" (Gonçalves and Erzini 2000; Mouine et al. 2007; Pajuelo et al. 2008). Four sexual types (allocation of male and female functions within a population/species) are distinguished in protandrous species (Fig. 3.2):

Type I: All individuals first mature as male and then change sex to female.

Type II: All individuals first mature as male, and some males then change sex to female, while others do not.

Type III: Individuals first mature either as male or female, and the males later change sex to female.

Type IV: Individuals first mature either as male or female, and then some males change sex to female, while other males do not.

The coexistence of two types of females in types III and IV is sometimes called "digyny" (Gonçalves and Erzini 2000), as the coexistence of two types of males is called diandry in protogynous fishes (see Chap. 4). All protandrous families contain species of type I (Table 3.1). The number of fish species known to exhibit type I, II, III, or IV, respectively, is 37, 7, 10, and 12. In nine species, two types of sexual patterns, which can also include gonochorism, have been reported from different populations: types I and II in one species, types I and III in one species, types I and

IV in one species, types III and IV in two species, type II and gonochorism in one species, and type IV and gonochorism in three species (Table 3.1).

Partially protandrous fishes can include gonochoristic individuals within the population, and in four species all individuals in some populations are gonochoristic. In general, gonochorism is favored if both sexes show a similar increase of fertility with size, when males and females form monogamous pairs matched by size or when males compete with each other to fertilize eggs and thus to produce the most sperm (Warner 1984). In this chapter, such mating system is called "ERS mating" that means equal reproductive success of females and males at each size (Fig. 3.1b). Species with group spawning will be gonochoristic because sperm competition in mass spawning results in greater reproductive success for larger males. For example, *Bodianus eclancheri* and four species of *Sparisoma* (Labridae), *Alphestes afer*, seven species of *Cephalopholis*, seven species of *Epinephelus*, four species of *Mycteroperca*, two species of *Plectropmus*, and *Rypticus saponaceus* (Epinephelidae) are gonochoristic with group spawning (Erisman et al. 2013). Small sneaking males, which invade territories of larger males to fertilize eggs, are also known to be gonochoristic because the small males will attain equal reproductive success with the females of the same size. For example, small males of *Symphodus ocellatus* (Labridae) and *Bathygobius fuscus* (Gobiidae) exhibit sneaking, and their sexual pattern is gonochoristic (Warner and Lejeune 1985; Taru et al. 2002).

In hermaphroditic fishes, the mating system of a species may vary between habitats with different conditions, and the sexual pattern is expected to change accordingly (Kuwamura et al. 2020). In the coral-dwelling damselfish *Dascyllus aruanus*, which exhibits harem polygyny and protogyny, the sexual pattern is gonochoristic in high-density populations in continuous coral-covered habitats, where females can move among the corals with low risk of movement, so they are not monopolized by large males (Kuwamura et al. 2016, 2020). Then, in partially protandrous species that include both protandrous and gonochoristic individuals, it is expected that the mating system could change according to the population density, resulting in alteration of the sexual pattern. Namely, protandry, partial protandry, and gonochorism will occur under random mating, both random mating and ERS mating, and ERS mating, respectively.

In the following sections, I describe the mating systems and sexual patterns of 10 species of *Amphiprion* (Pomacentridae), three species of Platycephalidae, and two species of Sparidae, for which the reproductive behavior has been reported, and consider whether the above prediction fits or not.

3.2 Anemonefish (*Amphiprion*; Pomacentridae)

3.2.1 Mating System and Proximate Cause of Sex Change

Among protandrous fishes, anemonefishes (*Amphiprion*: Fig. 3.3a) have been studied in the most detail. Anemonefishes establish a social group in a host sea anemone:

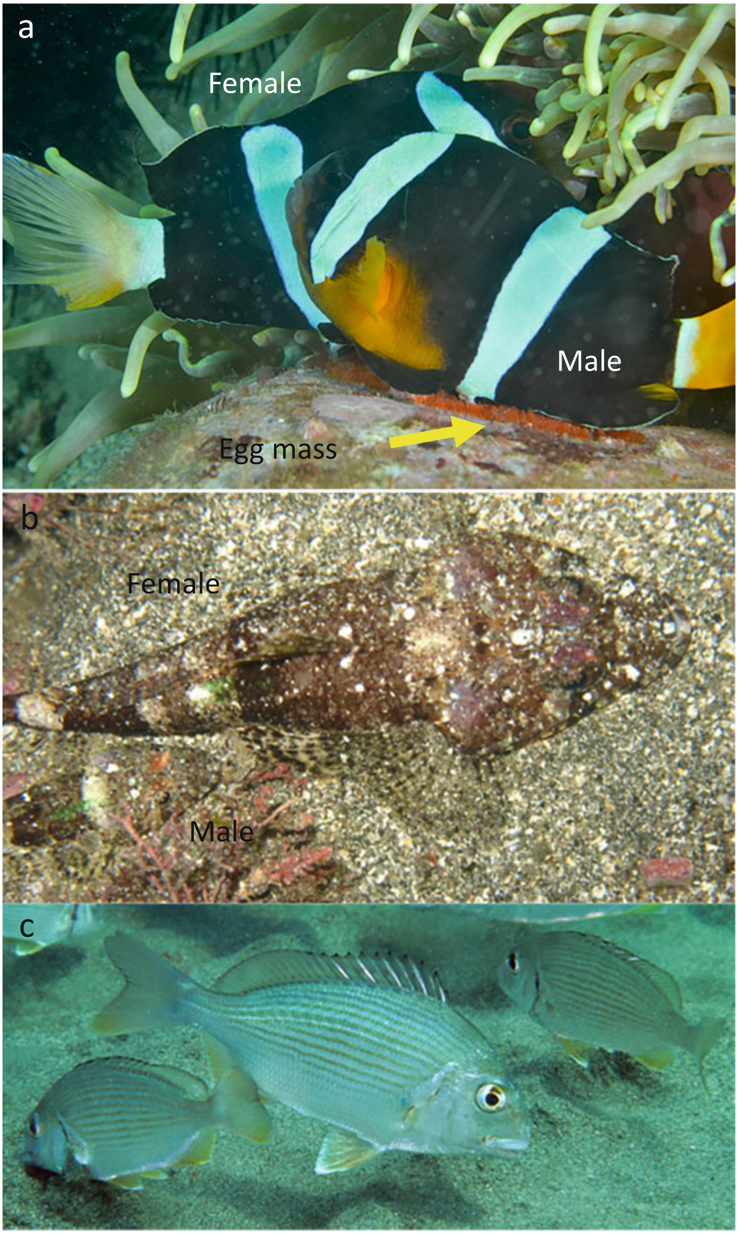


Fig. 3.3 (**a**) Spawning of *Amphiprion clarkii* (photo by T. Hirata); (**b**) *Thysanophrys celebica*: (photo by S. Sakaida); (**c**) *Rhabdosargus sarba* (photo by T. Hirata)

the largest and the second-largest individuals are female and male, respectively, and other smaller individuals are nonbreeders (immatures and juveniles). Therefore, their mating system is non-size-assortative monogamy (the term "size-assortative" is used in the narrow meaning of "matched by size" in the context of the SA model; Warner 1984), defined as "pair bonding of a male and a female which does not prefer a large male but accepts a smaller one" (Kuwamura et al. 2020). Females attack smaller individuals, including males, because there is a social order based on body size within the group. This seems to prevent males from changing sex. When females disappear, males change sex and become females, and the third-ranked individuals obtain breeding status as male (Fricke and Fricke 1977; Moyer and Nakazono 1978; Fricke 1979; Buston 2003; Hattori 2012). This evidence indicates that the sexual pattern of anemonefishes is type I. Another requisite for sex change to female is reaching a certain size in male, for instance, 100 mm in standard length (SL) in *A. bicinctus* and 75 mm SL in *A. frenatus* (Fricke 1983; Hattori 1991). Furthermore, single males evidently do not change sex: it has been shown in *A. bicinctus* that males require smaller subadults to change sex (Fricke 1983).

3.2.2 Why Monogamy?

It has been suggested that monogamy in anemonefishes is the result of resource limitation (Fricke and Fricke 1977). The host sea anemone provides shelter for anemonefishes, and eggs are spawned on the substrate near or under the tentacles of the host (Allen 1972; Moyer and Bell 1976; Ross 1978; Moyer and Steene 1979; Fautin 1991). Aggressive behavior between homosexuals of different groups is frequently observed in high-density populations of *A. akallopisos* and *A. clarkii* (Fig. 3.3a: Moyer and Sawyers 1973; Fricke 1979; Moyer 1980; Ochi 1989b), indicating that there is intrasexual competition. Thus, there will be competition among females for spawning sites (Ochi 1989a), whereas males will compete for breeding status because they often attack nonbreeders in the same group (Fricke and Fricke 1977; Buston 2003).

To test the above hypothesis, rearing experiments were conducted using *A. ocellaris* (Sunobe et al. 2022). If females compete each other over spawning sites, the frequency of aggressive behavior should decrease under conditions with more spawning sites. When two females were placed in a tank and given one or three flower pots as spawning nests, the results did not support the prediction as there was no significant difference in the frequency of attacks. The females seemed to defend the whole space including all the nest sites. When two males were paired, the larger of the two changed sex and eventually became a female, resulting in less aggressive behavior. However, if they were competitive for breeding status, the introduction of a female into the tank should increase the frequency of conflict. Indeed, the results showed that the frequency of attacks significantly increased, supporting the hypothesis. These results indicate that individuals of the same sex cannot cohabit in the same host anemone.

3.2.3 Non-size Assortative Monogamy and Evolution of Protandry

Monogamy seems to be the opposite of random mating in appearance. In this section, I will discuss how protandry have evolved under a monogamous mating system.

There are two main hypotheses to explain the evolution of protandry in anemonefishes (Fricke and Fricke 1977; Hattori 2012). Fricke and Fricke (1977) hypothesized that if the sex ratio of gonochoristic ancestral species was 1:1, homosexual and heterosexual pairings would be formed equally by randomly arriving juveniles or migrating adults into host anemones. Movement of individuals between hosts may be limited by a low density of hosts and predation pressure during migration. Therefore, it would be adaptive for a homosexual pair to be hermaphrodites, as one could then change sex to create a heterosexual pair. Among anemonefishes, smaller males can fertilize and guard the eggs of larger females because the eggs positioned under the host's tentacles are protected from egg predators (Fig. 3.3a), indicating that male size is not associated with reproductive success. In contrast, large females can produce more eggs than small females. Hence, non-size-assortative monogamy is established, and protandry should be advantageous to increase the number of fertilized eggs for an individual. Thus, in monogamy, the reproductive success of an individual would be maximized if the larger individual functions as female (Fricke and Fricke 1977).

The above hypothesis assumes random pairing in the gonochoristic ancestral species, but Hattori (2012) pointed out that random pairing does not occur in the extant anemonefishes and proposed "the body size composition model." This model predicts the size composition based on the number of individuals that the host can accommodate, and predicts the size differences and size ratios between individuals of adjacent ranks. Data on *A. frenatus*, *A. ocellaris*, and *A. perideraion* were used to compare the reproductive success of the largest individuals when the largest individual is female and monogamous or when the largest individual is male and polygynous. The results showed higher reproductive success under the former scenario. However, the model uses data from extant species, which may not reflect the size composition or reproductive success of ancestral species. In addition, as mentioned above, the coexistence of multiple females in one host is not possible and polygyny cannot occur irrespective of reproductive success.

To investigate the hypothesis of Fricke and Fricke (1977), simulations based on a mathematical model were performed (Sunobe et al. 2022), assuming the following preconditions: (1) the ancestral species is gonochoristic; (2) when an individual invades a host anemone occupied by another individual of the same sex, the larger one can stay in the host and the smaller one is eliminated; and (3) a pair is formed by random pairing (no mate choice) after settlement of the opposite sex. The results on the relationship between male and female reproductive success and body size corresponded well with the case of random mating in the SA model (Fig. 3.1a).

Monogamy appears to be very different from random mating, but if there is no mate choice at pairing, protandry will evolve independently of pair continuity.

3.2.4 Mating System and Sexual Pattern in High-Density Populations

The higher the density of hosts, the higher the density of resident anemonefish. In the high-density population of *A. clarkii*, males and females invade adjacent territories and temporarily establish bigamy or biandry, though monogamy is common (Ochi 1989a, 1989b; Hattori and Yanagisawa 1991). In *A. akallopisos* populations established around large anemone colonies, there are only monogamous pairs, despite the potential for polygamy (Fricke 1979). These findings indicate that the mating system of anemonefishes is monogamous in principle.

However, in areas with a dense population of host sea anemones, the sexual pattern of *A. clarkii* is type IV (Table 3.1), with a low frequency of sex change. Immature nonbreeders can establish a pair and occupy their own home ranges on the outskirts of adult territories. These immature individuals start as male or female when they can occupy the status of reproduction. The male after mate loss mates with a solitary female or invades another pair's territory with no risk of movement, and size-assortative pairs are formed. (Ochi 1989b; Hattori and Yanagisawa 1991). Therefore, the reproductive success of both sexes is nearly equal at all sizes, i.e., ERS mating, sex change rarely occurs, and gonochorists can exist.

3.3 Flatheads (Platycephalidae)

Protandry is confirmed in seven species of Platycephalidae (Table 3.1). Of these species, the mating system has been clarified only in three species: *Inegocia japonica*, *Thysanophrys celebica* (Fig. 3.3b), and *Platycephalus* sp. 2 of Nakabo (2013) (Shinomiya et al. 2003; Sunobe et al. 2016; Hara and Sunobe 2021).

The mating system of *I. japonica* was the first to be identified among protandrous fishes other than the anemonefishes (Shinomiya et al. 2003). All small individuals are male, and large individuals are predominantly female (Table 3.1). In 5 of 8 males from 116 to 168 mm in total length (TL), protandrous sex change was confirmed. However, of 16 males (98–256 mm TL) identified in the field, none of the six males larger than 183 mm TL were observed to change sex. Therefore, there is a possibility that some males do not change sex throughout their lifetime, indicating that the sexual type is type II (Table 3.1). The males less than 102 mm TL did not undergo sex change, suggesting that males must reach at least this size for sex change (Shinomiya et al. 2003).

In field observations of *I. japonica*, the home ranges of individuals of the same or opposite sex overlapped each other, and there was no aggressive interaction among them. Only pair spawning occurred. The mating system was random mating as predicted by the SA model, with the pairs being temporary, and both sexes established a pair with a different individual at the next spawning. There was no significant correlation between the sizes of males and females in the mating pairs, showing non-size-assortative mating (Shinomiya et al. 2003).

The mating system of *T. celebica* is also random mating, the home ranges of individuals of the same or opposite sex overlapping each other (Sunobe et al. 2016). The sexual pattern of this species is type I (Table 3.1). The longevity of *T. celebica* is ~5 years according to age estimations from scales. In rearing experiments, 1-year-old males did not change sex, and males did change sex after age 2. In contrast to the anemonefishes, in which the presence of females prevents sex change of males, the sex change of *T. celebica* males occurred even when reared with larger females. These results suggest that there is no social suppression of sex change based on size (Sunobe et al. 2016).

The mating system of *Platycephalus* sp. 2 is regarded as random mating, as in the two species mentioned above, based on temporal pair bonding, no territoriality, and non-size-assortative mating (Hara and Sunobe 2021). Even so, the number of individuals with bisexual gonad was relatively small, accounting for only 2 of 202 individuals. Because some individuals of the population do not change sex, and sexual type is classified into type IV (Table 3.1). The home ranges overlapped each other (Fig. 3.4) when they actively moved around. Therefore, other males can join a pair spawning by sneaking. In an aquarium under high-density conditions, multiple males followed a ripe female before spawning (Oikawa 1996). Hence, ERS mating is suggested through sneaking behavior and/or group spawning.

In rearing experiments with *Platycephalus* sp. 2, the smallest male (age 2 years) changed sex when kept with the larger and older five males and three females (Hara and Sunobe 2021). This shows that the larger individuals did not inhibit sex change of the smaller individual. The growth rate of *Platycephalus* sp. 2 varied among individuals up to age 2 years (Masuda et al. 2000; although they identified the species as *P. indicus*, it is regarded as *Platycephalus* sp. 2. by the collecting sites). Charnov (1982) predicts that a difference of growth rate between sexes favors sex change. For example, in the size-assortatively monogamous goby *Paragobiodon echinocephalus*, because females grow faster than males, the smaller individual in newly formed same-sex pairs should function as female to increase future reproductive success of the pair (Kuwamura et al. 1994). In *Lates calcarifer* (Latidae) there is a difference of growth rate among immature males, and those males with rapid growth change sex early during the juvenile phase to mature as female, which are therefore not derived from a functional male (Roberts et al. 2021). As the size of these young sex-changers is larger than the old sex-changers in their life time, the fitness of the former is higher than the latter. Similarly, otolith analysis of *Polydactylus quadrifilis* (Polynemidae) suggested that the males that change sex to female grow faster than the males that do not change sex (Butler et al. 2018).

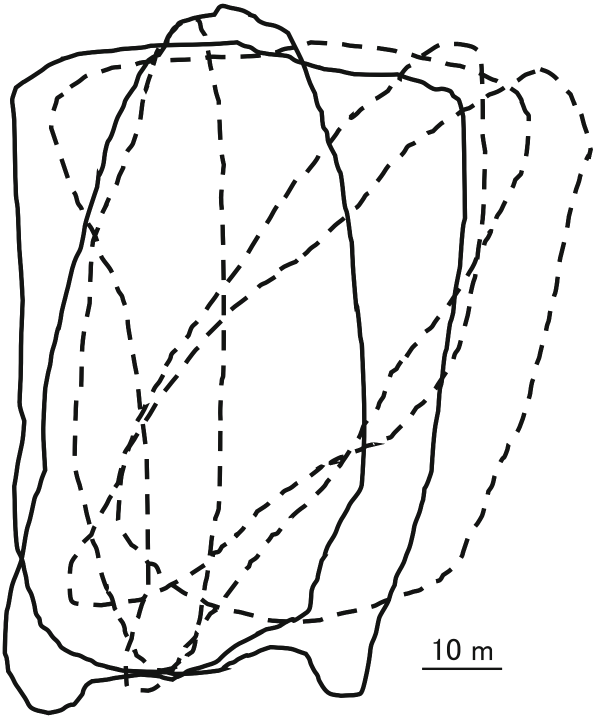


Fig. 3.4 Home ranges of *Platycephalus* sp. 2 in a study area of approximately 70 × 50 m on a sandy bottom at a depth of 20 m in Ito, Tateyama, Japan, observed by SCUBA from June 9 to September 30, 2014 (Hara N and Sunobe T, unpublished data). Solid and broken lines show the home ranges of females and males, respectively

Therefore, growth-advantage may facilitate sex change in *Platycephalus* sp. 2 as well as these three species.

3.4 Seabreams (Sparidae)

Twenty-two protandrous species are known among the Sparidae (Table 3.1). Their mating systems are mostly unknown, and spawning behavior has been observed under rearing conditions only in *Sparus aurata* (type II) and *Rhabdosargus sarba* (type II in Hong Kong; gonochorism in Australia: Fig. 3.3c).

S. aurata is the only sparid species for which the mating system has been reported (Ibarra-Zatarain and Duncan 2015). In aquaria, the individuals first formed aggregations near the bottom. Next, males became slightly darkened and rubbed and nudged the genital pore of females. There was no aggressive interaction among any individuals, whether between the same or different sex. After courtship at the bottom, the female dramatically increased its swimming speed and released eggs. According to the video attached to the research paper, one to four males participated in the spawning (Ibarra-Zatarain and Duncan 2015). These results show that the mating system of *S. aurata* includes both random mating and ERS mating.

In natural spawning of *R. sarba* in captivity, a female was followed by three or four males, and then the female and one of the males paired and spawned near the surface (Leu 1994); however, further details on the mating system are unknown because of the fragmentary observations. If there is no competition among males, mating will be random.

3.5 Plasticity of Sexual Patterns in the Protandrous Fishes

The diverse sexual patterns of protandrous fishes (Fig. 3.2) may be due to the occurrence of both random mating and ERS mating, resulting in the occurrence of both protandry and gonochorism, as depicted in Fig. 3.1. As predicted (see Sect. 3.1), if the density is low, there will be more protandrous individuals because there will be more opportunities for pair spawning, while at high density, there will be more gonochoristic individuals participating in ERS mating.

Among species exhibiting partial protandry, the mating system has been observed only in *A. clarkii*, *Platycephalus* sp. 2, and *S. aurata*, as mentioned above. In *A. clarkii*, there may be a tendency toward gonochorism under high-density conditions, because males after the mate loss can establish a new pair with a female in another host anemone. As a result, ERS mating occurs (see Sect. 3.2). In *Platycephalus* sp. 2, although group spawning has not been observed, there is a possibility of reproduction through group spawning (see Sect. 3.3). In *S. aurata*, both random pairing and group spawning took place in the same tank (see Sect. 3.4).

Although their spawning behavior and mating systems are unknown, different sexual patterns in populations of a species from different regions have also been reported in one species of tropical shad (Clupeidae), one loach (Cobitidae), and five sparids (Sparidae). These are: *Tenualosa macrura* (types I and III), *Cobitis taenia* (type IV and gonochorism), *Diplodus annularis* (type IV and gonochorism), *D. capensis* (type IV and gonochorism), *D. sargus* (type III and IV), *Pagellus bogaraveo* (types III and IV), and *R. sarba* (type II and gonochorism) (Table 3.1).

Even among individuals of a species within one region, fishing pressure has caused changes in the sexual pattern. *Polydactylus macrochir* (Polynemidae) is a large-sized species and commercially important in southern and eastern Australia. During the period 1986 to 1990, the females dominated the larger size classes and the males dominated the small ones, thus revealing type I (Moore et al. 2017). After a reduction of large individuals by overfishing of the larger and older females in the period 2007 to 2009, the sizes of males and females were mostly overlapped. These results indicate that some small males change sex, and some males do not change sex, showing transition to type II. Overfishing may have induced this transformation of sexual pattern (Moore et al. 2017). When the number of females declined from fishing, competition among males would have increased. Then, some males may have changed sex earlier to increase their future reproductive success.

The frequency of gonochoristic individuals within populations seems to increase in the order of types I, II, III, and IV. This may be attributable to a decrease in the frequency of random mating and an increase in that of ERS mating under higher population densities. Further comparative studies are needed to clarify the relationships among population densities, mating systems, and sexual types among regions.

3.6 Conclusions

1. Protandrous fishes include at least 62 species representing 14 families. In 37 of these species, all males change sex to females, but in 28 species some males do not change sex and/or primary females appear (partial protandry). Nine species exhibit different sexual types in different populations, and some are gonochorists. Information on the mating system is limited to 10 species of anemonefish (*Amphiprion*; Pomacentridae), three species of flatheads (Platycephalidae), and one species of sparid (Sparidae).
2. The size-advantage model predicts that protandry is favored under random mating (i.e., lack of female mate choice and/or monopolization of multiple females by large males) and gonochorism under ERS mating with equal reproductive success of females and males at each size.
3. In anemonefishes, eggs laid beneath the tentacles of the host sea anemone are guarded from egg predators; thus, even small males can complete egg guarding. Accordingly, there is no female mate choice, and protandry is favored. In areas with a high density of anemones, the density of *Amphiprion clarkii* is also high, and ERS mating occurs, resulting in a low frequency of sex change and a high number of gonochorists.
4. Three species of Platycephalidae are known to spawn in pairs. Mating occurs randomly and with a different mate each time the individual spawns. In *Platycephalus* sp. 2, males that do not change sex and primary females are expected to emerge.
5. In *Sparus aurata* (Sparidae), all individuals mature first as male, and thereafter some change sex to female, while others do not. This species exhibits pair spawning between a female and one of several males in a spawning aggregation. Formation of a pair may be established randomly. However, group spawning (ERS mating) is also possible.
6. Partial protandry is found in various protandrous species, and in some species all individuals are gonochorists in some populations. As background to this plasticity in sexual pattern, protandrous fishes may adopt random mating and/or ERS mating according to the given population density.

Acknowledgments I thank Tatsuru Kadota, Tetsuo Kuwamura, Yoichi Sakai, and Kota Sawada for helpful comments to improve the manuscript. I also thank Edanz (https://jp.edanz.com/user) for the English language review.

References

Abou-Seedo F, Wright JM, Clayton DA (1990) Aspects of the biology of *Diplodus sargus kotschyi* (Sparidae) from Kuwait Bay. Cybium 14:217–223

Abu-Hakima R (1984) Some aspects of the reproductive biology of *Acanthopagrus* spp. (family: Sparidae). J Fish Biol 25:515–526

Akazaki M (1962) Studies on the spariform fishes—anatomy, phylogeny, ecology and taxonomy. Misaki Marine Biological Institute, Kyoto University Special Reports 1:1–368

Allen GR (1972) The anemonefishes: their classification and biology. TFH Publications, Neptune City, New Jersey

Anam RO, Munga CN, Gonda JR (2019) The biology of Goldsilk Sea Bream (family: Sparidae) from the inshore waters of north coast Kenya. WIO J Mar Sci 18:77–86

Aoyama T, Kitajima T, Mizue K (1963) Study of the sex reversal of inegochi, *Cociella crocodila* (Tilesius). Bull Seikai Region Fish Res Lab 29:11–33

Badcock J (1986) Aspects of the reproductive biology of *Gonostoma bathyphilum* (Gonostomatidae). J Fish Biol 29:589–603

Badcock J, Merrett NR (1976) Midwater fishes in the eastern North Atlantic I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. Prog Oceanogr 7:3–58

Barazona CA, Demayo CG, Torres MAJ, Gorospe JG (2015) Landmark-based geometric morphometric analysis on bodyshape variation of *Mesopristes cancellatus* (Cuvier, 1829). Adv Environ Biol 9(19 S4):32–37

Besseau L, Bruslé-Sicard S (1995) Plasticity of gonad development in hermaphroditic sparids: ovotestis ontogeny in a protandric species, *Lithognathus mormyrus*. Environ Biol Fish 43:255–267

Blaber SJM, Milton DA, Pang J, Wong P, Boon-Teck O, Lolin N, Lubin D (1996) The life history of the tropical shad *Tenualosa toli* from Sarawak: first evidence of protandry in the Clupeiformes? Environ Biol Fish 46:225–242

Blaber SJM, Brewer DT, Milton DA, Merta GS, Efizon D, Fry G, van der Velde T (1999) The life history of the protandrous tropical shad *Tenualosa macrura* (Alosinae: Clupeidae): fishery implications. Estuar Coast Shelf Sci 49:689–701

Blaber SJM, Fry G, Milton DA, van der Velde T, Boon-Teck O, Pang J, Wong P (2005) The life history of *Tenualosa macrura* in Sarawak, further notes on protandry in the genus and management strategies. Fish Manag Ecol 12:201–210

Brickle P, Laptikhovsky V, Arkhipkin A (2005) Reproductive strategy of a primitive temperate notothenioid *Eleginops maclovinus*. J Fish Biol 66:1044–1059

Brusléa-Sicard S, Fourcault B (1997) Recognition of sex-inverting protandric *Sparus aurata*: ultrastructural aspects. J Fish Biol 50:1094–1103

Buston P (2003) Size and growth modification in clownfish. Nature 424:145–146

Butler EC, Childs A-R, Winkler AC, Milner MV, Potts WM (2018) Evidence for protandry in *Polydactylus quadrifilis* in the Kwanza Estuary, Angola, and its implications for local fisheries. Environ Biol Fish 101:301–313

Butler EC, Childs A-R, Milner MV, Farthing MW, Duncan MI, Winkler AC, Potts WM (2021) Do contemporary age-growth models overlook life-history complexities in protandrous fishes? A case study on the large protandrous polynemid, the giant African threadfin *Polydactylus quadrifilis*. Fish Res 233:105770

Chang CF, Yueh WS (1990) Annual cycle of gonadal histology and steroid profiles in the juvenile males and adult females of the protandrous black porgy, *Acanthopagrus schlegeli*. Aquaculture 91:179–196

Calvo J, Morriconi E, Rae GA, SanRoman A (1992) Evidence of protandry in a subantarctic notothenid, *Eleginops maclovinus* (Cuv. & Val., 1830) from the Beagle Channel, Argentina. J Fish Biol 40:157–164

Chaouch H, Hamida-Ben Abdallah O, Ghorbel M, Jarboui O (2013) Reproductive biology of the annular seabream, *Diplodus annularis* (Linnaeus, 1758), in the Gulf of Gabes (Central Mediterranean). J Appl Ichthyol 29:796–800

Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton, New Jersey

Costa e Silva GH, Freitas MO, Abilhoa V (2021) Reproductive biology of the fat Snook *Centropomus parallelus* Poey, 1860 (Teleostei, Centropomidae) and implications for its management in the southern Atlantic Ocean. J Fish Biol 99:669–672

David GS, Coutinho R, Quagio-Grassiotto I, Verani JR (2005) The reproductive biology of *Diplodus argenteus* (Sparidae) in the coastal upwelling system of Cabo Frio, Rio de Janeiro, Brazil. Afr J Mar Sci 27:439–447

Erisman BE, Petersen CW, Hastings PA, Warner RR (2013) Phylogenetic perspectives on the evolution of functional hermaphroditism in teleost fishes. Integr Comp Biol 53:736–754

Etessami S (1983) Hermaphroditism in one Sparidae of the Persian Gulf: *Acanthopagrus bifasciatus* (Forssk.). Cybium 7:87–91

Fautin DG (1991) The anemonefish symbiosis: what is known and what is not. Symbiosis 10:23–46

Fisher RA (1983) Protandric sex reversal in *Gonostoma elongatum* (Pisces: Gonostomatidae) from the eastern Gulf of Mexico. Copeia 1983:554–557

Fricke HW (1979) Mating system, resource defence and sex change in the anemonefish *Amphiprion akallopisos*. Z Tierpsychol 50:313–326

Fricke HW (1983) Social control of sex: field experiments with the anemonefish *Amphiprion bicinctus*. Z Tierpsychol 61:71–77

Fricke H, Fricke S (1977) Monogamy and sex change by aggressive dominance in coral reef fish. Nature 266:830–832

Fujii T (1970) Hermaphroditism and sex reversal in the fishes of the Platycephalidae I. Sex reversal of *Onigocia macrolepis* (Bleeker). Jpn J Ichthyol 17:14–21

Fujii T (1971) Hermaphroditism and sex reversal in the fishes of the Platycephalida II. *Kumococius detrusus* and *Inegocia japonica*. Jpn J Ichthyol 18:109–117

Garratt PA (1993) Spawning of riverbream, *Acanthopagrus berda*, in Kosi estuary. Afr Zool 28:26–31

Godwin J (1994a) Histological aspects of protandrous sex change in the anemonefish *Amphiprion melanopus* (Pomacentridae, Teleostei). J Zool Lond 232:199–213

Godwin J (1994b) Behavioural aspects of protandrous sex change in the anemonefish, *Amphiprion melanopus*, and endocrine correlates. Anim Behav 48:551–567

Gonçalves JMS, Erzini K (2000) The reproductive biology of the two-banded sea bream (*Diplodus vulgaris*) from the southwest coast of Portugal. J Appl Ichthyol 16:110–116

Guiguen Y, Cauty C, Fostier A, Fuchs J, Jalabert B (1994) Reproductive cycle and sex inversion of the seabass, *Lates calcarifer*, reared in sea cages in French Polynesia: histological and morphometric description. Environ Biol Fish 39:231–247

Hara N, Sunobe T (2021) Mating system and protandrous sex change in "Magochi" *Platycephalus* sp. 2 (Platycephalidae). Ichthyol Res 68:541–547

Hattori A (1991) Socially controlled growth and size-dependent sex change in the anemonefish *Amphiprion frenatus* in Okinawa, Japan. Jpn J Ichthyol 38:165–177

Hattori A (2000) Social and mating systems of the protandrous anemonefish *Amphiprion perideraion* under the influence of a larger congener. Austral Ecol 25:187–192

Hattori A (2012) Determinants of body size composition in limited shelter space: why are anemonefishes protandrous? Behav Ecol 23:512–520

Hattori A, Yanagisawa Y (1991) Life-history pathways in relation to gonadal sex differentiation in the anemonefish, *Amphiprion clarkii*, in temperate waters of Japan. Environ Biol Fish 31:139–155

Hesp SA, Potter IC (2003) Reproductive biology of *Rhabdosargus sarba* (Sparidae) in Western Australian waters, in which it is a rudimentary hermaphrodite. J Mar Biol Ass UK 83:1333–1346

Hesp SA, Potter IC, Hall NG (2004) Reproductive biology and protandrous hermaphroditism in *Acanthopagrus latus*. Environ Biol Fish 70:257–272

Ibarra-Zatarain Z, Duncan N (2015) Mating behaviour and gamete release in gilthead seabream (*Sparus aurata*, Linnaeus 1758) held in captivity. Span J Agric Res 13:e04-001

Joubert CSW (1981) Aspects of the biology of five species of inshore reef fishes on the Natal coast, South Africa. Invest Rep Oceanogr Res Ins 51:1–16

Junnan LAN, Youjun OU, Jiufu WEN, Junwei LI, Yingyue NIU, Jia'er LI (2020) A preliminary study on process of sex reversal in *Eleutheronema tetradactylum*. South China Fish Sci 16:67–74

Kawaguchi K, Marumo R (1967) Biology of *Gonostoma gracile* (Gonostomatidae). I. Morphology, life history, and sex reversal. In: Information Bulletin on Planktology in Japan, Commemoration Number of Dr Y Matsue's Sixtieth Birthday, pp 53–69

Kinoshita Y (1936) On the conversion of sex in *Sparus longispinis* (Temminck & Schlegel), (Teleostei). J Sci Hiroshima Univ, Ser B, Div 1 4:69–79

Kinoshita Y (1939) Studies on the sexuality of genus *Sparus* (Teleostei). J Sci Hiroshima Univ, Ser B, Div 1 7:25–38

Krug HM (1990) The Azorean blackspot seabream, *Pagellus bogaraveo* (Brünnich, 1768) (Teleostei, Sparidae). Reproductive cycle, hermaphroditism, maturity and fecundity. Cybium 14:151–159

Krug H (1998) Variation in the reproductive cycle of the blackspot seabream, *Pagellus bogaraveo* (Brünnich, 1768) in the Azores. ARQUIPÉLAGO Life Mar Sci Suppl 16:37–47

Kuwamura T, Nakashima Y, Yogo Y (1994) Sex change in either direction by growth-rate advantage in the monogamous coral goby, *Paragobiodon echinocephalus*. Behav Ecol 5:434–438

Kuwamura T, Suzuki S, Kadota T (2016) Male-to-female sex change in widowed males of the protogynous damselfish, *Dascyllus aruanus*. J Ethol 34:85–88

Kuwamura T, Sunobe T, Sakai Y, Kadota T, Sawada K (2020) Hermaphroditism in fishes: an annotated list of species, phylogeny, and mating system. Ichthyol Res 67:341–360

Lamrini A (1986) Sexualité de *Pagellus acarne* (Risso, 1826) (Teleosteen Sparidae) de la cote Atlantique Meridionale du Maroc (21°–26° N). Cybium 10:3–14

Langston RC (2004) Gonad morphology and sex change in sandburrowers (Teleostei: Creediidae). PhD dissertation, University of Hawaii, Honolulu

Law CSW, Sadovy de Mitheson Y (2017) Reproductive biology of black seabream *Acanthopagrus schlegelii*, threadfin porgy *Evynnis cardinalis* and red pargo *Pagrus major* in the northern South China Sea with consideration of fishery status and management needs. J Fish Biol 91:101–125

Lee YH, Du JL, Yueh WS, Lin BY, Huang JD, Lee CY, Lee MF, Lau EL, Lee FY, Morrey C, Nagahama Y, Chang CF (2001) Sex change in the protandrous black porgy, *Acanthopagrus schlegeli*: a review in gonadal development, estradiol, estrogen receptor, aromatase activity and gonadotropin. J Exp Zool 290:715–726

Leu MY (1994) Natural spawning and larval rearing of silver bream, *Rhabdosargus sarba* (Forsskål), in captivity. Aquaculture 120:115–122

Licandeo RR, Barrientos CA, Gonzalez MT (2006) Age, growth rates, sex change and feeding habits of notothenioid fish *Eleginops maclovinus* from the central-southern Chilean coast. Environ Biol Fish 77:51–61

Lissia-Frau AM, Pala M, Casu S (1976) Observations and considerations on protandrous hermaphroditism in some species of sparid fishes (Teleostei, Perciformes). Studi Sassar 54:147–167

Lodi E (1967) Sex reversal of *Cobitis taenia* L. (Osteichthyes, fam. Cobitidae). Experientia 23:446–447

Lodi E (1980) Hermaphroditic and gonochoric populations of *Cobitis taenia bilineata* Canestrini (Cobitidae Osteichthyes). Monit Zool Ital 14:235–243

Lone KP, Al-Marzouk A (2000) First observations on natural sex reversal in a protandrous bream (*Sparidentex hasta*: Sparidae) from Kuwait. Pakistan J Zool 32:229–243

Longhurst AR (1965) The biology of west African polynemid fishes. J Conseil 30:58–74

Lorenzo JM, Pajuelo JG, Méndez-Villamil M, Coca J, Ramos AG (2002) Age, growth, reproduction and mortality of the striped seabream, *Lithognathus mormyrus* (Pisces, Sparidae), off the Canary Islands (Central-east Atlantic). J Appl Ichthyol 18:204–209

Madhu K, Madhu R (2006) Protandrous hermaphroditism in the clown fish *Amphiprion percula* from Andaman and Nicobar islands. Indian J Fish 53:373–382

Madhu R, Madhu K, Venugopalan KM (2010) Sex change of hatchery produced *Amphiprion ocellaris*: influence of mating system removal on gonad maturation and nesting success. J Mar Biol Ass India 52:62–69

Mann BQ, Buxton CD (1998) The reproductive biology of *Diplodus sargus capensis* and *D. cervinus hottentotus* (Sparidae) off the south-east Cape coast, South Africa. Cybium 22:31–34

Masuda Y, Ozawa T, Onoue O, Hamada T (2000) Age and growth of the flathead, *Platycephalus indicus*, from the coastal waters of west Kyushu, Japan. Fish Res 46:113–121

Micale V, Maricchiolo G, Genovese L (2002) The reproductive biology of blackspot sea bream *Pagellus bogaraveo* in captivity. I. Gonadal development, maturation and hermaphroditism. J Appl Ichthyol 18:172–176

Miya M, Nemoto T (1985) Protandrous sex reversal in *Cyclothone atraria* (family Gonostomatidae). Japan J Ichthyol 31:438–440

Miya M, Nemoto T (1987) Reproduction, growth and vertical distribution of the meso-and bathypelagic fish *Cyclothone atraria* (Pisces: Gonostomatidae) in Sagami Bay, Central Japan. Deep-Sea Res 34:1565–1577

Moiseeva EB, Sachs O, Zak T, Funkenstein B (2001) Protandrous hermaphroditism in Australian silver perch, *Bidyanus bidyanus* (Mitchell, 1836). Israeli J Aquaculture–Bamidgeh 53:57–68

Moore BR, Stapley JM, Williams AJ, Welch DJ (2017) Overexploitation causes profound demographic changes to the protandrous hermaphrodite king threadfin (*Polydactylus macrochir*) in Queensland's Gulf of Carpentaria, Australia. Fish Res 187:199–208

Moser M, Whipple J, Sakanari J, Reilly C (1983) Protandrous hermaphroditism in striped bass from Coos Bay. Oregon T Am Fish Soc 112:567–569

Mouine N, Francour P, Ktari MH, Chakroun-Marzouk N (2007) The reproductive biology of *Diplodus sargus sargus* in the Gulf of Tunis (Central Mediterranean). Sci Mar 71:461–469

Moyer JT (1980) Influence of temperate waters on the behavior of the tropical anemonefish *Amphiprion clarkii* at Miyake-jima, Japan. Bull Mar Sci 30:261–272

Moyer JT, Bell LJ (1976) Reproductive behavior of the anemonefish *Amphiprion clarkii* at Miyake-Jima, Japan. Jpn J Ichthyol 23:23–32

Moyer JT, Nakazono A (1978) Protandrous hermaphroditism in six species of the anemonefish genus *Amphiprion* in Japan. Jpn J Ichthyol 25:101–106

Moyer JT, Sawyers CE (1973) Territorial behavior of the anemonefish *Amphiprion xanthurus* with a note on the life history. Jpn J Ichthyol 20:85–93

Moyer JT, Steene RC (1979) Nesting behavior of the anemonefish *Amphiprion polymus*. Jpn J Ichthyol 26:209–214

Nakabo T (ed) (2013) Fishes of Japan with pictorial keys to the species, 3rd edn. Tokai University Press, Tokyo

Ochi H (1989a) Acquisition of breeding space by nonbreeders in the anemonefish *Amphiprion clarkii* in temperate waters of southern Japan. Ethology 83:279–294

Ochi H (1989b) Mating behavior and sex change of the anemonefish, *Amphiprion clarkii*, in the temperate waters of southern Japan. Environ Biol Fish 26:257–275

Oikawa K (1996) Spawning of flathead, *Platycephalus indicus* under rearing condition. Bull Chiba Pref Fish Exp Sta 54:29–34

Pajuelo JG, Lorenzo JM (2001) Biology of the annular seabream, *Diplodus annularis* (Sparidae), in coastal waters of the Canary Islands. J Appl Ichthyol 17:121–125

Pajuelo JG, Lorenzo JM (2004) Basic characteristics of the population dynamic and state of exploitation of Moroccan white seabream *Diplodus sargus cadenati* (Sparidae) in the Canarian archipelago. J Appl Ichthyol 20:15–21

Pajuelo JG, Socorro J, González JA, Lorenzo JM, Pérez-Peñalvo JA, Martînez I, Hernández-Cruz CM (2006) Life history of the red-banded seabream *Pagrus auriga* (Sparidae) from the coasts of the Canarian archipelago. J Appl Ichthyol 22:430–436

Pajuelo JG, Lorenzo JM, Domínguez-Seoane R (2008) Gonadal development and spawning cycle in the digynic hermaphrodite sharpsnout seabream *Diplodus puntazzo* (Sparidae) off the Canary Islands, northwest of Africa. J Appl Ichthyol 24:68–76

Pla S, Benvenuto C, Capellini I, Piferrer F (2020) A phylogenetic comparative analysis on the evolution of sequential hermaphroditism in seabreams (Teleostei: Sparidae). Sci Rep 10:3606

Pollock BR (1985) The reproductive cycle of yellowfin bream, *Acanthopagrus australis* (Günther), with particular reference to protandrous sex inversion. J Fish Biol 26:301–311

Rasotto MB (1992) Gonadal differentiation and the mode of sexuality in *Cobitis taenia* (Teleostei; Cobitidae). Copeia 1992:223–228

Rattanayuvakorn S, Mungkornkarn P, Thongpan A, Chatchavalvanich K (2006) Gonadal development and sex inversion in saddleback anemonefish *Amphiprion polymnus* Linnaeus (1758). Kasetsart J (Nat Sci) 40:196–203

Richardson TJ, Potts WM, Sauer WHH (2011) The reproductive style of *Diplodus capensis* (Sparidae) in southern Angola: rudimentary hermaphroditism or partial protandry? Afr J Mar Sci 33:321–326

Roberts BH, Morrongiello JR, Morgan DL, King AJ, Saunders TM, Crook DA (2021) Faster juvenile growth promotes earlier sex change in a protandrous hermaphrodite (barramundi *Lates calcarifer*). Sci Rep 11:2276

Ross RM (1978) Reproductive behavior of the anemonefish *Amphiprion melanopus* on Guam. Copeia 1978:103–107

Shen SC, Lin RP, Liu FCC (1979) Redescription of a protandrous hermaphroditic moray eel (*Rhinomuaena quaesita* Garman). Bull Inst Zool Academia Sinica 18:79–87

Shihab I, Gopalakrishnan A, Vineesh N, Muktha M, Akhilesh KV, Vijayagopal P (2017) Histological profiling of gonads depicting protandrous hermaphroditism in *Eleutheronema tetradactylum*. J Fish Biol 90:2402–2411

Shinomiya A, Yamada M, Sunobe T (2003) Mating system and protandrous sex change in the lizard flathead, *Inegocia japonica* (Platycephalidae). Ichthyol Res 50:383–386

Shitamitsu T, Sunobe T (2017) Notes on protandry in the creediid fishes *Limnichthys fasciatus* and *L. nitidus* (Teleostei: Creediidae). Ichthyol Res 64:365–367

Shitamitsu T, Sunobe T (2018) Protandry of the flathead *Suggrundus meerdervoortii* (Teleostei: Platycephalidae). Ichthyol Res 65:507–509

Sunobe T, Iwata S, Shi C, Kuwamura T (2022) Monogamy and protandry caused by exclusion of the same sex and random pairing in anemonefishes: a simulation model and aquarium experiments. J Ethol 40:265–272

Sunobe T, Sakaida S, Kuwamura T (2016) Random mating and protandrous sex change of the platycephalid fish *Thysanophrys celebica* (Platycephalidae). J Ethol 34:15–21

Taru M, Kanda T, Sunobe T (2002) Alternative mating tactics of the gobiid fish *Bathygobius fuscus*. J Ethol 20:9–12

Taylor RG, Grier HJ, Whittington JA (1998) Spawning rhythms of common snook in Florida. J Fish Biol 53:502–520

Taylor RG, Whittington JA, Grier HJ, Crabtree RE (2000) Age, growth, maturation, and protandric sex reversal in common snook, *Centropomus undecimalis*, from the east and west coasts of South Florida. Fish Bull 98:612–624

Tobin AJ, Sheaves MJ, Molony BW (1997) Evidence of protandrous hermaphroditism in the tropical sparid *Acanthopagrus berda*. J Fish Biol 50:22–33

van der Walt BA, Mann BQ (1998) Aspects of the reproductive biology of *Sarpa salpa* (Pisces: Sparidae) off the east coast of South Africa. South African J Zool 33:241–248

Warner RR (1975) The adaptive significance of sequential hermaphroditism in animals. Am Nat 109:61–82

Warner RR (1984) Mating behavior and hermaphroditism in coral reef fishes. Am Sci 72:128–136

Warner RR, Lejeune P (1985) Sex change limited by paternal care: a test using four Mediterranean labrid fishes, genus *Symphodus*. Mar Biol 87:89–99

Yeung WSB, Chan STH (1987) The gonadal anatomy and sexual pattern of the protandrous sex-reversing fish, *Rhabdosargus sarba* (Teleostei: Sparidae). J Zool Lond 212:521–532

Young JM, Yeiser BG, Whittington JA, Dutka-Gianelli J (2020) Maturation of female common snook *Centropomus undecimalis*: implications for managing protandrous fishes. J Fish Biol 97:1317–1331

Zohar Y, Abraham M, Gordin H (1978) The gonadal cycle of the captivity-reared hermaphroditic teleost *Sparus aurata* (L.) during the first two years of life. Ann Biol Anim Bioch Biophys 18: 877–888

Chapter 4
Protogyny in Fishes

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Abstract Of approximately 480 hermaphroditic fish species, over 300 have been confirmed to undergo protogynous (female-to-male) sex changes. The occurrence of protogyny is strongly related to polygynous mating systems and follows the prediction of the size-advantage model based on the concept of life history strategies that maximize lifetime reproductive success. Sex change in females often occurs in a situation where females become dominant after the disappearance of dominant males in the local group. However, females are also observed to change their sex even in the presence of a dominant male (i.e., bachelor sex change and harem-fission sex change). Female tactics associated with sex change, for example, intergroup movement to improve the social condition and fast growth at the expense of spawning, are also known. This chapter introduces the results of widely studied protogynous sex changes in fish hermaphroditism and focuses on functional contexts and individual-level social mechanisms.

Keywords Bachelor sex change · Diandry and monandry · Harem-fission sex change · Mating systems · Sex change process · Social control

4.1 History of the Study of Protogynous Sex Change in Fish Biology

As mentioned in the previous chapter (see Chap. 1), sequential hermaphroditism (sex change) is a widely documented phenomenon in fishes, including in 41 families of teleost orders (Kuwamura et al. 2020). Of the approximately 480 hermaphroditic fish species, at least 314 species from 20 families of teleost orders have been confirmed to undergo protogynous sex changes (Table 4.1). This is the highest among the four

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T. Kuwamura et al. (eds.), *Hermaphroditism and Mating Systems in Fish*,
https://doi.org/10.1007/978-981-19-6095-6_4

Table 4.1 Number of protogynous species and methodology of confirmation in each fish family

Order-family	Number of species	Methodology		
		Histology	Aquarium experiment	Field surveys and/or experiments in nature
Gobiiformes				
Gobiidae	24	18	12	8
Uncertain orders in Ovalentaria				
Pomacentridae	6	6	1	2
Pseudochromidae	2	2	0	1
Cichliformes				
Cichlidae	1	0	1	0
Cyprinodontiformes				
Poeciliidae	1	1	1	0
Synbranchiformes				
Synbranchidae	4	4	1	0
Trachiniformes				
Pinguipedidae	7	7	2	2
Trichonotidae	1	1	0	0
Labriformes				
Labridae	99	94	9	9
Odacidae	1	1	0	0
Scaridae	36	36	0	1
Perciformes				
Serranidae	66	65	7	2
Pomacanthidae	22	9	11	6
Malacanthidae	1	1	0	1
Cirrhitidae	6	6	1	1
Scorpaeniformes				
Scorpaenidae	1	1	0	0
Spariformes				
Nemipteridae	2	2	0	0
Lethrinidae	11	11	0	0
Sparidae	22	19	0	0
Tetraodontiformes				
Balistidae	1	1	0	1
Total	314	285	46	34

Order and family names are arranged following Nelson et al. (2016)

The numbers of species in each family and methodology are summed up from data in Chap. 6. The number of species for which there is a report of female pre-maturity even in one population, even if there are different opinions, were counted

Species in which only bidirectional sex change has been reported and those with weak evidence of protogyny are excluded types of hermaphroditism (i.e., simultaneous, protandry, protogyny, and bidirectional; Kuwamura et al. 2020).

Atz (1964) initially summarized the documentation of hermaphroditism, mainly from anatomical and histological approaches in various taxa, representing the first step toward an integrated view of hermaphroditism in fish biology. Protogyny (female-to-male sex change) was recorded in at least 26 species including serranids, sparids, and labrids (Atz 1964). Similar to many other biological fields related to natural history, studies on sex change in fish have gradually increased since the 1960s. In a review by Reinboth (1970), 41 fish species were reported to be protogynous, including 16 from Serranidae, 3 from Sparidae, 12 from Labridae, and 3 from Scaridae. These four families are still recognized as the main groups displaying protogyny and constitute approximately 71% of all the 314 protogynous fish species (223 species; Table 4.1). In addition, these families include valuable fisheries resources, permitting scientists to obtain specimens via fishery activities for histological analysis. The gonad histology and size distribution pattern analyses remain the basic approaches to identifying the occurrence of sex change. Of the 314 species, 285 (91%) were confirmed to be protogynous by sampling analysis and gonad histology (Table 4.1).

After diving, including SCUBA, became popular in the 1960s, field researchers conducting underwater observations or experimental surveys have studied reef fishes that are not major targets of fisheries. In a review of hermaphroditism in fishes by Yogo (1987), protogyny was recorded in approximately 180 species, including 41 serranids, 84 labrids, and 33 scarids. The number of confirmed species has increased since the review by Reinboth (1970), based on the studies of reef fishes in diving surveys.

Underwater surveys are useful for understanding the processes and patterns of protogynous sex change at the individual level. In addition to providing a detailed understanding of the reproductive styles in fisheries resources, the methodology was synchronized with biology to reveal the adaptive significance of behavioral and ecological traits. A detailed understanding of the animal group, social structure, and mating patterns is a key concept in behavioral ecology studies. Long-term individual discrimination methodologies are adopted to reveal life history strategies or tactics, including sex change patterns. The best-known examples of protogynous fish, including the bluestreak cleaner wrasse *Labroides dimidiatus* in the Indo-Pacific reefs and the bluehead wrasse *Thalassoma bifasciatum* in the Caribbean reefs, are model animals for various topics in behavioral ecology. In addition, various wrasses, parrotfishes, gobies, *Dascyllus* damselfishes, *Parapercis* sandperches, and serranids, including *Pseudanthias squamipinnis* (formerly *Anthias squamipinnis*), *Centropyge* angelfishes, and cirrhitid hawkfishes, provided outstanding field data that significantly contributed to the nature of sex change as a mating strategy. Many researchers have ever conducted field studies on shallow reefs and confirmed functional protogynous sex changes in 34 fish species via observational surveys (Table 4.1). Thus, the phenomenon of sex change has been a central topic of reproduction and sexuality in reef fish since the 1970s.

The establishment of an underwater diving system has enabled observational researchers to collect live specimens from reefs in good condition for rearing in aquarium experiments (e.g., Suzuki et al. 1979; Hioki et al. 1982; Ross et al. 1983; Sunobe and Nakazono 1993). Aquarium experiments are useful for understanding the individual abilities of sex changes, revealing hermaphroditic sexualities, by controlling rearing conditions in terms of social combinations in simple cohabitated environments. This approach overcomes the difficulty in observing deep water or cryptic habitat (e.g., inside small holes or crevasses) fishes. However, the maintenance of reproductively active conditions in individual experimental fish is important for confirming sexual patterns. Demersal egg spawners, such as gobiid fishes, are one of the groups successfully used in rearing experiments; protogynous sexuality has been confirmed in 12 gobiid species in aquarium studies. Rearing experimental methods have often been applied to pelagic egg spawners such as labrids (9 species), serranids (7 species), and pomacanthid angelfishes (11 species). Overall, 46 fish species have been confirmed to be protogynous in aquarium experiments (Table 4.1).

4.2 Mating Systems of Protogynous Fishes

Protogyny occurs in various fish groups. Data on the mating systems of up to 131 protogynous fish species were obtained through observational field surveys (Table 4.2). The extensive data on mating systems indicated that protogynous sexuality was strongly related to polygynous mating systems (Robertson and Warner 1978; Warner and Robertson 1978; Kuwamura 1984; Warner 1984, 1988, 1991; Kuwamura et al. 2020). A recent phylogenetic approach revealed that the mating system was an important driver of evolutionary transition in sex allocation in labrid fishes (Hodge et al. 2020).

Mating systems in fishes can be classified using a combination of spatial relationships of individuals and their mating relationships within local populations (Kuwamura 1984, 1997). Males of various reef fishes often establish territories to protect females and/or their resources. Harem polygyny occurs when male territories almost completely encompass several female home ranges (or territories) to maintain a stable mating relationship with cohabiting females (Robertson 1972; Kuwamura 1984, 1997). The other major pattern of the polygynous mating system is called the male territory-visiting polygamy (MTV polygamy; Kuwamura 1997). Males establish mating territories as spawning sites and females visit the site during the mating period and have opportunities for mate choice. Males exhibiting preferable characteristics have opportunities for polygynous mating. MTV polygamy is called as lek-like polygamy in some labrids (Moyer and Yogo 1982; Moyer 1991). These two polygynous mating systems are widely known in reef fishes. Both harem polygyny and MTV polygamy were confirmed in 60 protogynous fish species, respectively (Table 4.2). The detailed characteristics and examples of each type are presented below.

Table 4.2 Mating systems of protogynous fishes with occurrence patterns of male types confirmed by field surveys

Order-family	Species	Occurrence pattern of male types	Mating system					References
			Size assortative monogamy	Harem	MTV polygamy	Group spawning	Spawning aggregation	
Gobiiformes								
Gobiidae	*Coryphopterus glaucofraenum*				X			Cole and Shapiro (1992) and Forrester et al. (2011)
Gobiidae	*Fusigobius neophytus*	Diandry			X			Tsuboi and Sakai (2016)
Gobiidae	*Gobiodon histrio*	Monandry	X					Munday et al. (1998)
Gobiidae	*Gobiodon okinawae*	Monandry	X					Cole and Hoese (2001)
Gobiidae	*Gobiodon quinquestrigatus*	Monandry	X					Nakashima et al. (1996) and Thompson et al. (2007)
Gobiidae	*Lythrypnus dalli*				X			St. Mary (1994)
Gobiidae	*Paragobiodon echinocephalus*	Monandry	X					Lassig (1976, 1977) and Kuwamura et al. (1994)
Gobiidae	*Paragobiodon xanthosomus*	Monandry	X					Wong et al. (2008)
Gobiidae	*Trimma okinawae*	Monandry		ND				Sunobe and Nakazono (1990)
Uncertain orders in Ovalentaria								
Pomacentridae	*Dascyllus aruanus*	Diandry		AF				Fricke and Holzberg (1974), Coates (1982), Shpigel and Fishelson (1986) and Cole (2002)
Pomacentridae	*Dascyllus carneus*	Diandry		AF				Asoh and Yoshikawa (2003)
Pomacentridae	*Dascyllus flavicaudus*			AF				Asoh (2004) and Godwin (1995)

(continued)

Table 4.2 (continued)

Order-family	Species	Occurrence pattern of male types	Mating system					References
			Size assortative monogamy	Harem	MTV polygamy	Group spawning	Spawning aggregation	
Pomacentridae	*Dascyllus marginatus*	Monandry		AF				Shpigel and Fishelson (1986) and Fricke (1980)
Pomacentridae	*Dascyllus melanurus*	Monandry		AF				Asoh (2005a)
Pomacentridae	*Dascyllus reticulatus*	Monandry		AF				Asoh (2005b) and Sakanoue and Sakai (2019)
Synbranchiformes								
Synbranchidae	*Monopterus albus*				X			Matsumoto et al. (2011)
Pinguipedidae	*Parapercis cylindrica*	Monandry		TF				Stroud (1982) and Walker and McCormick (2009)
Pinguipedidae	*Parapercis hexophtalma*	Monandry		TF				Stroud (1982) and Clark et al. (1991)
Pinguipedidae	*Parapercis snyderi*	Monandry		TF				Nakazono et al. (1985), Ohta (1987) and Ohnishi et al. (1997)
Labriformes								
Labridae	*Bodianus diplotaenia*	Monandry			X			Hoffman (1985)
Labridae	*Bodianus eclancheri*	Monandry				X		Hoffman (1985)
Labridae	*Bodianus mesothorax*	Monandry					X	Claydon (2005)
Labridae	*Bodianus rufus*	Monandry		CF				Hoffman (1985)
Labridae	*Cheilinus fasciatus*	Monandry		ND			X	Hubble (2003), Donaldson (1995) and Claydon (2004)

Labridae	*Cheilinus trilobatus*	Monandry		ND	X			Yogo (1987), Colin and Bell (1991) and Claydon (2004)
Labridae	*Cheilinus undulatus*	Monandry		ND	X		X	Colin and Bell (1991), Colin (2010), Claydon (2004) and Sadovy de Mitcheson et al. (2010)
Labridae	*Cirrhilabrus temmincki*	Monandry			X			Bell (1983) and Kohda et al. (2005)
Labridae	*Clepticus parrae*	Monandry					X	Warner and Robertson (1978) and Robertson and Hoffman (1977)
Labridae	*Coris dorsomacula*	Monandry		ND				Tribble (1982)
Labridae	*Coris gaimard*	Monandry			X			Sancho et al. (2000)
Labridae	*Coris julis*	Diandry			X			Lejeune (1987)
Labridae	*Epibulus insidiator*	Monandry		ND	X			Colin and Bell (1991) and Kuwamura et al. (2016b)
Labridae	*Gomphosus varius*	Monandry			X			Colin and Bell (1991) and Kuwamura et al. (2016b)
Labridae	*Halichoeres bivittatus*	Diandry			X	X		Warner and Robertson (1978) and Clavijo and Donaldson (1994)
Labridae	*Halichoeres garnoti*	Monandry			X			Robertson (1981)
Labridae	*Halichoeres maculipinna*	Diandry			X			Robertson (1981)
Labridae	*Halichoeres margaritaceus*	Monandry		ND				Walker and Ryen (2007)
Labridae	*Halichoeres marginatus*	Monandry			X	X		Shibuno et al. (1993)
Labridae	*Halichoeres melanochir*	Monandry			X			Moyer and Yogo (1982) and Yogo (1985)
Labridae	*Halichoeres melanurus*	Diandry		ND	X			Colin and Bell (1991), Kuwamura et al. (2000) and Karino et al. (2000)

(continued)

Table 4.2 (continued)

Order-family	Species	Occurrence pattern of male types	Mating system: Size assortative monogamy	Harem	MTV polygamy	Group spawning	Spawning aggregation	References
Labridae	*Halichoeres miniatus*	Monandry		TF				Munday et al. (2009)
Labridae	*Halichoeres semicinctus*	Monandry			X	X		Adreani and Allen (2008)
Labridae	*Halichoeres tenuispinnis*	Diandry			X			Nakazono (1979)
Labridae	*Halichoeres trimaculatus*	Diandry			X	X		Suzuki et al. (2008) and Suzuki et al. (2010)
Labridae	*Iniistius pentadactylus*	Monandry		TF				Nemtzov (1985)
Labridae	*Labrichthys unilineatus*	Monandry		ND				Colin and Bell (1991)
Labridae	*Labroides dimidiatus*	Monandry		CF				Robertson (1972) and Kuwamura (1984)
Labridae	*Lachnolaimus maximus*	Monandry		ND				McBride and Johnson (2007) and Colin (1982)
Labridae	*Macropharyngodon moyeri*	Monandry		ND				Moyer (1991)
Labridae	*Notolabrus celidotus*	Monandry			X			Jones (1980, 1981)
Labridae	*Parajulis poecilopterus*	Diandry			X	X		Nakazono (1979), Fukui et al. (1991) and Kimura and Kiriyama (1992)
Labridae	*Pseudocheilinus hexataenia*	Monandry		ND				Colin and Bell (1991)

Labridae	*Pseudolabrus sieboldi*	Diandry			X			Nakazono (1979)
Labridae	*Pteragogus aurigarius*	Monandry			X	X		Nakazono (1979), Moyer (1991) and Shimizu et al. (2022)
Labridae	*Semicossyphus pulcher*	Monandry			X			Adreani et al. (2004)
Labridae	*Stethojulis interrupta*	Diandry			X			Nakazono (1979)
Labridae	*Stethojulis trilineata*	Diandry			X			Kuwamura et al. (2016b) and Yogo (1987)
Labridae	*Suezichthys ornatus*	Monandry			X			Andrew et al. (1996)
Labridae	*Symphodus melanocercus*	Diandry			X			Warner and Lejeune (1985)
Labridae	*Symphodus tinca*	Diandry			X			Warner and Lejeune (1985)
Labridae	*Thalassoma bifasciatum*	Diandry			X	X		Warner and Robertson (1978) and Reinboth (1973)
Labridae	*Thalassoma cupido*	Diandry			X	X		Meyer (1977)
Labridae	*Thalassoma duperrey*	Diandry			X	X		Ross (1982)
Labridae	*Thalassoma hardwicke*	Diandry			X	X		Robertson and Choat (1974), Craig (1998) and Kuwamura et al. (2016b)
Labridae	*Thalassoma jansenii*	Diandry			X	X		Kuwamura et al. (2016b)
Labridae	*Thalassoma lucasanum*	Diandry			X	X		Warner (1982)
Labridae	*Thalassoma lunare*	Diandry			X	X		Robertson and Choat (1974)
Labridae	*Thalassoma lutescens*	Diandry			X	X		Shibuno et al. (1994a) and Kuwamura et al. (2016b)
Labridae	*Thalassoma pavo*	Diandry			X	X		Wernerus and Tessari (1991)

(continued)

Table 4.2 (continued)

Order-family	Species	Occurrence pattern of male types	Mating system					References
			Size assortative monogamy	Harem	MTV polygamy	Group spawning	Spawning aggregation	
Labridae	*Thalassoma quinquevittatum*				X	X		Craig (1998) and Kuwamura et al. (2016b)
Labridae	*Xyrichtys martinicensis*	Monandry		TF				Victor (1987)
Labridae	*Xyrichtys novacula*	Monandry		TF				Bentivegna and Rasotto (1987) and Marconato et al. (1995)
Scaridae	*Calotomus carolinus*	Monandry			X			Robertson et al. (1982)
Scaridae	*Calotomus japonicus*	Monandry			X			Shibuno et al. (1994b)
Scaridae	*Cetoscarus bicolor*	Diandry		ND				Colin and Bell (1991)
Scaridae	*Chlorurus sordidus*	Diandry			X	X		Yogo et al. (1980)
Scaridae	*Cryptotomus roseus*	Monandry			X			Robertson and Warner (1978)
Scaridae	*Scarus forsteni*	Diandry			X			Colin and Bell (1991) and Kuwamura et al. (2009)
Scaridae	*Scarus frenatus*	Monandry/ diandry		ND				Choat and Robertson (1975) and Gust (2004)
Scaridae	*Scarus globiceps*	Diandry			X	X		Choat and Robertson (1975) and Kuwamura et al. (2009)
Scaridae	*Scarus iseri*	Diandry		ND	X	X	X	Robertson and Warner (1978) and Colin (1978)
Scaridae	*Scarus niger*	Monandry			X	X		Kuwamura et al. (2009)
Scaridae	*Scarus oviceps*	Diandry			X			Claydon (2005)
Scaridae	*Scarus psittacus*	Diandry			X			Colin and Bell (1991), Claydon (2005) and Kuwamura et al. (2009)

Scaridae	*Scarus rivulatus*	Diandry			X	X		Choat and Robertson (1975) and Kuwamura et al. (2009)
Scaridae	*Scarus schlegeli*	Diandry			X			Colin and Bell (1991)
Scaridae	*Scarus sordidus*	Diandry			X	X		Yogo (1985)
Scaridae	*Scarus vetula*	Diandry		ND	X	X		Clavijo (1983)
Scaridae	*Sparisoma atomarium*	Monandry		ND (AF?)				Robertson and Warner (1978)
Scaridae	*Sparisoma aurofrenatum*	Monandry		ND (CF?)				Robertson and Warner (1978)
Scaridae	*Sparisoma chrysopterum*	Monandry			X			Robertson and Warner (1978)
Scaridae	*Sparisoma radians*	Monandry		ND (AF?)	X	X		Robertson and Warner (1978) and Muñoz and Warner (2003a, 2004)
Scaridae	*Sparisoma rubripinne*	Monandry			X	X		Robertson and Warner (1978)
Scaridae	*Sparisoma viride*	Monandry			X			Robertson and Warner (1978)
Perciformes								
Serranidae	*Cephalopholis argus*	Monandry		ND				Shpigel and Fishelson (1991) and Schemmel et al. (2016)
Serranidae	*Cephalopholis fulva*	Monandry		ND			X	Sadovy et al. (1994)
Serranidae	*Cephalopholis hemistiktos*	Monandry	X					Shpigel and Fishelson (1991)
Serranidae	*Cephalopholis miniata*	Monandry		TF				Shpigel and Fishelson (1991)
Serranidae	*Cephalopholis panamensis*	Monandry		ND				Erisman et al. (2010)
Serranidae	*Epinephelus adscensionis*	Monandry		ND (CF?)			X	Kline et al. (2011)

(continued)

Table 4.2 (continued)

Order-family	Species	Occurrence pattern of male types	Mating system					References
			Size assortative monogamy	Harem	MTV polygamy	Group spawning	Spawning aggregation	
Serranidae	*Epinephelus fuscoguttatus*	Monandry					X	Pears et al. (2007)
Serranidae	*Epinephelus guttatus*	Monandry					X	Shapiro et al. (1994), Sadovy et al. (1994) and Nemeth et al. (2007)
Serranidae	*Epinephelus marginatus*	Monandry			X			Zabala et al. (1997a, b)
Serranidae	*Epinephelus ongus*	Monandry					X	Nanami et al. (2013) and Ohta and Ebisawa (2015)
Serranidae	*Mycteroperca microlepis*	Monandry					X	Gilmore and Jones (1992) and Brulé et al. (2015)
Serranidae	*Mycteroperca olfax*	Monandry					X	Salinas-de-León et al. (2015) and Usseglio et al. (2015)
Serranidae	*Mycteroperca phenax*	Monandry					X	Gilmore and Jones (1992) and Harris et al. (2002)
Serranidae	*Mycteroperca rubra*	Monandry					X	Aronov and Goren (2008)
Serranidae	*Mycteroperca venenosa*	Monandry				X	X	Schärer et al. (2012) and García-Cagide and García (1996)
Serranidae	*Plectropomus leopardus*	Diandry					X	Samoilys and Squire (1994) and Adams (2003)
Serranidae	*Pseudoanthias squamipinnis*	Monandry		AF				Shapiro (1981) and Yogo (1985)
Pomacanthidae	*Centropyge bicolor*	Monandry		CF				Aldenhoven (1984)
Pomacanthidae	*Centropyge ferrugata*	Monandry		CF				Sakai and Kohda (1997)

Pomacanthidae	*Centropyge interruptus*	Monandry		CF				Moyer and Nakazono (1978)
Pomacanthidae	*Centropyge multispinis*	Monandry		ND				Moyer (1990)
Pomacanthidae	*Centropyge potteri*	Monandry		CF				Lutnesky (1994, 1996) and Lobel (1978)
Pomacanthidae	*Centropyge tibicen*	Monandry		CF				Moyer and Zaiser (1984) and Moyer (1987)
Pomacanthidae	*Centropyge vrolikii*	Monandry		CF				Sakai et al. (2003b)
Pomacanthidae	*Genicanthus caudovittatus*	Monandry		AF				Moyer (1990)
Pomacanthidae	*Genicanthus lamarck*	Monandry		AF				Moyer (1984)
Pomacanthidae	*Genicanthus melanospilos*	Monandry		AF				Moyer (1987, 1990)
Pomacanthidae	*Genicanthus semifasciatus*	Monandry		AF				Moyer (1987, 1990)
Pomacanthidae	*Holacanthus passer*	Monandry		ND				Moyer et al. (1983) and Arellano-Martínez (1997)
Pomacanthidae	*Holacanthus tricolor*	Monandry		CF				Hourigan and Kelley (1985), Hourigan (1986) and Moyer et al. (1983)
Malacanthidae	*Malacanthus plumieri*	Monandry		TF				Baird (1988)
Cirrhitidae	*Cirrhitichthys aprinus*	Monandry		TF				Kobayashi and Suzuki (1992), Sadovy and Donaldson (1995) and Donaldson (1990)
Cirrhitidae	*Cirrhitichthys falco*	Monandry		TF				Donaldson (1987) and Kadota et al. (2011)

(continued)

Table 4.2 (continued)

Order-family	Species	Occurrence pattern of male types	Mating system					References
			Size assortative monogamy	Harem	MTV polygamy	Group spawning	Spawning aggregation	
Cirrhitidae	*Cirrhitichthys oxycephalus*	Monandry		TF				Donaldson (1990)
Cirrhitidae	*Neocirrhites armatus*	Monandry		TF				Sadovy and Donaldson (1995) and Donaldson (1989, 1990)
Scorpaeniformes								
Scopaenidae	*Caracanthus unipinna*	Monandry		ND				Wong et al. (2005)
Tetraodontiformes								
Balistidae	*Sufflamen chrysopterus*			TF				Takamoto et al. (2003) and Seki et al. (2009)

X indicates that there are reported cases

For haremic groups, three types are shown; *CF* cohabiting female-type, *TF* territorial female-type, *AF* aggregating female-type, *ND* harem types unidentified, *?* weak evidence

4.2.1 Harem Polygyny

The cohabitation of multiple females within male territories and the establishment of stable mating relationships are the characteristics of harem polygyny. Large males maintain stable territories encompassing female home ranges or female territories and monopolize mating opportunities with cohabiting females. Pair spawning between territorial males and cohabiting females is the main form of mating in haremic fishes. Commonly, the largest individuals in each harem group function as males and the other smaller individuals function as females.

In *Parapercis* sandperches, pomacanthid angelfishes, and cirrhitid hawkfishes, all protogynous species ever examined their mating systems showed harem polygyny. Many harem species are also known in the Labridae (17 of 53 protogynous species whose mating system is known), Scaridae (7 of 22), and Serranidae (6 of 17) (Table 4.2). Harem polygyny is also confirmed in Gobiidae, Malacanthidae, Scorpaenidae, and Balistidae (Table 4.2) with one protogynous species record in each family.

In terms of spatial relationships among females, three types of group structures are distinguished in harem polygyny (Kuwamura 1984; Sakai and Kohda 1997).

4.2.1.1 Cohabiting Female-Type Harem

In the cohabiting female-type harem, the home ranges of females overlapped with each other (Fig. 4.1). This harem is recorded from *Bodianus rufus* and *L. dimidiatus*, *Centropyge* angelfishes, and *Holacanthus tricolor* (a total of nine species; Table 4.2). Frequent social interactions among harem members have been reported in this type of harem. Males repeatedly conduct patrols within their territories and have social contacts with females. The females meet with each other during the daytime and interact socially. The dominance order among harem members is based on body size (Kuwamura 1984; Sakai and Kohda 1997). Females of different body sizes cohabit, usually exhibiting a dominant linear relationship among harem members (linear-type harem; Fig. 4.1). Social interaction among cohabiting harem members is an important characteristic related to the mechanism of sex change in these fishes (see Sect. 4.5, Social control of sex change).

However, even in this type of harem, females of similar body sizes become mutually exclusive regarding their territories. Individuals with different body sizes overlap in their home ranges, whereas those with similar body sizes become territorial. Consequently, male territories are sometimes divided into two female subgroups (Robertson 1974; Kuwamura 1984; Hoffman 1985; Hourigan 1986; Sakai and Kohda 1997; Munday et al. 2009). The harem structure with female territoriality is found in harems of the cleaner wrasse *L. dimidiatus* (Kuwamura 1984) and *Centropyge* and *Holacanthus* angelfishes (Hourigan and Kelley 1985; Sakai and Kohda 1997) and is described as a branching-type harem (Fig. 4.1), related to the variation in the timing of sex change (see Sect. 4.6, Harem-fission sex change).

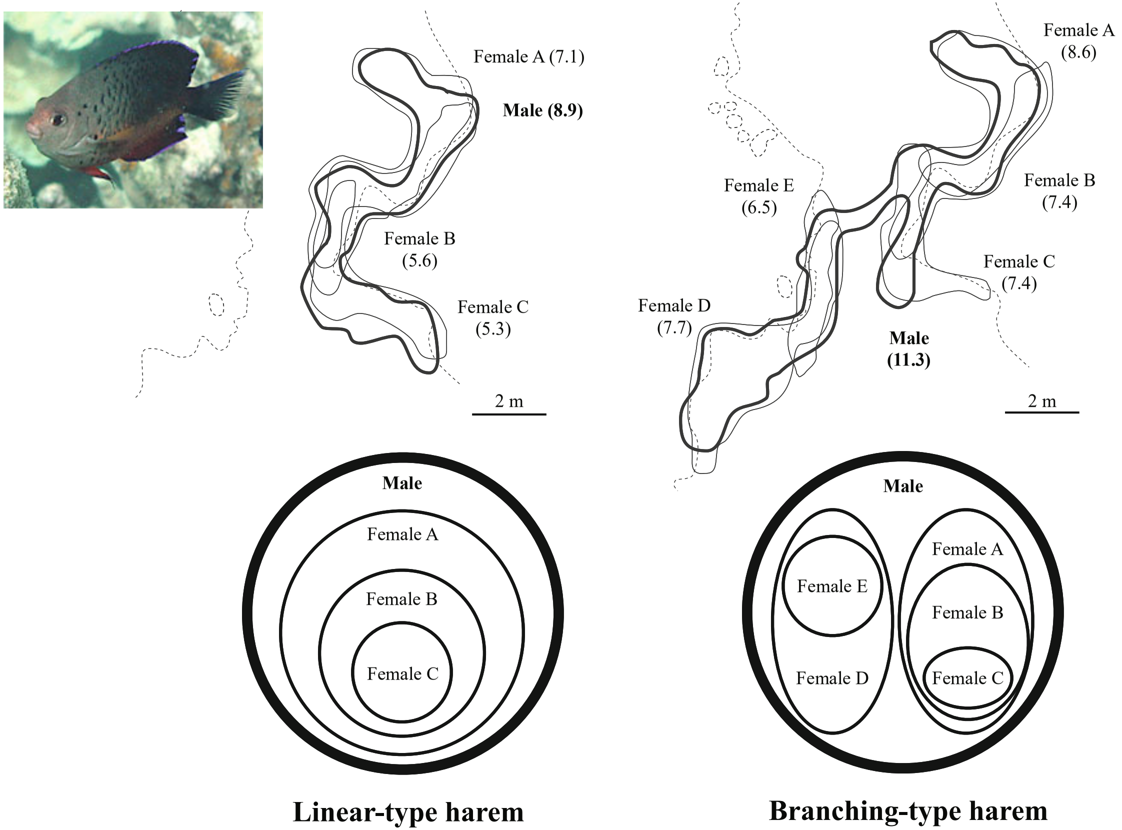

Fig. 4.1 Typical example of the spatial relationship of the cohabiting female-type harem. Male territories (*thick lines*) and female home ranges (*thin lines*) of two adjacent harems of the angelfish *Centropyge ferrugata* on reefs of Sesoko Island, Okinawa, are shown (redrawn from Sakai and Kohda 1997). Male territories encompass female home ranges, and female home ranges overlap. Total lengths (cm) are given in parentheses. Schematic models of two variation patterns of the cohabiting female-type harem are also shown; home ranges of females overlap within a male territory (the linear-type harem, *left*), while two dominant females that are exclusive of each other form subgroups within a male territory (the branching-type harem, *right*) (*photo* Yoichi Sakai)

4.2.1.2 Territorial Female-Type Harem

In this type, females maintained individual territories and divided the dominant male territory (Fig. 4.2), as confirmed in *Parapercis* sandperches, *Halichoeres*, *Iniistius* and *Xyrichtys* wrasses, the serranid *Cephalopholis miniata*, *Malacanthus* sand tilefish, cirrhitid hawkfish, and the triggerfish *Sufflamen chrysopterus* (a total of 14 species; Table 4.2). Exclusive territorialities among harem females are caused by the protection of shelter resources in open habitats (Clark 1983; Baird 1988), mating resources (Ishihara and Kuwamura 1996; Seki et al. 2009), and food resources (Shpigel and Fishelson 1991; Kadota et al. 2011). In contrast to the cohabiting female-type harem, social interactions among females occur infrequently, but dominant males often interact with females during territory patrols and courtship.

4.2.1.3 Aggregating Female-Type Harem

This is often seen in fish gregariously hovering in the water column to feed on zooplankton (Shapiro 1981; Moyer 1984; Yogo 1985; Sakanoue and Sakai 2019). No territorial relationship was found among the gregarious females, and a size-related spatial relationship was not found in the harem. This harem type was recorded in the coral-dwelling *Dascyllus* damselfishes, a serranid *P. squamipinnis*, and *Genicanthus* angelfishes (11 species; Table 4.2). The lack of apparent exclusive relationships among females in this harem is similar to that in cohabiting female-type harems. Females stably spawn with territorial males in each aggregating female-type harem, similar to the other two types of harems.

All the 11 protogynous species maintaining aggregating female-type harems showed a multi-male harem structure, where two or more territorial males dominated a female harem. The single male harem of the planktivorous serranid *P. squamipinnis* swimming in the water column includes up to nine females (Shapiro

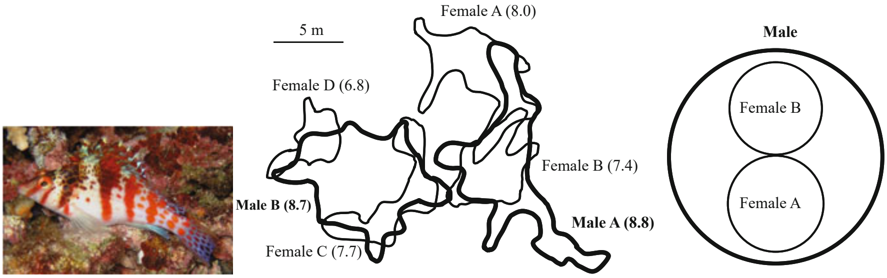

Fig. 4.2 Typical example of the spatial relationship of the territorial female-type harem. Male territories (*thick lines*) and female territories (*thin lines*) of two harems of the hawkfish *Cirrhitichthys falco* on the reefs of Kuchierabu-jima Island, southern Japan (*left*; redrawn from Kadota et al. 2011). Each male territory encompasses two female territories. Total lengths (cm) are given in parentheses. A schematic model of two female territories within a male territory is also shown (*right*; redrawn from Kuwamura 1984) (*photo* Tatsuru Kadota)

Fig. 4.3 Typical example of the spatial relationship of the aggregating female-type harem. Harem groups of the coral-dwelling damselfish *Dascyllus reticulatus* are formed on shelter corals. Single male harems often occur on corals with wide gaps between long branches (**a**), while multi-male groups often occur on corals with narrow gaps between fine short branches (**b**). A schematic model of a multi-male group is also shown (*right*); females often swim together and their home ranges (*thin lines*) overlap within male territories (*thick lines*) (*photo* Rei Sakanoue)

1977; Yogo 1985). In contrast, in the case of a harem with more individuals, multiple males cohabit, for example, a multi-male harem of *P. squamipinnis* included 15 males and 72 females (Yogo 1985). The females' home ranges overlap with multiple male home ranges providing opportunities to change spawning partners within a harem, suggesting the possibility of promiscuous mating. Thus, increased harem size often leads to multiple male groups.

High-density multi-male groups of the coral-dwelling *Dascyllus* damselfish often occur in high coral cover habitats (Fricke 1980; Shpigel and Fishelson 1986). However, multi-male harem groups sometimes occur, even in habitats with low coral cover (Asoh 2004). In *Dascyllus reticulatus*, the group structure strongly depends on the shelter spaces in the coral branches; single males tend to monopolize harems of large females in corals with long branches (Fig. 4.3a) ,providing wide shelter spaces suitable for large individuals, whereas relatively small adults inhabit corals with short branches providing narrow spaces in high density (short-branch groups; Fig. 4.3b). Multi-male group composition often occurs in short-branch groups even in the low coral cover habitats (Sakanoue and Sakai 2019).

The presence of multiple males within a harem group indicates the occurrence of sex change by a female in the presence of a dominant male. The process and social context of sex change in this harem type will be described later (Sect. 4.6).

4.2.2 Male Territory-Visiting Polygamy

In Labridae and Scaridae, MTV polygamy is the most frequent form of mating system (37 of 53 protogynous wrasses and 18 of 22 protogynous parrotfishes; Table 4.2). Phylogenetic analyses have found that the ancestral mating systems of labrid fish most likely belong to MTV polygamy (Hodge et al. 2020). These two families occupy 92% of the 60 MTV polygamy records. These labrids and scarids are fast swimmers; most are pelagic egg spawners, and hence use offshore spawning

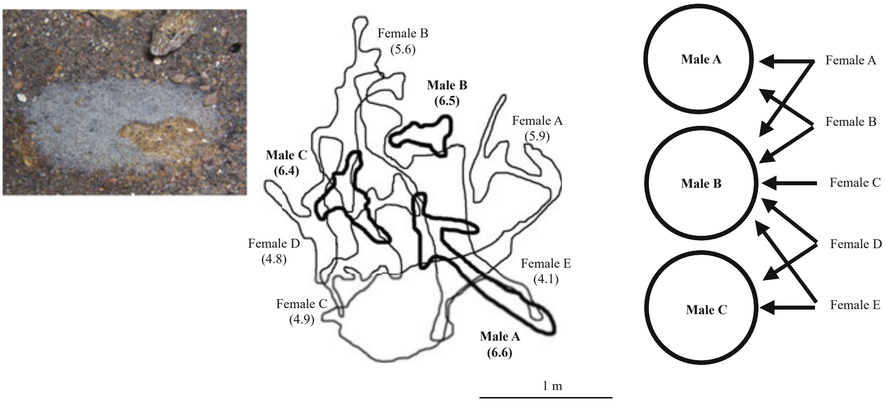

Fig. 4.4 Typical example of the spatial relationship of the male territory-visiting (MTV) polygamy. Home ranges of females (*thin lines*) and territories of nest-holding males (*thick lines*) of *Fusigobius neophytus* on the reefs of Kuchierabu-jima Island, southern Japan (*left*; redrawn from Tsuboi and Sakai 2016). Some females overlap their home ranges with multiple male territories. Total lengths (cm) are given in parentheses. A schematic model indicates mating relationships in MTV polygamy, in which females can change male mating territories for spawning (*right*; redrawn from Kuwamura 1997) (*photo* Miyuki Tsuboi)

sites for dispersing eggs and transporting them offshore (Colin and Bell 1991; Kuwamura et al. 2009). MTV polygamy has been found even in fishes showing paternal care for demersal eggs within their mating territories: *Symphodus* wrasses, *Coryphopterus*, *Fusigobius*, *Lythrypnus* gobies, and the synbranchid *Monopterus albus* (Table 4.2; Fig. 4.4).

In fish with MTV polygamy, territorial males frequently develop bright body coloration to attract females, similar to leks in birds. In contrast, territorial males with harem mating systems maintain large body sizes for resource and female defense, but do not generally show sexual dichromatism or dimorphism. These differences in male characteristics are consistent with the theory of sexual selection.

In MTV polygamy, the primary mating form involves pair spawning between territorial males and visiting females. Large individuals within a local population tend to become territorial males. It is well known that some territorial males often have the opportunity to spawn with many females (Warner 1984, 2001). In addition, alternative mating tactics such as sneaking, streaking, and group spawning are often observed in smaller males because of a relatively loose monopoly on mating opportunities with females by territorial males (Warner 1984, 2001; see Sect. 4.3). Some smaller males have pair spawning opportunities with females moving toward the male territorial spawning sites; this interception is called sneaking. The release of sperm by smaller males simultaneously with territorial males, coinciding with male-female pair spawning is called streaking.

In addition, small males often form groups to spawn with females (i.e., group spawning). The group spawning was exclusively confirmed in pelagic egg spawners and reported in at least 27 protogynous fish species (Table 4.2). Nearly all these cases are observed in labrids (17 species) and scarids (9 species). Of the 27 group spawning species, 93% (25 species) maintained MTV polygamy (Table 4.2). At spawning sites in MTV polygamy, group spawning is observed along with pair spawning, as females are ready to spawn together. In the high-density population site of the bluehead wrasse *T. bifasciatum*, the group-spawning males drive out territorial males from spawning sites, where females prefer to spawn and get frequent mating opportunities (Warner 1984, 2001).

Some labrids and scarids are reported to exhibit different mating systems among populations, including harem polygyny or MTV polygamy (two *Cheilinus* species, *Epibulus insidiator*, *Halichoeres melanurus*, two species of *Scarus*, and *Sparisoma radians*; Table 4.2). Although the mechanism promoting variation in mating system has not been revealed in many labroid fishes, one comparative field study on *H. melanurus* provides insight into this issue. The wrasse maintains reproduction by MTV polygamy, where females actively change their mates over a long mating trip visiting different males (Kuwamura et al. 2000). However, under high predation risks, females repeatedly spawn with nearby males, resulting in a mating system similar to that of harem polygyny (Karino et al. 2000). Under social or environmental conditions restricting female mate choice, mating based on MTV polygamy may flexibly shift to a harem-like group structure.

4.2.3 Monogamy

In protogynous gobies, the monogamous mating system is confirmed in coral-dwelling *Gobiodon* and *Paragobiodon* species (5 species; Table 4.2). In these monogamous gobies, males play an important role in egg guarding by covering the eggs spawned on the surface of coral branches (Kuwamura et al. 1994; Nakashima et al. 1996; Munday et al. 1998). The largest individuals function as males at the beginning of pair formation within local groups. These goby species are observed to form pairs of size-matched individuals. It has been reported that sex differences in growth (Kuwamura et al. 1994) and growth regulation between pairs (Munday et al. 2006a) are mechanisms that drive size-matched pairs. Details are described in the following chapter (Chap. 5).

The protogynous serranid *Cephalopholis hemistiktos* is reported to maintain a monogamous mating system with small territorial home ranges in small patch reef habitats isolated from sandy beds (Shpigel and Fishelson 1991). It is suggested that poor food availability in habitat restricts group size and forces monogamy in serranids. However, an exceptional example of a harem group comprising one male and two females has been observed (Shpigel and Fishelson 1991), suggesting the potential ability to establish harem polygyny when they settle in prey-rich habitats. Further field examination of mating systems of *C. hemistiktos* is expected to reveal whether it is obligately monogamous or facultatively monogamous and potentially harem polygynous, depending on the habitat conditions.

4.2.4 Spawning Aggregation

Spawning aggregation is reported in at least 164 species of coral reef fishes in 26 families (Claydon 2004) and occurs in the middle of the reproductive process just before spawning. It involves long-distance migration to offshore areas suitable for spawning and is often observed in those with a habit of spawning at limited and specific times (Robertson 1983; Claydon 2004). Spawning aggregation was recorded in 16 protogynous fishes, including 11 serranids in *Cephalopholis*, *Epinephelus*, *Mycteroperca*, and *Plectropomus* (Table 4.2). In addition, four protogynous labrids and one protogynous scarid species have also been recorded with spawning aggregation (Table 4.2). However, spawning aggregations cannot be considered under a comparable independent mating-system category.

Owing to the considerable difficulties in conducting field observation in offshore waters where spawning aggregations often occur, detailed individual-level data on mating behaviors are limited. Harem mating systems or MTV polygamy with records of spawning aggregation habits have been reported in two labrids (*Cheilinus fasciatus* and *Cheilinus undulatus*), a scarid *Scarus iseri*, and two protogynous serranids (*Cephalopholis fulva* and *Epinephelus adscensionis*) (Table 4.2). However, in most cases, whether the territorial structures of harems and MTV polygamy are formed in areas where individuals aggregate to spawn remains to be elucidated. Six serranids, namely, *C. fulva*, *Epinephelus guttatus*, *Epinephelus ongus*, *Mycteroperca microlepis*, *Mycteroperca phenax*, and *Plectropomus leopardus* perform pair spawning ascents (Erisman et al. 2009; Nanami et al. 2013), implying the broad occurrence of male territoriality to secure mating partners at the spawning sites where females form aggregates. In contrast, group spawning in *S. iseri* occurs following spawning aggregation (Colin 1978). Further research on spawning aggregates is needed to obtain data on spawning territoriality and mate fidelity (stable or promiscuous) with notes on their spawning forms, which clarify their actual status as mating systems.

4.3 Monandry and Diandry

Two types of males are known in protogynous fishes: primary males and secondary males derived from females (Reinboth 1970). The coexistence of small males and large territorial males within a local population occurs in several protogynous fishes. Histological approaches have revealed that small males not derived from sex changes in females occur in several protogynous fishes. The non-sex-changing males, called primary males, differ from males derived from sex change (secondary males) in terms of gonadal maturation or development. No remnants of the ovarian structure or ovarian cells were histologically verified in or around the testicular structure of primary males (Reinboth 1970; Sadovy and Shapiro 1987). Diandry is defined by the coexistence of two types of males in a population or species; in monandry, all males are derived from the sex change of females.

Table 4.3 Relationship between occurrence pattern of male types and mating systems of protogynous fishes

Occurrence pattern of male types	Size assortative monogamy ($n = 6$)	Harem polygyny ($n = 51$)	MTV polygamy ($n = 52$)
Monandry ($n = 71$)	6	46	19
Diandry ($n = 32$)	0	3	29
Unknown ($n = 6$)	0	2	4

Number of species summarized from Table 4.2, excluding species with more than one mating system records and those only with spawning aggregation

Monandry was confirmed in 89 protogynous species and diandry in 37 including various labrids and scarids (Table 4.2). The occurrence of both or only one of these types of males is related to the mating system of fish. The following discussion focuses on protogynous species with only one known mating system (i.e., monogamy, harem polygyny and MTV polygamy) for comparison, with the exception of species that exclusively exhibit spawning aggregation.

In total, 71 and 32 protogynous fish species are identified as monandrous and diandrous, respectively (Table 4.3). Monandry is broadly confirmed in fish maintaining stable mating relationships, that is, harem polygyny and monogamy. In all, 46 of the 51 species of harem fish (90%), and all 6 monogamous protogynous fishes are monandrous (Table 4.3). Territorial males monopolize mating in harems or secure mating opportunities within monogamous pairs in monandric fishes. Thus, pair spawning between territorial males and females is the primary form of mating. In most cases, sneaking or streaking is rare because of the strong territorial dominance of males (but see Ohnishi et al. 1997; Muñoz and Warner 2003a).

Some MTV polygamous fish species are monandric (19 species; Table 4.3). However, the number of monandric species with MTV polygamy may be overestimated, because the frequency of primary males within a population varies with population density in various diandric MTV polygamous fishes (Warner 1984). Therefore, reports of monandry in MTV polygamous fishes should be carefully re-examined for the possibility of the occurrence of primary males, depending on the population density.

Of the 32 diandric species 91% (29 species) exhibited MTV polygamy in their mating system (Table 4.3). Many diandrous wrasses and parrotfishes possess high free-swimming abilities and produce pelagic eggs in the water column. Diandric sexuality has also been confirmed in demersal egg spawners, i.e., a goby *Fusigobius neophytus* (Tsuboi and Sakai 2016) and some haremic *Dascyllus* damselfish (Cole 2002; Asoh and Yoshikawa 2003; Table 4.2).

Primary males of diandric labrids and scarids develop large testes even when they are small, providing an advantage during streaking or group spawning (Robertson and Warner 1978; Warner and Robertson 1978; Warner 1984, 2001). Primary males often maintain female-like body coloration and behave stealthily to sneak or streak, while avoiding attacks from territorial males performing courtship displays to approaching females for pair spawning. Sex-changing females and primary males of diandric labroid fishes can become territorial males after growth and exhibit secondary body coloration.

The occurrence of small males due to small female sex change (see Sect. 4.7) or immature female sex change (i.e., prematurational sex change) is not defined as diandry, as long as ovary-related tissues are histologically present. In the case of the monandric labrid *Notolabrus celidotus* (formerly *Pseudolabrus celidotus*), small males derived from protogynous sex change of immature females (prematurational sex change) coexist with large sex-changing males within a population showing MTV polygamy (Jones 1981). In addition, the occurrence of males via prematurational sex change has also been detected in *Bodianus eclancheri* (Labridae), *Sparisoma cretense* (Scaridae), *Lethrinus nebulosus* (Lethrinidae), and *Pagrus ehrenbergii* (Sparidae) (Chap. 6). Furthermore, the prematurational sex change may also occur in at least three labrids: *Cirrhilabrus temmincki*, *Labrus bergylta*, and *Labrus mixtus*; a serranid *Paralabrax maculatofasciatus*; a nemipterid *Scolopsis monogramma*; a lethrinid *Lethrinus atkinsoni*; and a sparid *Pagrus pagrus*.

The origin and sexuality of primary males in diandric fish have long been discussed. It has long been believed that primary males are gonochoric without sexual plasticity. However, primary males of the genera *Halichoeres* and *Parajulis* have recently been shown to have the ability to change sex to females (Kuwamura et al. 2007; Miyake et al. 2008). In addition, juveniles of the famous diandric wrasse, *T. bifasciatum*, have been confirmed to become primary males or females, depending on social conditions, for example, conspecific densities (Munday et al. 2006c). Since plastic sexuality has been confirmed in the primary males of some diandric wrasses, it may not be necessary to distinguish between males by prematurational sex change and those by direct maturation to primary males. Research to elucidate the details of the social and environmental conditions under which prematurational sex change occurs is expected to provide an integrated understanding of the mechanisms of small male emergence in protogynous fishes.

4.4 Adaptive Significance of Protogyny Explained by the Size-Advantage Model

Protogyny is recorded mainly in fishes that maintain harem polygyny or MTV polygamy, where large dominant males can obtain polygynous mating opportunities. This condition coincides with the prediction of the adaptive significance of protogynous sexuality using the size-advantage model (SA model; see Chap. 1). The SA model predicts that protogynous (female to male) sex change will be selectively favored in fishes with polygynous mating systems, where large males monopolize mating to the detriment of small ones (Warner 1975, 1984, 1988).

Small young males generally have poor mating opportunities in polygynous mating groups dominated by large territorial males. In contrast, females maintain mating opportunities, even when their body size is small. In this social context, it is predicted that individuals can maximize their lifetime reproductive success by maturing as females first and changing sex into males after growing larger. For many protogynous fishes that maintain harem polygyny or MTV polygamy, it has been widely confirmed that large territorial males obtain high reproductive success via multiple spawning opportunities in local groups. Therefore, the prediction of the SA model fits well with the social and mating conditions of the polygynous mating groups.

The emergence of primary males in situations that favor protogyny, in which large males dominate reproduction, is also theoretically well explained. Warner's (1975) SA model shows that the characteristics of the mating system, such as mate choice by females and the degree of monopoly of reproductive opportunities by males, determine the direction and frequency of the sex change phenomenon. In the bluehead wrasses *T. bifasciatum*, the number of individuals living in a patch reef varies greatly depending on its size. On large reefs harboring large populations of the wrasse, large numbers of small primary males that do not have a territory group together to interfere with the spawning of territorial males and then conduct group spawning at females' favorite spawning sites (Warner 1984). This shows that in a population where it is difficult for territorial males to monopolize reproduction, the proportion of primary males will be high. This is consistent with the predictions of the SA model. Based on this concept, Charnov (1982) also successfully accounted for variation among populations in the proportion of primary male bluehead wrasses in field data using an ESS model that predicts an optimal value for the proportion of primary males occurring under the influence of the reproductive success of territorial males. In other words, the frequency of the occurrence of primary males may mutate depending on the advantage of primary males in terms of their mating tactics in the local habitat.

It has been hypothesized that sexual differences in life history traits, such as mortality or growth rates, may also favor the evolution of protogynous sex change (Charnov 1982; Warner 1988; Iwasa 1991). In general, individuals maximize fitness by first maturing with lower mortality or higher growth rate and later changing into the other sex. For the coral-dwelling goby *Paragobiodon echinocephalus* with a size-assortative monogamous mating system, where size-fecundity relationships are equal in both sexes, the adaptive significance of protogynous sexuality (despite the ability to reverse sex change; Table 4.4, see Sect. 4.5) is explained by the growth rate advantage: females grow faster than males in each pair (Kuwamura et al. 1994). Because the reproductive success of a monogamous pair of *P. echinocephalu*s is limited by the body size of the smaller mate, regardless of sex and male body size, which strongly determines reproductive success in the parental care role, a smaller individual will become a female in the newly formed pair, and adult females will undergo sex changes in males when they form new pairs (Kuwamura et al. 1994). In the case of another coral-dependent monogamous goby, *Gobiodon histrio*, the effect of sex-specific growth differences on sex change is limited (Munday 2002; Munday et al. 2006a).

In a monandric scarid, *S. radians*, in addition to pair spawning by territorial brightly colored males (terminal phase: TP) with drab-colored females (initial phase: IP), non-territorial bachelor IP-colored secondary males derived from females conduct streaking and group spawning (Muñoz and Warner 2003a, 2004). By incorporating sperm competition within local groups (i.e., possibilities of paternity loss suffered from streaking) and size-fecundity skew (i.e., future expected fecundity of the other females remaining in the harem), the SA model was extended to predict that large females maintaining high fecundity do not always undergo sex change (Muñoz and Warner 2003b) with a field test of the hypothesis using the parrotfish *S. radians* harem (Muñoz and Warner 2004). The new version of the SA model may explain variations in the timing of sex change among populations or species, especially in MTV polygamous fishes, which sometimes show intense sperm competition.

In addition, an ESS model incorporating sex-specific growth rates and the effect of female nutritional status on the clutch size as life history parameters predicts that well-nourished females achieve high reproductive success as they change sex on attaining a larger size than poorly nourished ones (Yamaguchi et al. 2013). In some situations, well-nourished females no longer change sex (i.e., lifelong females). This notional approach also explains tactical variations in the size and timing of protogynous sex change (Sect. 4.7).

The foregoing reports reveal the adaptive significance of protogynous sexuality in fishes explained through the maximization of lifetime reproductive success.

4.5 Social Control of Sex Change: Broad Occurrence of Takeover Sex Change

Experimental manipulations and underwater observational surveys have significantly contributed to studies on the processes, patterns, and conditions of protogynous sex change. In various haremic protogynous fishes, the male body size varies among local groups (Warner 1988). Furthermore, males are always the largest in each local group, and thus the most dominant in size-based dominance order within a group (Robertson 1972; Moyer and Nakazono 1978; Kuwamura 1984; Sakai and Kohda 1997; Kadota et al. 2011). Therefore, the timing of protogynous sex changes is determined by the relative body size and dominance in groups, rather than the absolute body size. Even in MTV polygamous fishes, similar relative body size-based dominance order and size-based sexuality have been confirmed (Warner and Swearer 1991; Sakai et al. 2002, 2007). If females begin sex change at a fixed body size or a certain age, then local group member composition related to body size would not be observed in nature.

As protogynous sex change is mediated by relative size and dominance, females may not change sex unless they become relatively larger than their group members, even when they attain the absolute size at which many other females change sex. As a result, females do not often undergo sex changes in natural conditions, as revealed by many demographic studies. For example, in the haremic angelfish *Centropyge ferrugata* on the reefs of Okinawa, southern Japan, 9 of 31 females underwent protogynous sex changes in a 3-year-long demographic survey (Sakai 1997). In the case of cleaner wrasse *L. dimidiatus*, 8 of 31 females showed sex changes in a 3-year-long survey on the reefs of southern Japan (Sakai et al. 2001). Kadota et al. (2012) observed protogynous sex changes in 3 *Cirrhitichthys falco* females in a 3-year survey of the population, including 11 females on the reefs of southern Japan. Aldenhoven (1984) conducted demographic surveys in four populations of *Centropyge bicolor* on reefs of Great Barrier Reef to follow 36 harems (2–3 females in each harem) for 2.5 years and confirmed sex reversal of 1 or 2 individuals in most populations, although there was an exceptional population with frequent sex changes (20 sex changes; Aldenhoven 1984) (see Sect. 4.6, Bachelor sex change). These findings suggest that females change sex in situations that make them dominant in the local group, many cases, the disappearance of dominant males.

Robertson (1972) first highlighted the importance of social interactions in the sex change of protogynous fish. He conducted experiments on males removed from harems and showed that the loss of the dominant male is an important social factor that promotes female sex change. In a 2.5-year demographic survey, Robertson (1974) found that females of the cleaner wrasse *L. dimidiatus* often showed sex changes in harems where the dominant males disappeared. In each cohabiting female-type harem (Table 4.2), a dominance order based on relative body size through behavioral interactions was found (Robertson 1974; Kuwamura 1984; Sakai and Kohda 1997). The dominance rank affects the timing of sex change by females adopting a conditional strategy, "if dominant, be a male; if not, be a female." The importance of social status within a local group, affecting the start or delay of sex change, is often called the "social control of sex change" (Robertson 1972).

After discovering the social control of sex change, male removal from a polygynous group or female-only cohabitation is often used to confirm protogynous sex change in field or aquarium experiments using various fishes. In fish whose sex change patterns have been surveyed in nature, the most common example is that of the largest female changing sex after the disappearance of the dominant male to take over the harem, called takeover sex change (Sakai 1997). Eleven protogynous species are known to undergo takeover sex change in nature (Table 4.4). In addition, male removal experiments in fields or male-loss conditions in aquariums showed takeover sex changes by females in a total of 57 species (25 and 41 species, respectively; Table 4.4). In total, 60 protogynous fish species were confirmed to undergo sex change by females after the loss of males, implying the broad occurrence of social control of sex change.

The rationale behind this observation is that if females started sex changes when the male was present, they would be chased out of the group by the territorial male (but see Sects. 4.6 and 4.7). If females do not conduct sex change even after the disappearance of the dominant male, the harem would be taken over by another male that has intruded into the territory or group members would leave the territory to search for new mates. In either case, the future reproductive success of females is considerably lower than that of individuals undergoing takeover sex change

Table 4.4 A list of fishes that have been confirmed to conduct protogynous sex change under the male-loss conditions by rearing experiment in aquarium (A) or field experiment (F), with notes on takeover sex change after the male disappearance observed in natural conditions

Order/family/ species	Mating system	Experiments	Takeover sex change observed in nature	References
Gobiiformes				
Gobiidae				
Coryphopterus dicrus		A		Cole and Shapiro (1990)
Coryphopterus glaucofraenum	MTV	A		Cole and Shapiro (1992)
Coryphopterus hyalinus		A		Cole and Shapiro (1990)
Coryphopterus lipernes		A		Cole and Shapiro (1990)
Coryphopterus personatus		A		Cole and Robertson (1988)
Eviota epiphanes		A		Cole (1990)
Fusigobius neophytus	MTV		X	Tsuboi and Sakai (2016)
Gobiodon histrio	MG	F[a]		Munday et al. (1998)
Gobiodon okinawae		A[a]		Cole and Hoese (2001)
Gobiodon quinquestrigatus	MG	F, A[a]		Nakashima et al. (1996)
Lythrypnus dalli	MTV	F (artificial habitat), A[a]		Reavis and Grober (1999), Black et al. (2005) and Lorenzi et al. (2006)
Paragobiodon echinocephalus	MG	F, A[a]	X[a]	Kuwamura et al. (1994), Nakashima et al. (1995) and Lassig (1977)
Paragobiodon xanthosomus	MG	F		Lassig (1977)
Rhinogobiops nicholsi		A		Cole (1983)
Trimma okinawae	ND harem	F, A[a]	X[a]	Sunobe and Nakazono (1990, 1993) and Manabe et al. (2007b)
Uncertain orders in Ovalentaria				
Pomacentridae				
Dascyllus aruanus	AF harem, MTV	F[a]		Kuwamura et al. (2016a) and Asoh (2003)

(continued)

Table 4.4 (continued)

Order/family/species	Mating system	Experiments	Takeover sex change observed in nature	References
Dascyllus reticulatus	AF harem, MTV	A	X[a]	Tanaka (1999), Asoh (2005b) and Sakanoue and Sakai (2022)
Cichliformes				
Cichlidae				
Metriaclima cf. *livingstoni*		A		Stauffer Jr and Ruffing (2008)
Cyprinodontiformes				
Poeciliidae				
Xiphophorus helleri		A		Lodi (1980)
Trachiniformes				
Pinguipedidae				
Parapercis cylindrica	TF harem	F	X	Stroud (1982)
Parapercis snyderi	TF harem	F, A	X	Nakazono et al. (1985) and Ohnishi (1998)
Labriformes				
Labridae				
Bodianus rufus	CF harem	F		Hoffman (1983, 1985) and Hoffman et al. (1985)
Choerodon schoenleinii		A		Sato et al. (2018)
Halichoeres melanurus	ND harem, MTV	F		Sakai et al. (2002)
Halichoeres miniatus	TF harem	F		Munday et al. (2009)
Iniistius pentadactylus	TF harem	F, A		Nemtzov (1985)
Labroides dimidiatus	CF harem	F[a], A[a]	X	Robertson (1972), Kuwamura et al. (2002, 2011) and Sakai et al. (2001)
Macropharyngodon moyeri	ND harem	F		Moyer (1991)
Parajulis poecilopterus	MTV	A		Sakai et al. (2007)
Pteragogus aurigarius	MTV	A		Shimizu et al. (2022)
Thalassoma bifasciatum	MTV	F		Warner and Swearer (1991) and Hoffman et al. (1985)

(continued)

Table 4.4 (continued)

Order/family/ species	Mating system	Experiments	Takeover sex change observed in nature	References
Thalassoma duperrey	MTV	A		Ross et al. (1983)
Thalassoma lucasanum	MTV	A		Warner (1982)
Scaridae				
Sparisoma radians	ND harem, MTV	F		Muñoz and Warner (2003a, 2004)
Perciformes				
Serranidae				
Cephalopholis boenak		A		Liu and Sadovy (2004)
Epinephelus adscensionis		A		Kline et al. (2011)
Epinephelus akaara		A[a]		Okumura (2001)
Epinephelus coioides		A[a]		Quinitio et al. (1997), Chen et al. (2019, 2020, 2021)
Epinephelus rivulatus		F		Mackie (2003)
Pseudoanthias pleurotaenia		A		Hioki et al. (2001)
Pseudoanthias squamipinnis	AF harem	F, A	X	Fishelson (1970), Yogo (1985), Shapiro (1981) and Shapiro and Boulon Jr (1982)
Pomacanthidae				
Apolemichthys trimaculatus		A[a]		Hioki and Suzuki (1995)
Centropyge acanthops	CF harem	A		Hioki and Suzuki (1996)
Centropyge bicolor	CF harem		X	Aldenhoven (1984, 1986)
Centropyge ferrugata	CF harem	F[a], A[a]	X	Sakai (1997), Sakai et al. (2003a) and Kuwamura et al. (2011)
Centropyge fisheri		A[a]		Hioki and Suzuki (1996)
Centropyge heraldi		A		Hioki (2002)
Centropyge interruptus	CF harem	F		Moyer and Nakazono (1978)
Centropyge potteri	CF harem	F (artificial habitat)		Lutnesky (1994, 1996)

(continued)

Table 4.4 (continued)

Order/family/ species	Mating system	Experiments	Takeover sex change observed in nature	References
Centropyge vrolikii	CF harem	F		Sakai et al. (2003b)
Genicanthus bellus		A		Hioki et al. (1995)
Genicanthus lamarck	AF harem	A		Suzuki et al. (1979)
Genicanthus melanospilos	AF harem	A		Hioki et al. (1982)
Genicanthus persomatus		A		Carlson (1982)
Genicanthus semifasciatus	AF harem	A		Suzuki et al. (1979)
Genicanthus watanabei		A		Hioki et al. (1995)
Malacanthidae				
Malacanthus plumieri	TF harem	F		Baird (1988)
Cirrhitidae				
Cirrhitichthys aureus		A[a]		Kobayashi and Suzuki (1992)
Cirrhitichthys falco	TF harem		X[a]	Kadota et al. (2012)
Tetraodontiformes				
Balistidae				
Sufflamen chrysopterus	TF harem	F		Takamoto et al. (2003)

MG size-assortative monogamy, *MTV* male territory-visiting polygamy, *CF harem* cohabiting female-type harem, *TF harem* territorial female-type harem, *AF harem* aggregating female-type harem, and *ND harem* harem types unidentified (see Table 4.2)

X indicates that there are reported cases

[a] Reversed sex change (male to female) was also confirmed

immediately after male loss. Thus, regardless of the mating system, subordinate females broadly adopt takeover sex change as a life history tactic for protogynous fish (Table 4.4).

The SA model was mathematically formulated as a life history strategy model to explain the adaptive significance of the direction and timing of sex change, viewed as an evolutionary response to demographic parameters of the entire population (Warner 1975, 1984). The social control of sex change is an individual-level mechanism that drives variations in the timing of sex change within and between species. However, the SA model can also be applied at the scale of the local mating group and explain the advantage of sex change based on the reproductive values of individuals as males or females relative to the size of the other individuals in the mating group (Munday et al. 2006b). Thus, the validity of the SA model as a theory to explain the advantage of sex change remains unchanged, even in fishes that demonstrate socially controlled sex changes. However, empirical studies of fishes that exhibit social control of sex change have revealed variations in the timing of sex change within species. How they relate to the reproductive, social, and environmental conditions of local groups will be discussed in the next section.

4.6 Alternative Examples of Protogynous Sex Change

Mating systems of protogynous fishes, including harem polygyny and MTV polygamy, where large territorial males monopolize mating opportunities, may favor the evolution of the conditional strategy "if dominant, be male." However, to achieve a dominant status, females sometimes adopt sex changes without waiting for the disappearance of males. In other words, females do not always wait until they become dominant (i.e., the largest) in the original local group because of the disappearance of males. Although sex change after the male loss has already been observed in a wide range of protogynous fish species, it is emphasized that sex change starts earlier than the timing of male loss, the pattern initially referred to as "early sex change" (Moyer and Zaiser 1984).

In protogynous fishes demonstrating socially controlled sex change (i.e., takeover sex change after male loss), females of 18 species changed sex even in the presence of the dominant male (Table 4.5). In addition, three haremic species without any observation records of takeover sex change (*C. tibicen*, *H. tricolor*, and *Xyrichtys martinicensis*; Table 4.5) have records of sex change in male presence. With the empirical data accumulation, it became clear that the early sex change initially mentioned by Moyer and Zaiser (1984) could be divided into two major processes: bachelor sex change and harem-fission sex change. For two gobies *Rhinogobiops nicholsi* and *F. neophytus* and a wrasse *Choerodon schoenleinii*, detail processes of the sex change under the male presence were unrevealed. For the remaining 15 species, either or both patterns of bachelor sex change or harem-fission sex change have been identified (Table 4.5). This view of the phenotypic flexibility of sex change is an alternative life history tactic determined by field studies, in which identified individuals were observed continuously over time. In addition, tactical behaviors of females that may favor the acquisition of sex change opportunities through group migration and fast growth has also been reported. Three perspectives on alternative tactics (i.e., bachelor sex change, harem-fission sex change, and female tactics toward the faster acquisition of sex change) are introduced below.

4.6.1 Bachelor Sex Change

One of the processes of protogynous sex change demonstrated in the presence of a male is becoming a bachelor male. A female leaves the male's territory and changes sex to become a bachelor male that will spend a reproductively inactive period (Aldenhoven 1984, 1986; Moyer and Zaiser 1984; Hoffman et al. 1985; Moyer 1987; Warner 1988). This is called "bachelor sex change" as described by Sakai (1997). Bachelor sex changers have been reported in the haremic goby *Trimma okinawae*, the damselfish *D. reticulatus*, the sandperch *Parapercis snyderi*, the temperate wrasse *N. celidotus*, the bluehead wrasse *T. bifasciatum*, the bucktooth parrotfish *Scarus radians*, and three *Centropyge* angelfishes (*C. bicolor*, *C. interruptus*, and *C. tibicen*) (9 species; Table 4.5).

Bachelor sex change was found earlier in harem species of *Centropyge* angelfishes, and its advantages have been discussed (Moyer and Zaiser 1984; Aldenhoven 1984, 1986). Bachelor sex changers were subsequently identified in harem fish species of various taxa (Table 4.5). Sex-changing females undergoing a period similar to bachelor males have also been confirmed in MTV polygamous wrasses and parrotfishes, under the effective social control of sex change (Table 4.5). In the case of the MTV polygamous labrids *N. celidotus and T. bifasciatum*, and a scarid *S. radians*, females would abandon their home ranges and become nonterritorial males before reaching territorial male status (Jones 1981; Warner 1984; Hoffman et al. 1985; Muñoz and Warner 2003a).

Since bachelor sex changers could have continued to breed as females if they had not changed sex, they would have incurred significant opportunity costs if the period of bachelorhood until taking over the harem was long. However, the cost can be compensated by high reproductive success after taking over the harem (Aldenhoven 1984, 1986; Moyer and Zaiser 1984; Warner 1991). To acquire a reproductive position, a sex-changing individual must (1) wait for the territorial male to disappear, (2) wait for a new female (or juvenile) to settle in its home range, or (3) deprive the territorial male of some of its females (Moyer 1987). The last option is often adopted as another type of sex change tactic, called "harem-fission sex change," described later. Of these, the first tactic appears to be the most successful for bachelor males. In this case, bachelor males have to enter the group earlier than the completion of takeover sex change by the group's largest female after the territorial male's disappearance to mate with the females. In *C. bicolor*, seven cases were identified in which bachelor males took over a harem that lost its male (Aldenhoven 1984).

Moyer and Zaiser (1984) observed bachelor sex changers wandering over a wide area as a floater to visit several harems in two *Centropyge* angelfish harems, suggesting that they assess the surrounding group conditions to find harems without males where they could take over. It is believed that it is not easy for a bachelor male to displace a larger territorial male. The floating behavior of bachelor males is important in detecting the loss of territorial males (Moyer and Zaiser 1984; Moyer 1987). However, reports on the behavioral patterns of bachelor sex changers are very limited.

Table 4.5 List of fishes that have been confirmed to conduct protogynous sex change in the presence of males, i.e., bachelor sex change, harem-fission sex change, and other patterns, by aquarium experiments or field observation on natural populations

			Sex change in the male presence			
Family/species	Mating system	Takeover sex change	Bachelor sex change	Harem-fission sex change	Remarks	References
Aquarium experiments						
Gobiidae						
Rhinogobiops nicholsi		X	Details unknown		Details unknown	Cole (1983)
Labridae						
Choerodon schoenleinii		X	Details unknown		Female-biased harem	Sato et al. (2018)
Pomacanthidae						
Centropyge potteri	CF harem	X		Female-biased harem in low-density conditions		Lutnesky (1994, 1996)
Field observational surveys						
Gobiidae						
Fusigobius neophytus	MTV	X	Details unknown		Sex change during the non-breeding season	Tsuboi and Sakai (2016)
Trimma okinawae	ND harem	X	Moved to vacant spaces			Manabe et al. (2007b)
Pomacentridae						
Dascyllus reticulatus	AF harem, MTV	X	Behavioral crypticity of bachelor males	High-density groups		Tanaka (1999), Asoh (2005b) and Sakanoue and Sakai (2022)
Pinguipedidae						

(continued)

Table 4.5 (continued)

Family/species	Mating system	Takeover sex change	Sex change in the male presence			References
			Bachelor sex change	Harem-fission sex change	Remarks	
Parapercis cylindrica	TF harem	X		Large harems		Stroud (1982)
Parapercis snyderi	TF harem	X	Synchronized bachelor sex change in the late breeding season			Nakazono et al. (1985) and Ohnishi (1998)
Labridae						
Labroides dimidiatus	CF harem	X		Large harems		Robertson (1972), Sakai et al. (2001) and Kuwamura et al. (2011)
Macropharyngodon moyeri	ND harem	X		Large harems		Moyer (1991)
Notolabrus celidotus	MTV	X	Non-territorial bachelor males			Jones (1981)
Thalassoma bifasciatum	MTV	X	Non-territorial bachelor males with high growth			Warner and Swearer (1991) and Hoffman et al. (1985)
Xyrichtys martinicensis	TF harem			A large harem including 35 females		Victor (1987)
Scaridae						
Sparisoma radians	ND harem, MTV	X	Non-territorial bachelor males			Muñoz and Warner (2003a, 2004)
Serranidae						
Pseudoanthias squamipinnis	AF harem	X		Density-dependent sex change		Fishelson (1970), Yogo (1985), Shapiro (1981) and Shapiro and Boulon Jr (1982)

Pomacanthidae						
Centropyge bicolor	CF harem	X	High density conditions with high male mortality	Large harems		Aldenhoven (1984, 1986)
Centropyge ferrugata	CF harem	X		Large harems		Sakai (1997) and Kuwamura et al. (2011)
Centropyge interruptus	CF harem	X	Floating bachelors in low-density conditions			Moyer and Nakazono (1978)
Centropyge tibicen	CF harem		Floating bachelors in low-density conditions	Infrequent social interaction in low-density conditions		Moyer and Zaiser (1984)
Holacanthus tricolor	CF harem			Infrequent social interaction		Hourigan and Kelley (1985)
Cirrhitidae						
Cirrhitichthys falco	TF harem	X		Large harems		Kadota et al. (2012)

The circumstances under which the sex change tactic occurred and the behavioral characteristics of the sex change individual are described (see text)

X indicates that there are reported cases of takeover sex change via manipulation experiments or field observational surveys

MTV male territory-visiting polygamy, *CF harem* cohabiting female-type harem, *TF harem* territorial female-type harem, *AF harem* aggregating female-type harem, and *ND harem* harem types unidentified

A 2.5-year demographic study by Aldenhoven (1984) in four populations of *C. bicolor* confirmed the frequent occurrence of bachelor males in a population exhibiting high mortality and high harem density. For population conditions promoting bachelor sex changers, high mortality rates in both territorial males and reproductively active females may increase the chances of group takeover by bachelor males having low mortality rates. The annual mortality rate of males in the population with frequent bachelor sex change was 2–13 times higher than that in populations where only takeover sex change was observed (Aldenhoven 1984, 1986). High harem density also favors the occurrence of bachelor sex changers, because the conditions of many harems could be easily assessed (Aldenhoven 1984, 1986; Warner 1988, 1991). In a population where 19 bachelor males appeared, each harem was in close proximity to an average of 4.1 harems (Aldenhoven 1984).

In contrast, Moyer and Zaiser (1984) and Moyer (1987) suggested the advantages of low-density conditions for obtaining females from male territories. Although subsequent studies have confirmed that harems with increased size are more likely to experience sex change and group splitting by sex changers when the male is present (Lutnesky 1994; Sakai 1997), these processes are distinct from bachelor sex change (for details, see Sect. 4.7, the harem-fission sex change). Moyer's view as a pioneer of field observations of various sex change patterns appears to be based on sex change in the presence of males being lumped together as early sex change. Field experiments that followed bachelor males (not bachelor sex changers but widowed after mate loss) under low-density conditions have confirmed cases of pairing with other males, resulting in reversed sex change to females, although they sometimes acquire females (Kuwamura et al. 2002, 2011; Kadota et al. 2012). Hence, it is probable that low density is not an effective condition for bachelor sex changers.

A high growth rate is an important characteristic of bachelor sex changers in *Centropyge* angelfish harems (Moyer and Zaiser 1984), which would be advantageous in dominating the harem of females and obtaining preferred mating territories through competition among males. In the case of the MTV polygamous wrasse *T. bifasciatum*, sex changers spend considerable time as nonterritorial bachelor males (Hoffman et al. 1985), and nonterritorial males exhibit 1.5 times higher growth than females (Warner 1984). Large body size is generally crucial to dominate the harem of females and maintain mating territories in polygynous fishes (Warner and Schultz 1992; Kuwamura et al. 2000). Bachelor sex changers grow at the expense of their current reproductive opportunities to achieve a faster male reproductive status (Moyer and Zaiser 1984; Moyer 1987; Warner 1988).

Similarly, many small females left the harem and proceeded to change sex to bachelor males in the late breeding season in territorial female-type harems of the sandperch *P. snyderi*, where females maintain exclusive territories (Nakazono et al. 1985; Ohnishi 1998). This might be called "synchronized bachelor sex change." Bachelor sandperch males achieve high growth during the nonbreeding season and become territorial in the next breeding season (Ohnishi 1998). The body size of sex-changing females of *P. snyderi* was within 86% of the male body size, suggesting that the relative size threshold between dominant males and females may affect the start of synchronous sex change in females in the presence of males

(Ohnishi 1998). Thus, high growth is a key characteristic for acquiring territorial male status.

Bachelor sex changers may obtain growth or survivorship advantages during their nonbreeding status, potentially increasing their possibility of taking over a harem. Using field observations and mathematical models, Aldenhoven (1986) showed that even in populations with high harem density and survival advantages of bachelor males, not all females undergo a bachelor sex change. It is expected that the respective advantages of takeover and bachelor sex changes are strongly influenced by each other's frequency (frequency-dependent selection). However, no other study has been able to make a similar tactical assessment and evaluation of bachelor sex changers.

Moreover, the social conditions of females promoting bachelor sex change remain uncertain due to the lack of observational studies on individual bachelor sex changers. In an observational field survey of a population of *T. okinawae*, sex-changing females that moved out of the harems where dominant males were present became bachelor males in the vacant space (Manabe et al. 2007b). In addition, it is common for a female of similar size to a female that underwent a bachelor sex change to be present in the original harem. Although changes in social relationships between a dominant male and females within the local group are involved in the occurrence of female sex change in the presence of males (see the harem-fission sex change section), competitive and exclusive relationships between females in the harem over sex change opportunities may be involved in triggering bachelor sex change.

A new form of bachelor sex change was recently detected in the female aggregation-type harems of the coral-dwelling damselfish *D. reticulatus*. Some subordinate females undergo gonadal sex changes in the presence of larger males or females, and the sex changers become bachelor males that do not show any sexual behaviors and continue to stay in the original harem, called "cryptic bachelor sex change" (Sakanoue and Sakai 2022). Cryptic bachelor males do not engage in wandering behaviors as reported in some *Centropyge* angelfishes (Moyer and Zaiser 1984) or leave the original groups (i.e., male territories) as seen in *T. bifasciatum* (Hoffman et al. 1985) and *P. snyderi* (Ohnishi 1998). Sakanoue and Sakai (2022) found a growth rate advantage of the sex changers over females, which is similar to a possible advantage in bachelor sex changers of other fishes. A fast growth condition during the bachelor male phase may help conduct intergroup movements to obtain mating opportunities. It was confirmed that some bachelor sex changers subsequently obtained mating opportunities as territorial males or reproductively active females (via reverse sex change) after their harem changes.

Yamaguchi et al. (2013) theoretically tested the hypothesis that variation in female fecundity caused sex change in less fertile females using the ESS model and predicted that less fertile females, even if they are not the largest, may change sex earlier than well-nourished females. The nutritional status of females, measured as the body width relative to its length, affects the number of eggs laid in the protogynous triggerfish *S. chrysopterus* on which this ESS model is based (Yamaguchi et al. 2013). In the case of *D. reticulatus*, female individuals were confirmed to have poor mating opportunities before conducting a bachelor sex change (Sakanoue and Sakai 2022). Regardless of the differences in the causes of low spawning success in females, the hypothesis may be applicable for explaining the cases of small bachelor sex changers. Low spawning frequency has also been reported in bachelor sex change in larger females (Moyer and Zaiser 1984; Moyer 1987). Hamaguchi et al. (2002), using a different ESS model approach, predicted from field data on a *Centropyge* angelfish that large females would adjust their spawning frequency lower in response to social and environmental conditions and, in some circumstances, a complete cessation of spawning would occur like bachelor sex changers. Though there is a process difference of females lowering their reproductive success between the two theories, it may be noteworthy as a female trait related to the onset of sex change. Field studies are needed to examine whether current spawning success affects the timing of sex changes in females.

4.6.2 Harem-Fission Sex Change

Another example of protogynous sex change in the presence of a dominant male (i.e., early sex change) goes that females begin to change sex while in a male's territory and acquire a portion of the harem immediately after completion of the sex change. This sex change process is called "harem-fission sex change" and has been reported in 12 harem species, including cohabiting female-type (*L. dimidiatus*, *C. bicolor*, *C. ferrugata*, *C. potteri*, *C. tibicen*, and *H. tricolor*), territorial female-type (*Parapercis cylindrica*, *Xyrichtys martinicensis*, and *Cirrhitichthys falco*), aggregating female-type (*D. reticulatus* and *P. squamipinnis*), and unknown type (*Macropharyngodon moyeri*) types (Table 4.5). For aggregating female-type harems, harem-fission sex change is not the result of harem-fission but because of living in a multi-male harem (see below). Data on the social change process of the harem-fission sex change are more detailed than for bachelor sex change because the process proceeds without the sex-changing individual leaving the group.

In cohabiting female-type harem, harem-fission sex change was observed in harem groups with a considerable female-biased sex ratio or large male territory where males could not frequently interact with females (Robertson 1974; Aldenhoven 1984; Sakai 1997). The harem-fission sex change in territorial female-type and aggregating female-type harems has also been observed in group situations with large harem sizes or a high number (Shapiro 1981; Stroud 1982; Victor 1987; Moyer 1991; Kadota et al. 2012; Sakanoue and Sakai 2022). Such harems are formed when a territorial male disappears and adjacent harem males quickly invade the territory to dominate over both harems, where some females set up their home ranges at an extreme distance from other harem females (Moyer and Zaiser 1984; Moyer JT personal communication) or when females become overly settled within male territories (Robertson 1974; Stroud 1982; Victor 1987; Sakai 1997). Females have been observed to change sex in the presence of males and set up new territories to incorporate solitary females that grew from juveniles near a harem group (Aldenhoven 1984). This is also considered to be a similar social situation, in which the number of females increased in a harem.

As seen in the case of takeover sex change, insufficient social interactions between sexes are thought to be an important trigger for inducing protogynous sex change in dominant male presence. Lutnesky (1994) experimentally promoted sex change in female *Centropyge potteri* in the presence of a dominant male in a large cage (3 × 34 m), including 1 male and 15 females. The males did not maintain frequent social interactions with all females because of low-density conditions with widespread distribution of females within the tank. In contrast, no females underwent sex changes in a small cage (3 m × 4 m), including a harem with the same number of fish at high density. In a tank experiment on the wrasse *Choerodon schoenleinii*, rearing conditions with a larger number of females (one male and five to six females) promoted protogynous sex change in the presence of the male (Sato et al. 2018). This indicates that a decrease in the interaction with the dominant male is important for the initiation of sex change in the females of both species.

In the case of harem-fission sex change in *C. ferrugata* in nature, it has been observed that when a male begins to dominate the large harem after the conjunction of two harems, it actively engages in social and courtship behaviors toward new females. This results in a decrease in the frequency of social and courtship behaviors toward the largest female of the original harem. They then cease to spawn and starts an aggressive struggle with the males (Sakai 1997). Similarly, during harem-fission sex change in *H. tricolor*, a female that subsequently underwent sex change was observed to hide most of the time to avoid social contact with the dominant male (Hourigan and Kelley 1985).

In aggregating female-type harems of the anthias serranid *P. squamipinnis*, females in large groups undergo sex changes in the presence of dominant males, resulting in the formation of multi-male harem groups, as mentioned above. Sex changers become reproductive males, obtain mating opportunities, and subsequently, turn into single-male groups (Shapiro 1984; Yogo 1985). This situation is identical to the harem-fission sex change regarding the immediate acquisition of mating status in males. Females that subsequently engaged in sex change were observed to hide behind rocky shelters during the mating period and did not spawn (Yogo 1985). Although the detailed conditions of social interactions between females and males are unknown, the attitude of avoiding sexual behaviors from males appears similar to that of harem-fission sex changers in harem angelfish. In addition, the sex ratio threshold hypothesis has been proposed to explain the natural occurrence of sex changers in the harems of *P. squamipinnis* exceeding a certain sex ratio (Shapiro and Lubbock 1980).

In the case of high-density aggregating female-type harems of *D. reticulatus*, harem-fission sex changes were observed in females that did not have spawning opportunities within the local group (Sakanoue and Sakai 2022). These conditions are similar to those promoting harem-fission sex changers in cohabiting female-type harems in terms of the difficulties of males providing adequate social contact with too many females.

Thus, the social conditions in which harem-fission sex change occurs are suggested to have extensive similarities with takeover sex change, in which the dominant male disappears from the harems. Therefore, this type of protogynous sex change in the presence of males can be considered to occur in a condition-dependent manner in fish species, where social control of sex change is normally effective.

4.6.3 Females' Tactics for Faster Acquisition of Sex Change Opportunity

Some protogynous fishes show tactics for the faster acquisition of sex change. It is generally considered that the females that stably settle in male territories in the cohabiting female-type harem fishes can secure the possibility of future sex change via maintaining their social ranks in the local group (Robertson 1974; Moyer and Nakazono 1978; Kuwamura 1984). However, in populations where harems are closely adjacent, females of the cleaner wrasse *L. dimidiatus* may move out of the original harem to a site where they can improve their social rank, which is considered a tactic for faster sex change (Sakai et al. 2001). A total of 24 inter-harem moves by 15 females were identified through a 2.5-year survey. This indicated that subordinate females tended to move to harems where they were higher in rank, whereas dominant females moved to harems where there were no individuals close in size to their body sizes (Sakai et al. 2001). Similar intergroup moving tactics by females have been reported in *T. okinawae* goby harems (Manabe et al. 2007a). Therefore, females do not just wait for an opportunity to change their sex after the loss of dominant individuals.

Yet another example of female refusal to spawn has been reported as a tactic for faster sex change. In harems of the cleaner wrasse, *L. dimidiatus*, and *Centropyge* angelfishes, females of the same size class are territorially exclusive of each other (Fig. 4.1). This territoriality among females is thought to occur because individuals of similar sizes are rivals to future opportunities for sex change. Furthermore, in the case of *C. ferrugata*, it has been reported that females inhabiting close to similar-sized individuals tend to spawn less frequently. Such females with low spawning frequencies grow faster, suggesting that they invest more energy in growth for faster sex change (Sakai 1997; Hamaguchi et al. 2002). This tactic is observed in large harems resulting from the merger of adjacent harems and is considered a preliminary stage of harem-fission sex change.

The rapid growth of females during sex change has been reported in various fish species (Ohnishi 1998; Walker and McCormick 2004; Walker and Ryen 2007; Munday et al. 2009; Sakanoue and Sakai 2022). Fast growth may have resulted from the cessation of spawning, in addition to being released from social control by dominant individuals. To acquire mating territory and females, sex-changing individuals need to grow larger. Earlier growth competition for future sex change opportunities among females should be considered, especially in harem fish with a strong social hierarchy among females.

4.7 Individual-Level Process of Takeover Sex Change After Male Loss

During takeover sex change in protogynous fishes, females are unable to produce gametes and switch over from ovarian to testicular structures. This means that they cannot produce offspring during gonadal sex change. Loss of reproductive opportunity is considered an obligatory cost for sex change. In addition, they switch to sexual behaviors typical of males, including territorial defense and courtship (i.e., behavioral sex change). Furthermore, some species require the development of secondary morphological characteristics in males to obtain mating opportunities (Hoffman et al. 1985; Muñoz and Warner 2003a).

Once the males disappear or are removed from the mating group, gonadal sex change usually lasts from 1 to 4 weeks (Table 4.6). Two types of developmental patterns of the testis are known: inside (undelimited type) and outside (delimited type) the ovary (Sadovy and Shapiro 1987). Species with delimited gonads usually change their sex for a shorter duration (Yamaguchi and Iwasa 2017). Observational surveys of gonadal sex change duration in pelagic spawners have provided fairly accurate values because reproductive behaviors are displayed daily, and the completion of gonadal sex change is directly judged by the fertilization of daily spawned eggs (Nakashima et al. 2000; Sakai et al. 2003b; Table 4.6).

Some demersal egg spawners, such as *F. neophytus*, *Dascyllus aruanus*, and *S. chrysopterus*, have considerably long gonadal sex change durations (Table 4.6). In addition, sexual behaviors seemed to occur close to the day of the completion of gonadal sex change in the cases of *Gobiodon quinquestrigatus*, *T. okinawae*, and *D. reticulatus*, suggesting no precedence of behavioral sex change (Table 4.6). These tendencies, which are different from those of pelagic egg spawners, are partially due to the mating habits exhibiting spawning rhythms following lunar cycles (i.e., tidal conditions), resulting in potential difficulties in confirming the exact timing of the start of behavioral sex change and the completion of gonadal sex change in demersal egg spawners with the cyclic spawning interval.

It has been confirmed that some protogynous sex changers start to exhibit male-type sexual behaviors and spawning behaviors with females before the completion of gonadal sex change, especially in daily pelagic egg spawners (Fig. 4.5; Table 4.6), resulting in unfertilized spawned eggs. The adaptive significance of the faster precedence of behavioral sex change before the completion of gonadal sex change can be explained as a tactic for future mate acquisition (Nakashima et al. 2000). The female also responds to egg release in the usual spawning form with a sex-changing individual if the sexual behavior of the individual is complete (Godwin et al. 1996; Nakashima et al. 2000). If sex changers (i.e., the largest females) do not engage in

Table 4.6 Duration period needed for protogynous sex change after the male disappearance

Family/species	Behavioral sex change		Gonadal sex change	Body coloration change	References
	Courtship (male role)	Spawning (male role)			
Demersal egg spawners					
Gobiidae					
Coryphopterus glaucofraenum			10–20 days		Cole and Shapiro (1992)
Coryphopterus hyalinus			15 days		Cole and Shapiro (1990)
Coryphopterus lipernes			21 days		Cole and Shapiro (1990)
Coryphopterus personatus			9–20 days		Cole and Robertson (1988)
Fusigobius neophytus			<62–70 days		Tsuboi and Sakai (2016)
Gobiodon histrio			<28 days		Munday et al. (1998)
Gobiodon quinquestrigatus	<1 month	1 month	1 month		Nakashima et al. (1996)
Lythrypnus dalli			5.71 ± 1.70 days		Reavis and Grober (1999)
Paragobiodon echinocephalus			24 days		Nakashima et al. (1995)
Trimma okinawae	7 days	12 days	6–14 days		Sunobe and Nakazono (1993)
Pomacentridae					
Dascyllus aruanus			<50–60 days		Coates (1982) and Kuwamura et al. (2016a)
Dascyllus reticulatus	<10 days	10 days	<19 days		Tanaka (1999) and Sakanoue and Sakai (2022)
Balistidae					
Sufflamen chrysopterus	71 days		<90–94 days	9–19 days	Takamoto et al. (2003)
Pelagic egg spawners					
Pinguipedidae					
Parapercis cylindrica	5–11 days		20–31 days	17–24 days	Stroud (1982)
Parapercis snyderi			23 days	10–13 days	Nakazono et al. (1985)
Labridae					
Bodianus rufus		0–10 days	7–10 days		Hoffman et al. (1985)
Halichoeres melanurus	0 day	0 day	2–3 weeks		Sakai et al. (2002)

(continued)

Table 4.6 (continued)

Family/species	Behavioral sex change		Gonadal sex change	Body coloration change	References
	Courtship (male role)	Spawning (male role)			
Iniistius pentadactylus			14 days	14 days	Nemtzov (1985)
Labroides dimidiatus	0 day	0 day	14–18 days		Robertson (1972) and Nakashima et al. (2000)
Macropharyngodon moyeri		<23 days	<23 days		Moyer (1991)
Parajulis poecilopterus	2–11 days		2 weeks	2–6 weeks	Sakai et al. (2007) and Miyake et al. (2012)
Thalassoma bifasciatum	0 day	0 day	8–28 days	8–28 days	Warner and Swearer (1991)
Thalassoma lucasanum			2–6 weeks	2–6 weeks	Warner (1982)
Scaridae					
Sparisoma radians		7–12 days	12–18 days	7–11 days	Muñoz and Warner (2003a)
Serranidae					
Epinephelus coioides			214–298 days		Quinitio et al. (1997)
Epinephelus rivulatus			20–27 days		Mackie (2003)
Pseudoanthias squamipinnis	2–7 days		2–4 weeks	26–53 days	Fishelson (1970) and Shapiro (1981)
Pseudoanthias pleurotaenia	4 days	9 days	18 days		Hioki et al. (2001)
Pomacanthidae					
Apolemichthys trimaculatus		11 days	25 days		Hioki and Suzuki (1995)
Centropyge acanthops	4 days	6 days	8 days		Hioki and Suzuki (1996)
Centropyge bicolor	3 days		<20 days		Aldenhoven (1984)
Centropyge fisheri	2 days	3 days	6 days		Hioki and Suzuki (1996)
Centropyge interruptus	1–7 days		20–39 days	12 days	Moyer and Nakazono (1978)
Centropyge vrolikii	0 day	1–3 days	10–16 days		Sakai et al. (2003b)
Genicanthus bellus	4 days	31–38 days	31–38 days	38 days	Hioki et al. (1995)
	11 days	11 days	11 days	13 days	Suzuki et al. (1979)

(continued)

Table 4.6 (continued)

Family/species	Behavioral sex change Courtship (male role)	Behavioral sex change Spawning (male role)	Gonadal sex change	Body coloration change	References
Genicanthus lamarck					
Genicanthus melanospilos	8–19 days	19 days		12–19 days	Hioki et al. (1982)
Genicanthus watanabei		15 days	25 days		Hioki et al. (1995)

Days, weeks or months from experimental male removal or natural male disappearance from mating groups to the start of behavioral sex change including courtship and spawning as males, to the completion of gonadal sex change (sperm release), and the completion of sexual body color transformation are shown

In behavioral sex change, 0 day means that the behavioral expression was confirmed on the day when the male was removed

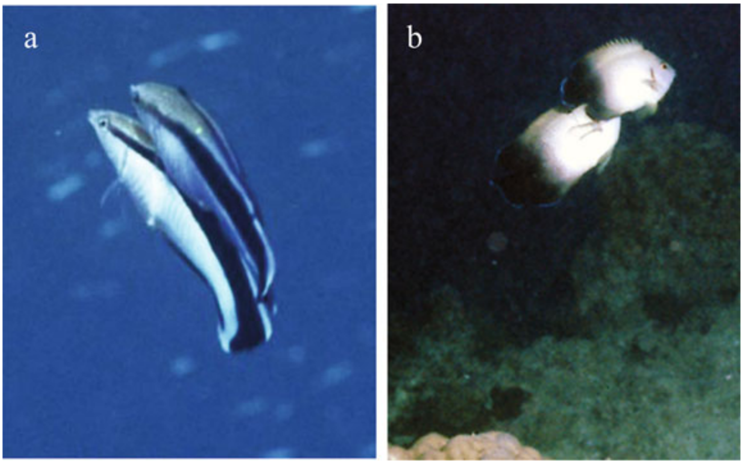

Fig. 4.5 Spawning behaviors by a pair consisting of a sex-changing female and a smaller female in haremic fishes. The largest females of *Labroides dimidiatus* (**a**; above of ascending pair) and *Centropyge vrolikii* (**b**; below of ascending pair) started male sexual behaviors and spawned with subordinate females in the process of gonadal sex change after the dominant male removal (*photos* Tetsuo Kuwamura)

any sexual behavior toward smaller females in the local group during gonadal sex change, then the smaller females will leave the group to look for new mates. Though harem fishes usually maintain stable mating relationships, females may move to other harems (Sakai et al. 2001; Manabe et al. 2007a), or females that are not given the opportunity to spawn may change sex (Moyer and Zaiser 1984; Sakai 1997;

Sakanoue and Sakai 2022). The immediate start of behavioral sex change during gonadal sex change is suggested to play a role in securing mates and smooth takeover of the harem (Nakashima et al. 2000; Sakai et al. 2002, 2003b).

During the male removal experiment in the cleaner wrasse *L. dimidiatus* and the haremic angelfish *C. vrolikii*, ripened females with swollen abdomens quickly initiated male sexual behaviors and spawned in the male role with smaller females of the harem (Nakashima et al. 2000; Sakai et al. 2003b; Fig. 4.5). It was also confirmed that large females of the bluehead wrasse *T. bifasciatum*, whose gonadal tissues had been surgically removed, exhibited male sexual behaviors just after male removal (Godwin et al. 1996). In addition, Nakashima et al. (2000) found that females initiating male sexual behaviors on the day of male removal resumed female-type sexual behaviors immediately after the original dominant males returned to the harem. Therefore, sexual behavior can change within an hour or a few hours. These results suggest that gonadal females can immediately initiate male sexual behaviors. This implies an important role for the brain and neuroendocrine mechanisms in promoting behavioral sex changes. Casas and Saborido-Rey (2021) reviewed environmental cues and endocrinological mechanisms of sex change.

The succession of a sex-changing female to a position after the disappearance of the dominant male (i.e., the effectiveness of takeover sex change) will depend on the mating system and social/environmental conditions. In cases where sex changers have to spend time acquiring mating territories because of competition among males or developing secondary male morphological characteristics to attract females, delays in the start of sexual behaviors by sex changers have been reported. In the case of sex-changing females of the bucktooth parrotfish *S. radians*, the appearance of male coloration is followed by the development of male behavior, which is fully expressed approximately 20 days after the disappearance of the male (Muñoz and Warner 2003a). In the case of the bluehead wrasse *T. bifasciatum*, males initially spent an average of 81 days as non-territorial individuals after changing sex and required more than 32 days to attain territorial status as terminal-phase males (Hoffman et al. 1985). Male removal experiments to induce sexual change have confirmed that the larger the female in *Halichoeres melanurus*, the more is it likely to develop male sexual behavior (Sakai et al. 2002). This suggests that the social status of female individuals, which is related to the ease of acquiring mating territory, determines whether they should exhibit an early onset of sexual behavior.

Recent studies on social cognitive abilities of cleaner wrasse *L. dimidiatus* have confirmed their ability to perceive and recognize a reflected mirror image as self (mirror self-recognition; Kohda et al. 2019, 2022) and their capability of transitive inference, that is, logical prediction from previous information (Hotta et al. 2020). These abilities may contribute to the mechanism of stable maintenance of dominant relationships among harem members, as well as the detection of changes in the social situation of nearby harems, affecting the social control of sex change and the variation in sex change patterns.

4.8 Future Research Directions

The foregoing results presented on the nature of sex change in various protogynous fishes were achieved through the excellent observation skills and persistent efforts of researchers in the empirical and theoretical fields. Field surveys have provided many insights, and various approaches have been developed, such as empirical studies using captive and field experiments and the construction of theoretical systems using mathematical models. We expect that research on fish under natural conditions will continue to contribute to scientific knowledge in the future. Especially, research to confirm the relationship between sex change and mating systems in these fish species is required.

In this chapter, the fish species identified as protogynous were determined based on Kuwamura et al. (2020). However, even among those identified as bidirectional sex changers, many species, such as *Gobiodon* and *Trimma* gobies, often show protogynous sex changes. It has been confirmed that social dominance influences the switch in these sex changers (Sunobe and Nakazono 1993; Nakashima et al. 1996; Munday 2002), and the phenomenon can be understood as an extension of the sex change strategies introduced in this chapter. In addition, it has become clear that many protogynous fishes can reverse sex change in at least 16 species, including *Gobiodon*, *Lythrypnus*, *Paragobiodon*, *Trimma* gobies, *Dascyllus* damselfishes, *Labroides* labrid, *Epinephelus* serranids, *Apolemichthys* and *Centropyge* angelfishes, and *Cirrhitichthys* hawkfishes (Table 4.4). By comparing this with the information on mating systems and life histories accumulated in protogynous fishes, it may be possible to understand the advantages of bidirectional sex change in fish (see Chap. 5 for details).

4.9 Conclusions

In this chapter, the following topics related to protogynous fishes were introduced

1. Numerous protogynous fishes (at least 314 species from 20 families) have been reported through histology, aquarium experiments, and field studies. They form the core of the scientific knowledge related to sex change.
2. The mating system has been documented in 131 protogynous fishes, many of which are polygynous, including harem polygyny (60 species) and MTV polygamy (60 species). This is consistent with the predictions of the SA model, in which the sex-change advantage is explained by sexual differences in the changed characteristics of reproductive success with growth.
3. Histological studies and field surveys have confirmed that two male patterns, monandry (only males derived from females by sex change: secondary males; 89 species) and diandry (coexistence of secondary males and non-sex-changing males called primary males; 37 species), emerge in response to harem polygyny

and MTV polygamy, respectively, and have been linked to the diversity of male mating tactics and the strength of female mate choice. Primary males are also thought to have sexual plasticity as they undergo sex change.

4. Manipulation experiments (57 species) and field observations (11 species) have confirmed that sex changes frequently occur after the loss of the dominant male (a total of 60 species).
5. Field studies and rearing experiments focusing on how sex change occurs have confirmed cases of females changing sex in the presence of males in 18 protogynous species. These include bachelor sex changes, in which a female abandons reproductive function and becomes a bachelor male (9 species), and harem-fission sex changes, in which a sex-changing female takes over part of the original harem (12 species). These tactics are considered to be advantageous for future reproductive success.
6. Studies on the process of protogynous sex change have confirmed that behavioral sex change (i.e., male sexual behavior) often occurs earlier than gonadal change, especially in harem fish. Interspecific differences in the onset of behavioral sex change can be explained in terms of the immediate availability of females and the maintenance of mating territories.
7. It has been observed that protogynous fish (at least 16 species) can revert to females after a sex change (see Chap. 5 for details), indicating potential sexual plasticity.

Acknowledgements I thank Tatsuru Kadota, Tetsuo Kuwamura, Kota Sawada, and Tomoki Sunobe for their helpful comments on improving the manuscript. I also thank Editage (www.editage.jp) for the English language review.

References

Adams S (2003) Morphological ontogeny of the gonad of three plectropomid species through sex differentiation and transition. J Fish Biol 63:22–36

Adreani MS, Allen LG (2008) Mating system and reproductive biology of a temperate wrasse, *Halichoeres semicinctus*. Copeia 2008:467–475

Adreani MS, Erisman BE, Warner RR (2004) Courtship and spawning behavior in the California sheephead, *Semicossyphus pulcher* (Pisces: Labridae). Environ Biol Fishes 71:13–19

Aldenhoven JM (1984) Social organization and sex change in an angelfish, *Centropyge bicolor* on the Great Barrier Reef. PhD dissertation, Macquarie University, North Ryde

Aldenhoven JM (1986) Different reproductive strategies in a sex-changing coral reef fish *Centropyge bicolor* (Pomacanthidae). Aust J Mar Freshw Res 37:353–360

Andrew TG, Buxton CD, Hecht T (1996) Aspects of the reproductive biology of the concha wrasse, *Nelabrichthys ornatus*, at Tristan da Cunha. Environ Biol Fishes 46:139–149

Arellano-Martínez M (1997) Biología reproductiva del ángel rey *Holacanthus passer* Valenciennes, 1864 y del ángel de cortés *Pomacanthus zonipectus* (Gill, 1863) (Teleostei: Pomacanthidae), en la coasta sur-occidental del Golfo de California. México. Master thesis, Instituto Politécnico Nacional, La Paz

Aronov A, Goren M (2008) Ecology of the mottled grouper (*Mycteroperca rubra*) in the eastern Mediterranean. Electron J Ichthyol 2:43–55

Asoh K (2003) Gonadal development and infrequent sex change in a population of the humbug damselfish, *Dascyllus aruanus*, in continuous coral-cover habitat. Mar Biol 142:1207–1218

Asoh K (2004) Gonadal development in the coral reef damselfish *Dascyllus flavicaudus* from Moorea, French Polynesia. Mar Biol 146:167–179

Asoh K (2005a) Frequency of functional sex change in two populations of *Dascyllus melanurus* conforms to a prediction from sex allocation theory. Copeia 2005:732–744

Asoh K (2005b) Gonadal development and diandric protogyny in two populations of *Dascyllus reticulatus* from Madang, Papua New Guinea. J Fish Biol 66:1127–1148

Asoh K, Yoshikawa T (2003) Gonadal development and an indication of functional protogyny in the Indian damselfish (*Dascyllus carneus*). J Zool 260:23–39

Atz JW (1964) Intersexuality in fishes. In: Armstrong CN, Marshall AJ (eds) Intersexuality in vertebrates including man. Academic Press, London, pp 145–232

Baird TA (1988) Female and male territoriality and mating system of the sand tilefish, *Malacanthus plumieri*. Environ Biol Fishes 22:101–116

Bell LJ (1983) Aspects of the reproductive biology of the wrasse, *Cirrhilabrus temminckii*, at Miyake-jima, Japan. Jpn J Ichthyol 30:158–167

Bentivegna F, Rasotto MB (1987) Protogynous hermaphroditism in *Xyrichthys novacula* (L. 1758). Cybium 3:75–78

Black MP, Moore B, Canario AVM, Ford D, Reavis RH, Grober MS (2005) Reproduction in context: field testing a laboratory model of socially controlled sex change in *Lythrypnus dalli* (Gilbert). J Exp Mar Biol Ecol 318:127–143

Brulé T, Caballero-Arango D, Renán X, Colás-Marrufo T (2015) Confirmation of functional hermaphroditism in six grouper species (Epinephelidae: Epinephelinae) from the Gulf of Mexico. Cybium 40:83–92

Carlson BA (1982) The masked angelfish *Genicanthus personatus* Randall 1974. Freshw Mar Aquar 5:31–32

Casas L, Saborido-Rey F (2021) Environmental cues and mechanisms underpinning sex change in fish. Sex Dev 15(1–3):108–121. https://doi.org/10.1159/00515274

Charnov EL (1982) The theory of sex allocation. Princeton University Press, Princeton

Chen J, Xiao L, Peng C, Ye Z, Wang D, Yang Y, Zhang H, Zhao M, Li S, Lin H, Zhang Y (2019) Socially controlled male-to-female sex reversal in the protogynous orange-spotted grouper, *Epinephelus coioides*. J Fish Biol 94:414–421

Chen J, Chen H, Peng C, Ye Z, Zhao M, Xiao L, Zhang H, Li S, Lin H, Zhang Y (2020) A highly efficient method of inducing sex change using social control in the protogynous orange-spotted grouper (*Epinephelus coioides*). Aquaculture 517:734787

Chen J, Peng C, Huang J, Shi H, Xiao L, Tang L, Lin H, Li S, Zhang Y (2021) Physical interactions facilitate sex change in the protogynous orange-spotted grouper, *Epinephelus coioides*. J Fish Biol 98:1308–1320

Choat JH, Robertson DR (1975) Protogynous hermaphroditism in fishes of the family Scaridae. In: Reinboth R (ed) Intersexuality in the animal kingdom. Springer, New York, pp 263–283

Clark E (1983) Sand-diving behavior and territoriality of the red sea razorfish, *Xyrichtys pentadactylus*. Bull Inst Oceanogr Fish Cairo 9:225–242

Clark E, Pohle M, Rabin J (1991) Stability and flexibility through community dynamics of the spotted sandperch. Natl Geogr Res Explor 7:138–155

Clavijo IE (1983) Pair spawning and formation of a lek-like mating system in the parrotfish *Scarus vetula*. Copeia 1983:253–256

Clavijo IE, Donaldson PL (1994) Spawning behavior in the labrid, *Halichoeres bivittatus*, on artificial and natural substrates in Onslow Bay, North Carolina, with notes on early life history. Bull Mar Sci 55:383–387

Claydon J (2004) Spawning aggregations of coral reef fishes: characteristics, hypotheses, threats and management. Oceanogr Mar Biol Annu Rev 42:265–302

Claydon JAB (2005) The structure and dynamics of spawning aggregations of coral reef fish. PhD dissertation, James Cook University, Townsville

Coates D (1982) Some observations on the sexuality of humbug damselfish, *Dascyllus aruanus* (Pisces, Pomacentridae) in the field. Z Tierpsychol 59:7–18

Cole KS (1983) Protogynous hermaphroditism in a temperate zone territorial marine goby, *Coryphopterus nicholsi*. Copeia 1983:809–812

Cole KS (1990) Patterns of gonad structure in hermaphroditic gobies (Teleostei Gobiidae). Environ Biol Fishes 28:125–142

Cole KS (2002) Gonad morphology, sexual development, and colony composition in the obligate coral-dwelling damselfish *Dascyllus aruanus*. Mar Biol 140:151–163

Cole KS, Hoese DF (2001) Gonad morphology, colony demography and evidence for hermaphroditism in *Gobiodon okinawae* (Teleostei, Gobiidae). Environ Biol Fishes 61:161–173

Cole KS, Robertson DR (1988) Protogyny in the Caribbean reef goby, *Coryphopterus personatus*: gonad ontogeny and social influences on sex-change. Bull Mar Sci 42:317–333

Cole KS, Shapiro DY (1990) Gonad structure and hermaphroditism in the gobiid genus *Coryphopterus* (Teleostei: Gobiidae). Copeia 1990:996–1003

Cole KS, Shapiro DY (1992) Gonadal structure and population characteristics of the protogynous goby *Coryphopterus glaucofraenum*. Mar Biol 113:1–9

Colin PL (1978) Daily and summer-winter variation in mass spawning of the striped parrotfish, *Scarus croicensis*. Fish Bull 76:117–124

Colin PL (1982) Spawning and larval development of the hogfish, *Lachnolaimus maximus* (Pisces: Labridae). Fish Bull 80:853–862

Colin PL (2010) Aggregation and spawning of the humphead wrasse *Cheilinus undulatus* (Pisces: Labridae): general aspects of spawning behaviour. J Fish Biol 76:987–1007

Colin PL, Bell LJ (1991) Aspects of the spawning of labrid and scarid fishes (Pisces: Labroidei) at Enewetak Atoll, Marshall Islands with notes on other families. Environ Biol Fishes 3:229–260

Craig PC (1998) Temporal spawning patterns of several surgeon fishes and wrasses in American Samoa. Pac Sci 52:35–39

Donaldson TJ (1987) Social organization and reproductive behavior of the hawkfish *Cirrhitichthys falco* (Cirrhitidae). Bull Mar Sci 41:531–540

Donaldson TJ (1989) Facultative monogamy in obligate coral-dwelling hawkfishes (Cirrhitidae). Environ Biol Fishes 26:295–302

Donaldson TJ (1990) Reproductive behavior and social organization of some Pacific hawkfishes (Cirrhitidae). Jpn J Ichthyol 36:439–458

Donaldson TJ (1995) Courtship and spawning of nine species of wrasses (Labridae) from the Western Pacific. Jpn J Ichthyol 42:311–319

Erisman BE, Craig MT, Hastings PA (2009) A phylogenetic test of the size-advantage model: evolutionary changes in mating behavior influence the loss of sex change in a fish lineage. Am Nat 174:E83–E99

Erisman BE, Craig MT, Hastings PA (2010) Reproductive biology of the Panama graysby *Cephalopholis panamensis* (Teleostei: Epinephelidae). J Fish Biol 76:1312–1328

Fishelson L (1970) Protogynous sex reversal in the fish *Anthias squamipinnis* (Teleostei, Anthiidae) regulated by the presence or absence of a male fish. Nature 227:90–91

Forrester G, Harmon L, Helyer J, Holden W, Karis R (2011) Experimental evidence for density-dependent reproductive output in a coral reef fish. Popul Ecol 53:155–163

Fricke HW (1980) Control of different mating systems in a coral reef fish by one environmental factor. Anim Behav 28:561–569

Fricke HW, Holzberg S (1974) Social units and hermaphroditism in a pomacentrid fish. Naturwissenschaften 61:367–368

Fukui Y, Gushima K, Kakuda S, Hashimoto H (1991) Growth-related changes in color and sex in *Halichoeres poecilopterus*. Jpn J Ichthyol 37:395–401

García-Cagide A, García T (1996) Reproducción de *Mycteroperca bonaci* y *Mycteroperca venenosa* (Pisces: Serranidae) en la plataforma Cubana. Rev Biol Trop 44:771–780

Gilmore RG, Jones RS (1992) Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode & Bean) and *M. phenax* (Jordan & Swain). Bull Mar Sci 51: 83–103

Godwin J (1995) Phylogenetic and habitat influences on mating system structure in the humbug damselfishes (*Dascyllus*, Pomacentridae). Bull Mar Sci 57:637–652

Godwin J, Crews D, Warner RR (1996) Behavioural sex change in the absence of gonads in a coral reef fish. Proc R Soc Lond B 263:1683–1688

Gust N (2004) Variation in the population biology of protogynous coral reef fishes over tens of kilometres. Can J Fish Aquat Sci 61:205–218

Hamaguchi Y, Sakai Y, Takasu F, Shigesada N (2002) Modeling spawning strategy for sex change under social control in haremic angelfishes. Behav Ecol 13:75–82

Harris PJ, Wyanski DM, White DB, Moore JL (2002) Age, growth, and reproduction of scamp, *Mycteroperca phenax*, in the southwestern North Atlantic, 1979–1997. Bull Mar Sci 70:113–132

Hioki S (2002) Sexuality in angelfishes of the genus *Centropyge* (Teleostei, Pomacanthidae) with special reference to gonadal structure and subgeneric relationship. Sci Rep Mus Tokai Univ 4: 37–43

Hioki S, Suzuki K (1995) Spawning behavior, eggs, larvae, and hermaphroditism of the angelfish, *Apolemichthys trimaculatus*, in captivity. Bull Inst Ocean Res Dev Tokai Univ 16:13–22

Hioki S, Suzuki K (1996) Sex changing from male to female on the way of protogynous process in three *Centropyge* angelfishes (Pomacanthidae: Teleostei). Bull Inst Ocean Res Dev Tokai Univ 17:27–34

Hioki S, Suzuki K, Tanaka Y (1982) Spawning behavior, egg and larval development, and sex succession of the hermaphroditic pomacanthine, *Genicanthus melanospilos*, in the aquarium. J Fac Mar Sci Tech Tokai Univ 15:359–366

Hioki S, Tanaka Y, Suzuki K (1995) Reproductive behavior, eggs, larvae, and sexuality of two angelfishes, *Genicanthus watanabei* and *G. bellus*, in an aquarium. J Fac Mar Sci Tech Tokai Univ 40:151–171

Hioki S, Oyama T, Yoshinaka A (2001) Reproductive behavior, eggs, larvae, and sexuality in the anthiine fish, *Pseudoanthias pleurotaenia* (Serranidae; Teleostei), in the aquarium. Sci Rep Mus Tokai Univ 3:19–27

Hodge J, Santini F, Wainwright PC (2020) Correlated evolution of sex allocation and mating system in wrasses and parrotfishes. Am Nat 196:57–73

Hoffman SG (1983) Sex-related foraging behavior in sequentially hermaphroditic hogfishes (*Bodianus* spp.). Ecology 64:798–808

Hoffman SG (1985) Effects of size and sex on the social organization of reef-associated hogfishes, *Bodianus* spp. Environ Biol Fishes 14:185–197

Hoffman SG, Schildhauer MP, Warner RR (1985) The costs of changing sex and the ontogeny of males under contest competition for mates. Evolution 39:915–927

Hotta T, Ueno K, Hataji Y, Kuroshima H, Fujita K, Kohda M (2020) Transitive inference in cleaner wrasses (*Labroides dimidiatus*). PLoS One 15(8):e0237817

Hourigan TF (1986) A comparison of haremic social systems in two reef fishes. In: Dickamer LC (ed) Behavioral ecology and population biology, readings from the 19th International Ethological Conference. Privat, Toulouse, pp 23–28

Hourigan TF, Kelley CD (1985) Histology of the gonads and observations on the social behavior of the Caribbean angelfish *Holacanthus tricolor*. Mar Biol 88:311–322

Hubble M (2003) The ecological significance of body size in tropical wrasses (Pisces: Labridae). PhD dissertation, James Cook University, Townsville

Ishihara M, Kuwamura T (1996) Bigamy or monogamy with maternal egg care in the triggerfish, *Sufflamen chrysopterus*. Ichthyol Res 43:307–313

Iwasa Y (1991) Sex change evolution and cost of reproduction. Behav Ecol 2:56–68

Jones GP (1980) Growth and reproduction in the protogynous hermaphrodite *Pseudolabrus celidotus* (Pisces: Labridae) in New Zealand. Copeia 1980:660–675

Jones GP (1981) Spawning-site choice by female *Pseudolabrus celidotus* (Pisces: Labridae) and its influence on the mating system. Behav Ecol Sociobiol 8:129–114

Kadota T, Osato J, Hashimoto H, Sakai Y (2011) Harem structure and female territoriality in the dwarf hawkfish *Cirrhitichthys falco* (Cirrhitidae). Environ Biol Fishes 92:79–88

Kadota T, Osato J, Nagata K, Sakai Y (2012) Reversed sex change in the haremic protogynous hawkfish *Cirrhitichthys falco* in natural conditions. Ethology 118:226–234

Karino K, Kuwamura T, Nakashima Y, Sakai Y (2000) Predation risk and the opportunity for female mate choice in a coral reef fish. J Ethol 18:109–114

Kimura S, Kiriyama T (1992) Natural spawning of the labrid fish, *Halichoeres poecilopterus* in a tank. Suisanzoushoku 40:81–85

Kline RJ, Khan IA, Holt GJ (2011) Behavior, color change and time for sexual inversion in the protogynous grouper (*Epinephelus adscensionis*). PLoS One 6(5):e19576

Kobayashi K, Suzuki K (1992) Hermaphroditism and sexual function in *Cirrhitichthys aureus* and the other Japanese hawkfishes (Cirrhitidae: Teleostei). Jpn J Ichthyol 38:397–410

Kohda M, Sasaki K, Sakai Y, Ohnishi N, Matsumoto K (2005) Preliminary study on female choice of mates versus sites in a wrasse, *Cirrhilabrus temminckii*. Ichthyol Res 52:406–409

Kohda M, Hotta T, Takeyama T, Awata S, Tanaka H, Asai J, Jordan AL (2019) If a fish can pass the mark test, what are the implications for consciousness and self-awareness testing in animals? PLoS Biol 17(2):e3000021

Kohda M, Sogawa S, Jordan AL, Kubo N, Awata S, Satoh S, Kobayashi T, Fujita A, Bshary R (2022) Further evidence for the capacity of mirror self-recognition in cleaner fish and the significance of ecologically relevant marks. PLoS Biol 20(2):e3001529

Kuwamura T (1984) Social structure of the protogynous fish *Labroides dimidiatus*. Publ Seto Mar Biol Lab 29:117–177

Kuwamura T (1997) The evolution of parental care and mating systems among Tanganyikan cichlids. In: Kawanabe H, Hori M, Nagoshi M (eds) Fish communities in Lake Tanganyika. Kyoto University Press, Kyoto, pp 57–86

Kuwamura T, Nakashimn Y, Yogo Y (1994) Sex change in either direction by growth-rate advantage in the monogamous coral goby, *Paragobiodon echinocephalus*. Behav Ecol 5:434–438

Kuwamura T, Karino K, Nakashima Y (2000) Male morphological characteristics and mating success in a protogynous coral reef fish, *Halichoeres melanurus*. J Ethol 18:17–23

Kuwamura T, Tanaka N, Nakashima Y, Karino K, Sakai Y (2002) Reversed sex-change in the protogynous reef fish *Labroides dimidiatus*. Ethology 108:443–450

Kuwamura T, Suzuki S, Tanaka N, Ouchi E, Karino K, Nakashima Y (2007) Sex change of primary males in a diandric labrid *Halichoeres trimaculatus*: coexistence of protandry and protogyny within a species. J Fish Biol 70:1898–1906

Kuwamura T, Sagawa T, Suzuki S (2009) Interspecific variation in spawning time and male mating tactics of the parrotfishes on a fringing coral reef at Iriomote Island, Okinawa. Ichthyol Res 56:354–362

Kuwamura T, Suzuki S, Kadota T (2011) Reversed sex change by widowed males in polygynous and protogynous fishes: female removal experiments in the field. Naturwissenschaften 98:1041–1048

Kuwamura T, Suzuki S, Kadota T (2016a) Male-to-female sex change in widowed males of the protogynous damselfish *Dascyllus aruanus*. J Ethol 34:85–88

Kuwamura T, Suzuki S, Kadota T (2016b) Interspecific variation in the spawning time of labrid fish on a fringing reef at Iriomote Island, Okinawa. Ichthyol Res 63:460–469

Kuwamura T, Sunobe T, Sakai Y, Kadota T, Sawada K (2020) Hermaphroditism in fishes: an annotated list of species, phylogeny, and mating system. Ichthyol Res 67:341–360

Lassig BR (1976) Field observations on the reproductive behaviour of *Paragobiodon* spp. (Osteichthyes: Gobiidae) at Heron Island Great Barrier Reef. Mar Behav Physiol 3:283–293

Lassig BR (1977) Socioecological strategies adopted by obligate coral-dwelling fishes. In: Proceedings of the 3rd International Coral Reef Symposium. University of Miami, Miami, pp 565–570

Lejeune P (1987) The effect of local stock density on social behavior and sex change in the Mediterranean labrid *Coris julis*. Environ Biol Fishes 18:135–141

Liu M, Sadovy Y (2004) The influence of social factors on adult sex change and juvenile sexual differentiation in a diandric, protogynous epinepheline, *Cephalopholis boenak* (Pisces, Serranidae). J Zool 264:239–248

Lobel PS (1978) Diel, lunar, and seasonal periodicity in the reproductive behavior of the pomacanthud fish, *Centropyge potteri*, and some other reef fishes in Hawaii. Pac Sci 32:193–207

Lodi E (1980) Sex inversion in domesticated strains of the swordtail *Xiphophorus helleri* Heckel (Pisces, Osteichthyes). Bull Zool 47:1–8

Lorenzi V, Earley R, Grober M (2006) Preventing behavioural interactions with a male facilitates sex change in female bluebanded gobies, *Lythrypnus dalli*. Behav Ecol Sociobiol 59:715–722

Lutnesky MMF (1994) Density-dependent protogynous sex change in territorial-haremic fishes: models and evidence. Behav Ecol 5:375–383

Lutnesky MMF (1996) Size-dependent rate of protogynous sex change in the pomacanthid angelfish, *Centropyge potteri*. Copeia 1996:209–212

Mackie MC (2003a) Socially controlled sex-change in the half-moon grouper, *Epinephelus rivulatus*, at Ningaloo Reef, Western Australia. Coral Reefs 22:133–142

Manabe H, Ishimura M, Shinomiya A, Sunobe T (2007a) Inter-group movement of females of the polygynous gobiid fish *Trimma okinawae* in relation to timing of protogynous sex change. J Ethol 25:133–137

Manabe H, Ishimura M, Shinomiya A, Sunobe T (2007b) Field evidence for bi-directional sex change in the polygynous gobiid fish *Trimma okinawae*. J Fish Biol 70:600–609

Marconato A, Tessari V, Marin G (1995) The mating system of *Xyrichthys novacula*: sperm economy and fertilization success. J Fish Biol 47:292–301

Matsumoto S, Takeyama T, Ohnishi N, Kohda M (2011) Mating system and size advantage of male mating in the protogynous swamp eel *Monopterus albus* with paternal care. Zool Sci 28:360–367

McBride RS, Johnson MR (2007) Sexual development and reproductive seasonality of hogfish (Labridae: *Lachnolaimus maximus*), an hermaphroditic reef fish. J Fish Biol 71:1270–1292

Meyer KA (1977) Reproductive behavior and patterns of sexuality in the Japanese labrid fish *Thalassoma cupido*. Jpn J Ichthyol 24:101–112

Miyake Y, Fukui Y, Kuniyoshi H, Sakai Y, Hashimoto H (2008) Examination of the ability of gonadal sex change in primary males of the diandric wrasses *Halichoeres poecilopterus* and *Halichoeres tenuispinus*: estrogen implantation experiments. Zool Sci 25:220–224

Miyake Y, Nishigakiuchi J, Sakai Y, Kuniyoshi H (2012) Ovarian degeneration during the female-to-male sex change in the protogynous hermaphroditic fish, *Halichoeres poecilopterus*. Ichthyol Res 59:276–281

Moyer JT (1984) Reproductive behavior and social organization of the pomacanthid fish *Genicanthus lamarck* at Mactan Island, Philippines. Copeia 1984:194–200

Moyer JT (1987) Social organization and protogynous hermaphroditism in marine angelfishes (Pomacanthidae). In: Nakazono A, Kuwamura T (eds) Sex change in fishes. Tokai University Press, Tokyo, pp 120–147

Moyer JT (1990) Social and reproductive behavior of *Chaetodontoplus mesoleucus* (Pomacanthidae) at Bantayan Island, Philippines, with notes on pomacanthid relationships. Jpn J Ichthyol 36:459–467

Moyer JT (1991) Comparative mating strategies of labrid fishes. Watanabe Ichthyol Inst Monogr 1: 1–90

Moyer JT, Nakazono A (1978) Population structure, reproductive behavior and protogynous hermaphroditism in the angelfish *Centropyge interruptus* at Miyake-jima, Japan. Jpn J Ichthyol 25:25–39

Moyer JT, Yogo Y (1982) The lek-like mating system of *Halichoeres melanochir* (Pisces: Labridae) at Miyake-jima, Japan. Z Tierpsychol 60:209–226

Moyer JT, Zaiser MJ (1984) Early sex change: a possible mating strategy of *Centropyge* angelfishes (Pisces: Pomacanthidae). J Ethol 2:63–67

Moyer JT, Thresher RE, Colin PL (1983) Courtship, spawning and inferred social organization of American angelfishes (genera *Pomacanthus*, *Holacanthus* and *Centropyge*; Pomacanthidae). Environ Biol Fishes 9:25–39

Munday PL (2002) Bi-directional sex change: testing the growth-rate advantage model. Behav Ecol Sociobiol 52:247–254

Munday PL, Caley MJ, Jones GP (1998) Bi-directional sex change in a coral-dwelling goby. Behav Ecol Sociobiol 43:371–377

Munday PL, Buston PM, Warner RR (2006a) Diversity and flexibility of sex-change strategies in animals. Trends Ecol Evol 21:89–95

Munday PL, Cardoni AM, Syms C (2006b) Cooperative growth regulation in coral-dwelling fishes. Biol Lett 2:355–358

Munday PL, White JW, Warner RR (2006c) A social basis for the development of primary males in a sex-changing fish. Proc R Soc B 273:2845–2851

Munday PL, Ryen CA, McCormick MI, Walker SPW (2009) Growth acceleration, behavior and otolith check marks associated with sex change in the wrasse *Halichoeres miniatus*. Coral Reefs 28:623–634

Muñoz RC, Warner RR (2003a) Alternative contexts of sex change with social control in the bucktooth parrotfish, *Sparisoma radians*. Environ Biol Fishes 68:307–319

Muñoz RC, Warner RR (2003b) A new version of the size-advantage hypothesis for sex changer: incorporating sperm competition and size-fecundity skew. Am Nat 161:749–761

Muñoz RC, Warner RR (2004) Testing a new version of the size-advantage hypothesis for sex change: sperm competition and size-skew effects in the bucktooth parrotfish, *Sparisoma radians*. Behav Ecol 15:129–136

Nakashima Y, Kuwamura T, Yogo Y (1995) Why be a both-ways sex changer? Ethology 101:301–307

Nakashima Y, Kuwamura T, Yogo Y (1996) Both-ways sex change in monogamous coral gobies, *Gobiodon* spp. Environ Biol Fishes 46:281–288

Nakashima Y, Sakai Y, Karino K, Kuwamura T (2000) Female–female spawning and sex change in a haremic coral-reef fish, *Labroides dimidiatus*. Zool Sci 17:967–970

Nakazono A (1979) Studies on the sexual reversal and spawning behavior of five species of Japanese labrid fishes. Rep Fish Res Lab Kyushu Univ 4:1–64

Nakazono A, Nakatani H, Tsukahara H (1985) Reproductive ecology of the Japanese reef fish, *Parapercis snyderi*. In: Proceedings of the 5th International Coral Reef Congress, Tahiti, vol 5. ICRC, Tahiti, pp 355–360

Nanami A, Sato T, Ohta I, Akita Y, Suzuki N (2013) Preliminary observations of spawning behavior of white-streaked grouper (*Epinephelus ongus*) in an Okinawan coral reef. Ichthyol Res 60:380–385

Nelson JS, Grande TC, Wilson MVH (2016) Fishes of the world, 5th edn. Wiley, New York

Nemeth RS, Blondeau J, Herzlieb S, Kadison E (2007) Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. Environ Biol Fishes 78:365–381

Nemtzov SC (1985) Social control of sex change in the Red Sea razorfish *Xyrichtys pentadactylus* (Teleostei, Labridae). Environ Biol Fishes 14:199–211

Ohnishi N (1998) Studies on the life history and the reproductive ecology of the polygynous sandperch *Parapercis snyderi.* Doctoral dissertation, Osaka City University, Osaka

Ohnishi N, Yanagisawa Y, Kohda M (1997) Sneaking by harem masters of the sandperch, *Parapercis snyderi*. Environ Biol Fishes 50:217–223

Ohta K (1987) Study on life history and sex change in a haremic protogynous sandperch, *Parapercis snyderi*. Bull Biol Soc Hiroshima Univ 53:11–19

Ohta I, Ebisawa A (2015) Reproductive biology and spawning aggregation fishing of the white-streaked grouper, *Epinephelus ongus*, associated with seasonal and lunar cycles. Environ Biol Fishes 98:1555–1570

Okumura S (2001) Evidence of sex reversal towards both directions in reared red spotted grouper *Epinephelus akaara*. Fish Sci 67:535–537

Pears R, Choat JH, Mapstone BD, Beggs GA (2007) Reproductive biology of a large, aggregation-spawning serranid, *Epinephelus fuscoguttatus* (Forskål): management implications. J Fish Biol 71:795–817

Quinitio GF, Caberoy NB, Reyes DM (1997) Induction of sex change in female *Epinephelus coioides* by social control. Isr J Aquac 49:77–83

Reavis RH, Grober MS (1999) An integrative approach to sex change: social, behavioural and neurochemical changes in *Lythrypnus dalli* (Pisces). Acta Ethol 2:51–60

Reinboth R (1970) Intersexuality in fishes. Mem Soc Endocrinol 18:515–543

Reinboth R (1973) Dualistic reproductive behavior in the protogynous wrasse *Thalassoma bifasciatum* and some observations on its day-night changeover. Helgoländer wiss Meeresunters 24:174–191

Robertson DR (1972) Social control of sex reversal in a coral-reef fish. Science 177:1007–1009

Robertson DR (1974) A study of the ethology and reproductive biology of the labrid fish, *Labroides dimidiatus*, at Heron Island, Great Barrier Reef. PhD dissertation, University of Queensland, Brisbane

Robertson DR (1981) The social and mating systems of two labrid fishes, *Halichoeres maculipinna* and *H. garnoti*, off the Caribbean coast of Panama. Mar Biol 64:327–340

Robertson DR (1983) On the spawning behavior and spawning cycles of eight surgeonfishes (Acanthuridae) from the Indo-Pacific. Environ Biol Fishes 9:193–223

Robertson DR, Choat JH (1974) Protogynous hermaphroditism and social systems in labrid fish. In: Proceedings of the 2nd International Coral Reef Symposium, vol 1. Smithsonian Tropical Research Institute, Panama City, pp 217–224

Robertson DR, Hoffman SG (1977) The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. Z Tierpsychol 45:298–320

Robertson DR, Warner RR (1978) Sexual patterns in the labroid fishes of the western Caribbean, II: the parrotfishes (Scaridae). Smithson Contr Zool 255:1–26

Robertson DR, Reinboth R, Bruce RW (1982) Gonochorism, protogynous sex-change and spawning in three sparisomatinine parrotfishes from the western Indian Ocean. Bull Mar Sci 32:868–879

Ross RM (1982) Sex change in the endemic Hawaiian labrid *Thalassoma duperrey* (Quoy and Gaimard): a behavioral and ecological analysis. PhD dissertation, University of Hawaii, Honolulu

Ross RM, Losey GS, Diamond M (1983) Sex change in a coral-reef fish: dependence of stimulation and inhibition on relative size. Science 221:574–575

Sadovy de Mitcheson Y, Liu M, Suharti S (2010) Gonadal development in a giant threatened reef fish, the humphead wrasse *Cheilinus undulatus*, and its relationship to international trade. J Fish Biol 77:706–718

Sadovy Y, Donaldson TJ (1995) Sexual pattern of *Neocirrhites armatus* (Cirrhitidae) with notes on other hawkfish species. Environ Biol Fishes 42:143–150

Sadovy Y, Shapiro DY (1987) Criteria for the diagnosis of hermaphroditism in fishes. Copeia 1987: 136–156

Sadovy Y, Rosario A, Román A (1994) Reproduction in an aggregating grouper, the red hind, *Epinephelus guttatus*. Environ Biol Fishes 41:269–286

Sakai Y (1997) Alternative spawning tactics of female angelfish according to two different contexts of sex change. Behav Ecol 8:372–377

Sakai Y, Kohda M (1997) Harem structure of the protogynous angelfish, *Centropyge ferrugatus* (Pomacanthidae). Environ Biol Fishes 49:333–339

Sakai Y, Kohda M, Kuwamura T (2001) Effect of changing harem on timing of sex change in female cleaner fish *Labroides dimidiatus*. Anim Behav 62:251–257

Sakai Y, Karino K, Nakashima Y, Kuwamura T (2002) Status-dependent behavioural sex change in a polygynous coral-reef fish, *Halichoeres melanurus*. J Ethol 20:101–105

Sakai Y, Karino K, Kuwamura T, Nakashima Y, Maruo Y (2003a) Sexually dichromatic protogynous angelfish *Centropyge ferrugata* (Pomacanthidae) males can change back to females. Zool Sci 20:627–633

Sakai Y, Tsujimura C, Nakata Y, Tanabe H, Maejima G (2003b) Rapid transition in sexual behaviors during protogynous sex change in the haremic angelfish *Centropyge vroliki* (Pomacanthidae). Ichthyol Res 50:30–35

Sakai Y, Kuniyoshi H, Yoshida M, Fukui Y, Hashimoto H, Gushima K (2007) Social control of terminal phase transition in primary males of the diandric wrasse, *Halichoeres poecilopterus* (Pisces: Labridae). J Ethol 25:57–61

Sakanoue R, Sakai Y (2019) Dual social structures in harem-like colony groups of the coral-dwelling damselfish *Dascyllus reticulatus* depending on body size and sheltering coral structures. J Ethol 37:175–186

Sakanoue R, Sakai Y (2022) Cryptic bachelor sex change in harem colonial groups of the coral-dwelling damselfish *Dascyllus reticulatus*. J Ethol 40:181–192

Salinas-de-León P, Rastoin E, Acuña-Marrero D (2015) First record of a spawning aggregation for the tropical eastern Pacific endemic grouper *Mycteroperca olfax* in the Galapagos marine reserve. J Fish Biol 87:179–186

Samoilys MA, Squire LC (1994) Preliminary observations on the spawning behavior of coral trout *Plectropomus leopardus* (Pisces: Serranidae), on the Great Barrier Reef. Bull Mar Sci 54:332–342

Sancho G, Solow AR, Lobel P (2000) Environmental influences on the diel timing of spawning in coral reef fishes. Mar Ecol Prog Ser 206:193–212

Sato T, Kobayashi M, Takebe T, Hirai N, Okuzawa K, Sawaguchi S, Matsubara T, Yamaguchi T, Shinoda R, Koiso M, Teruya K (2018) Induction of female-to-male sex change in a large protogynous fish, *Choerodon schoenleinii*. Mar Ecol 39:e12484

Schärer MT, Nemeth MI, Mann D, Locascio J, Appeldoorn RS, Rowell TJ (2012) Sound production and reproductive behavior of yellowfin grouper, *Mycteroperca venenosa* (Serranidae) at a spawning aggregation. Copeia 2012:135–144

Schemmel EM, Donovan MK, Wiggins C, Anzivino M, Friedlander AM (2016) Reproductive life history of the introduced peacock grouper *Cephalopholis argus* in Hawaii. J Fish Biol 89:1271–1284

Seki S, Kohda M, Takamoto G, Karino K, Nakashima Y, Kuwamura T (2009) Female defense polygyny in the territorial triggerfish *Sufflamen chrysopterum*. J Ethol 27:215–220

Shapiro DY (1977) The structure and growth of social groups of the hermaphroditic fish *Anthias squamipinnis* (Peters). In: Proceedings of the 3rd international coral reef symposium. University of Miami, Miami, pp 571–577

Shapiro DY (1981) Size, maturation and the social control of sex reversal in the coral reef fish *Anthias squamipinnis*. J Zool 193:105–128

Shapiro DY (1984) Sex reversal and sociodemographic processes in coral reef fishes. In: Potts GW, Wootton RJ (eds) Fish reproduction: strategies and tactics. Academic Press, London, pp 103–118

Shapiro DY, Boulon RH Jr (1982) The influence of females on the initiation of female to male sex change in a coral reef fish. Horm Behav 16:66–75

Shapiro DY, Lubbock R (1980) Group sex ratio and sex reversal. J Theor Biol 82:411–426

Shapiro DY, Garcia-Moliner G, Sadovy Y (1994) Social system of an inshore stock of the red hind grouper, *Epinephelus guttatus* (Pisces: Serranidae). Environ Biol Fishes 41:415–422

Shibuno T, Gushima K, Kakuda S (1993) Female spawning migrations of the protogynous wrasse, *Halichoeres marginatus*. Jpn J Ichthyol 39:357–362

Shibuno T, Chiba I, Hashimoto H, Gushima K (1994a) Reproductive behavior of the wrasse, *Thalassoma lutescens*, at Kuchierabu-jima. J Fac Appl Biol Sci Hiroshima Univ 33:43–50

Shibuno T, Ogata S, Hashimoto H, Gushima K (1994b) Reproductive behavior of the parrotfish, *Calotomus japonicus*, at Kuchierabu-jima. J Fac Appl Biol Sci Hiroshima Univ 33:37–41

Shimizu S, Endo S, Kihara S, Sunobe T (2022) Size, age, and social control of protogynous sex change in the labrid fish *Pteragogus aurigarius*. Ichthyol Res 69:75–81

Shpigel M, Fishelson L (1986) Behavior and physiology of coexistence in two species of *Dascyllus* (Pomacentridae, Teleostei). Environ Biol Fishes 17:253–265

Shpigel M, Fishelson L (1991) Territoriality and associated behaviour in three species of the genus *Cephalopholis* (Pisces: Serranidae) in the Gulf of Aqaba, Red Sea. J Fish Biol 38:887–896

St. Mary CM (1994) Sex allocation in a simultaneous hermaphrodite, the blue-banded goby (*Lythrypnus dalli*): the effects of body size and behavioral gender and the consequences for reproduction. Behav Ecol 5:304–313

Stauffer JR Jr, Ruffing RA (2008) Behaviorally induced sex reversal of *Metriaclima* cf. *livingstoni* (Cichlidae) from Lake Malawi. Copeia 2008:618–620

Stroud GJ (1982) The taxonomy and biology of fishes of the genus *Parapercis* (Teleostei: Mugiloididae) in Great Barrier Reef waters. PhD dissertation. James Cook University, Townsville

Sunobe T, Nakazono A (1990) Polygynous mating system of *Trimma okinawae* (Pisces: Gobiidae) at Kagoshima, Japan with a note of sex change. Ethology 84:133–143

Sunobe T, Nakazono A (1993) Sex change in both directions by alteration of social dominance in *Trimma okinawae* (Pisces: Gobiidae). Ethology 94:339–345

Suzuki K, Hioki S, Tanaka Y, Iwasa K (1979) Spawning behavior, eggs, larvae, and sex reversal of two pomacanthine fishes, *Genicanthus lamarck*, and *G. semifasciatus*, in the aquarium. J Fac Mar Sci Tech Tokai Univ 12:149–165

Suzuki S, Toguchi K, Makino Y, Kuwamura T, Nakashima Y, Karino K (2008) Group spawning results from the streaking of small males into a sneaking pair: male alternative reproductive tactics in the threespot wrasse *Halichoeres trimaculatus*. J Ethol 26:397–404

Suzuki S, Kuwamura T, Nakashima Y, Karino K, Kohda M (2010) Social factors of group spawning as an alternative mating tactic in the territorial males of the threespot wrasse *Halichoeres trimaculatus*. Environ Biol Fishes 89:71–77

Takamoto G, Seki S, Nakashima Y, Karino K, Kuwamura T (2003) Protogynous sex change in the haremic triggerfish *Sufflamen chrysopterus* (Tetraodontiformes). Ichthyol Res 50:281–283

Tanaka Y (1999) Reproductive behavior, eggs and larvae of four *Dascyllus* species in the aquarium. J Sch Mar Sci Technol Tokai Univ 47:223–244

Thompson VJ, Munday PL, Jones GP (2007) Habitat patch size and mating system as determinants of social group size in coral-dwelling fishes. Coral Reefs 26:165–174

Tribble GW (1982) Social organization, patterns of sexuality, and behavior of the wrasse *Coris dorsomaculata* at Miyake-jima, Japan. Environ Biol Fishes 7:29–38

Tsuboi M, Sakai Y (2016) Polygamous mating system and protogynous sex change in the gobiid fish *Fusigobius neophytus*. J Ethol 34:263–275

Usseglio P, Friedlander AM, DeMartini EE, Schuhbauer A, Schemmel E, Salinas de Léon P (2015) Improved estimates of age, growth and reproduction for the regionally endemic Galapagos sailfin grouper *Mycteroperca olfax* (Jenyns, 1840). PeerJ 3:e1270

Victor BC (1987) The mating system of the Caribbean rosy razorfish, *Xyrichtys martinicensis*. Bull Mar Sci 40:152–160

Walker SPW, McCormick MI (2004) Otolith-check formation and accelerated growth associated with sex change in an annual protogynous tropical fish. Mar Ecol Prog Ser 266:201–212

Walker SPW, McCormick MI (2009) Sexual selection explains sex-specific growth plasticity and positive allometry for sexual size dimorphism in a reef fish. Proc R Soc B 276:3335–3343

Walker SPW, Ryen CA (2007) Opportunistic hybridization between two congeneric tropical reef fish. Coral Reefs 26:539–539

Warner RR (1975) The adaptive significance of sequential hermaphroditism in animals. Am Nat 109:61–82

Warner RR (1982) Mating systems, sex change and sexual demography in the rainbow wrasse, *Thalassoma lucasanum*. Copeia 1982:653–661

Warner RR (1984) Mating behavior and hermaphroditism in coral reef fish. Am Sci 72:128–136

Warner RR (1988) Sex change in fishes: hypotheses, evidence, and objections. Environ Biol Fishes 22:81–90

Warner RR (1991) The use of phenotypic plasticity in coral reef fishes as tests of theory in evolutionary ecology. In: Sale P (ed) The ecology of coral reef fishes. Academic Press, New York, pp 387–398

Warner RR (2001) Synthesis: environment, mating systems, and life history allocations in the bluehead wrasse. In: Dugatkin LA (ed) Model systems in behavioral ecology. Princeton University Press, Princeton, pp 227–244

Warner RR, Lejeune P (1985) Sex change limited by paternal care: a test using four Mediterranean labrid fishes, genus *Symphodus*. Mar Biol 87:89–99

Warner RR, Robertson DR (1978) Sexual patterns in the labroid fishes of the western Caribbean, I: the wrasses (Labridae). Smithson Contr Zool 254:1–27

Warner RR, Schultz ET (1992) Sexual selection and male characteristics in the blue-head wrasse, *Thalassoma bifasciatum*: mating site acquisition, mating site defense, and female choice. Evolution 46:1421–1442

Warner RR, Swearer SE (1991) Social control of sex change in the bluehead wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). Biol Bull 181:199–204

Wernerus FM, Tessari V (1991) The influence of population density on the mating system of *Thalassoma pavo*, a protogynous Mediterranean labrid fish. Mar Ecol 12:361–368

Wong MYL, Munday PL, Jones GP (2005) Habitat patch size, facultative monogamy and sex change in a coral-dwelling fish, *Caracanthus unipinna*. Environ Biol Fishes 74:141–150

Wong MYL, Munday PL, Buston PM, Jones GP (2008) Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish. Behav Ecol 19:353–361

Yamaguchi S, Iwasa Y (2017) Advantage for the sex changer who retains the gonad of the nonfunctional sex. Behav Ecol Sociobiol 71:39

Yamaguchi S, Seki S, Sawada K, Takahashi S (2013) Small and poor females change sex: a theoretical and empirical study on protogynous sex change in a triggerfish under varying resource abundance. J Theor Biol 317:186–191

Yogo Y (1985) Studies on the sexual maturation and reproductive ecology in three protogynous fishes. Rep Fish Res Lab Kyushu Univ 7:37–83

Yogo Y (1987) Hermaphroditism and the evolutionary aspects of its occurrences in fishes. In: Nakazono A, Kuwamura T (eds) Sex change in fishes. Tokai University Press, Tokyo, pp 1–47

Yogo Y, Nakazono A, Tsukahara H (1980) Ecological studies on the spawning behavior of the parrotfish, *Scarus sordidus* Forsskål. Sci Bull Fac Agric Kyushu Univ 34:105–114

Zabala M, García-Rubies A, Louisy P, Sala E (1997a) Spawning behaviour of the Mediterranean dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Pisces: Serranidae) in the Medes Islands Marine Reserve (NW Mediterranean, Spain). Sci Mar 61:65–77

Zabala M, Louisy P, García-Rubies A, Gracia V (1997b) Socio-behavioural context of reproduction in the Mediterranean dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Pisces: Serranidae) in the Medes Islands Marine Reserve (NW Mediterranean, Spain). Sci Mar 61:79–89

Chapter 5
Bidirectional Sex Change in Fishes

Tatsuru Kadota

Abstract This chapter explains the distribution of bidirectional sex change among teleost fishes, the social context of bidirectional sex change in each mating system, and the adaptive significance. Of a total of 481 hermaphroditic fish species, 69 species have been confirmed to perform bidirectional sex change. Their mating systems are size-assortative monogamy, harem polygyny, or male-territory-visiting (MTV) polygamy. In size-assortative monogamous fish, bidirectional sex change occurs when a new same-sex pair is formed after movements between social groups following mate loss. Widowed individuals tend to prefer pairing with a nearby individual of the same sex rather than moving a longer distance to pair with an individual of the opposite sex. Therefore, bidirectional sex change can increase the reproductive value by reducing the risk of movement to seek a new mate. In haremic and MTV polygamous fish, the size-advantage model predicts protogyny (female-to-male sex change), but reversed (male-to-female) sex change occurs in some specific social situations. In haremic fish, males change back to females when they move to a mating group dominated by a larger male after all females have disappeared from their mating group. The widowed males need not conduct reversed sex change if new females or juveniles immigrate to their mating group or when they can take a female from a neighboring harem. Thus, the widowed males use reversed sex change as a last resort when they cannot gain new mating opportunities in any other way. Such a social context is predicted to be more likely to occur in low-density populations because the number of females in mating groups tends to become small and immigrations rarely occur. Some field studies have supported this low-density hypothesis for reversed sex change. In MTV polygamous fish, a small male, which has performed alternative mating tactics like group spawning, changes sex to perform pair spawning with a larger male. This sex change would be derived from the decrease in advantage of alternative tactics owing to decreased population density.

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T. Kuwamura et al. (eds.), *Hermaphroditism and Mating Systems in Fish*,
https://doi.org/10.1007/978-981-19-6095-6_5

Keywords Bidirectional sex change · Low-density hypothesis for reversed sex change · Male-to-female sex change · Reversed sex change

5.1 New Prospects Opened by the Discovery of Bidirectional Sex Change

Sex change (sequential hermaphroditism) is a life-history strategy and usually occurs in one direction in a species: either protogyny (i.e., female to male) or protandry (i.e., male to female). The adaptive significance of these sex-change patterns is explained by the size-advantage (SA) model (Ghiselin 1969; Warner 1975; see Chap. 1). The SA model predicts that protogyny will evolve in polygynous mating systems, while protandry will evolve in random mating. To test this hypothesis, many field studies on mating systems and sex change were conducted in the 1980s and 1990s. As a result, a good relationship between the type of mating system and the direction of sex change was confirmed in many reef fishes (Warner 1984; Nakazono and Kuwamura 1987; Kuwamura et al. 2020; see Chaps. 3 and 4). However, a few research teams working in the early 1990s discovered bidirectional sex change: the occurrence of both female-to-male and male-to-female in a species. The discovery that individuals of some fish species can change sex more than once is impactful because many ichthyologists had supposed that there were physiological constraints or no selective advantage in reverting to the original sex (Munday et al. 2010).

Japanese ichthyologists have greatly contributed to the progress of research on bidirectional sex change (Kuwamura and Nakashima 1998). Tanaka et al. (1990) were the first to report (although only briefly described) the occurrence of bidirectional sex change, in a protogynous grouper, *Epinephelus akaara* (Fig. 5.1a), held in aquaria. Subsequently, Kobayashi and Suzuki (1992) and Sunobe and Nakazono (1993) confirmed the ability of *Cirrhitichthys aureus* (Fig. 5.1b) and *Trimma okinawae*, respectively, to undergo bidirectional sex change, through aquarium experiments in which two or more individuals of the same sex were held in a tank. Bidirectional sex change in a natural population was first reported by Kuwamura et al. (1994a) from observations of *Paragobiodon echinocephalus*, a monogamous goby that lives among the branches of corals. Following that study, many other monogamous gobies with similar ecology were confirmed to exhibit bidirectional sex change by field and aquarium experiments (Nakashima et al. 1996; Munday 2002). For haremic fishes, Manabe et al. (2007a) reported bidirectional sex change in *T. okinawae* under natural conditions. In *Labroides dimidiatus*, another haremic fish well-known for undergoing protogynous sex change once in its lifetime (Robertson 1972), Kuwamura et al. (2011, 2014) succeeded to induce male-to-female sex change by female-removal experiments in the field. Male-to-female sex change is termed “reversed sex change” because the predominant pattern of sex change is protogyny. Reversed sex change has now been confirmed in many polygynous and protogynous fishes, either under natural conditions or by field/aquarium experiments (e.g., Kadota et al. 2012; Kuwamura et al. 2016a, 2020; Fukuda et al. 2017; Sunobe

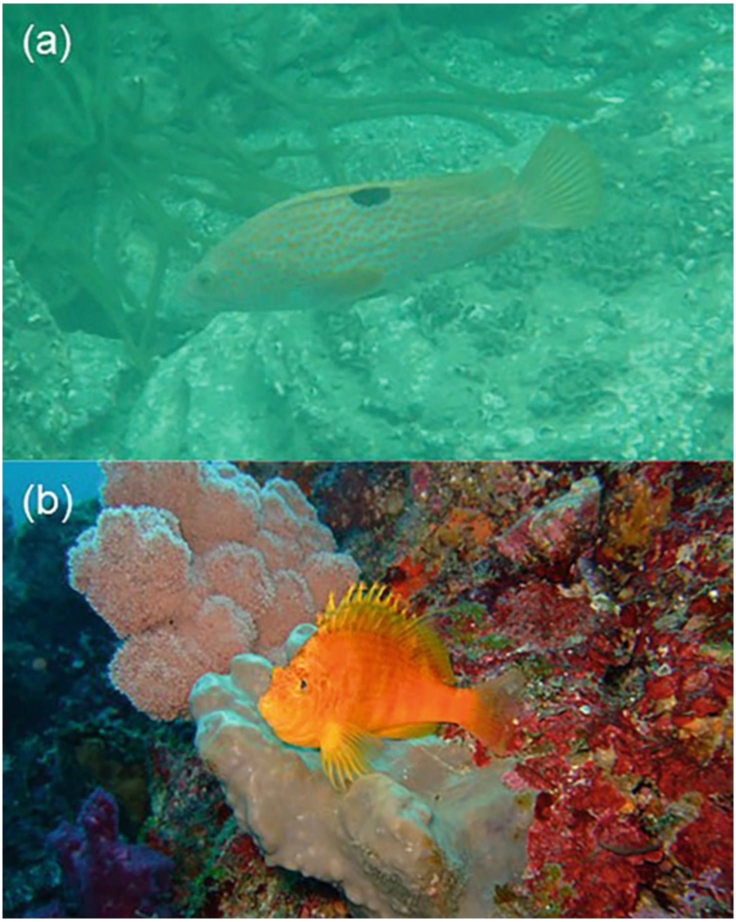

Fig. 5.1 *Epinephelus akaara* (**a**) and *Cirrhitichthys aureus* (**b**) are the first and second species in which bidirectional sex change has been confirmed in aquarium

et al. 2017). Furthermore, reversed sex change in male-territory-visiting polygamy (MTV polygamy) has been reported in a diandric protogynous wrasse, *Halichoeres trimaculatus*, through field observations and aquarium experiments (Kuwamura et al. 2007). Nonetheless, the existence of bidirectional sex change and reversed sex change seem to conflict with predictions of the SA model. Thus, solving the discrepancy has become a critical challenge in studies on sex change in fishes.

This chapter reviews the distribution of bidirectional sex change among teleost fishes and evaluates the relation between bidirectional sex change and the mating system or predominant sexual pattern in a species. Next, it gives a brief overview of aquarium experiments on bidirectional sex change conducted especially to investigate proximate mechanisms controlling sex change and the time required for sex change. Finally, the chapter discusses the social context of bidirectional sex change in each mating system and considers its adaptive significance. A review by Munday et al. (2010) covered the adaptive significance of bidirectional sex change, possible proximate mechanisms, and inherent physiological changes. However, since that review, numerous studies on bidirectional sex change have advanced our knowledge, especially as regards polygynous and protogynous fishes; therefore, those studies are emphasized here.

5.2 Distribution of Bidirectional Sex Change Among Teleost Fishes

To date, the ability to undergo bidirectional sex change has been confirmed in 7 families, 15 genera, and 69 species of teleosts (14% of 481 hermaphroditic species). Bidirectional sex change is most abundant in the Gobiidae (51 species), followed by in the Pomacanthidae (4 species) and Pseudochromidae (4 species). All these families belong to the clade Percomorpha (Kuwamura et al. 2020; see Chap. 1). The percentage of species confirmed to exhibit bidirectional sex change is relatively high in the families Cirrhitidae (6%), Pomacanthidae (4%), and Gobiidae (4%). However, the number of species and the percentage in each family represent lower limits because the sexual patterns of all species have not been investigated.

From investigations in the field and/or aquaria, the mating system has been reported for just 24 species or less than 35% of species known to exhibit bidirectional sex change (Table 5.1). Size-assortative monogamy is known in nine species, harem polygyny in nine species, and MTV polygamy in three species. In addition, two species (*Dascyllus aruanus* and *D. reticulatus*) and one species (*Halichoeres trimaculatus*) change the mating system between harem polygyny and MTV polygamy and between MTV polygamy and group spawning, respectively. Size-assortative monogamy is reported only in the Gobiidae, while harem polygyny and MTV polygamy are reported in various families (harem polygyny, Gobiidae, Pomacentridae, Labridae, Serranidae, Pomacanthidae, and Cirrhitidae; MTV polygamy, Gobiidae, Pomacentridae, and Labridae; Table 5.1). Harem polygyny is the most prevalent mating system (46% of 24 spp.; Table 5.1). In these mating systems, protogyny will be favored according to the SA model (Ghiselin 1969; Warner 1975) or the growth-rate-advantage model (Iwasa 1991). As predicted by these models (see Chap. 1), all species whose sexual patterns are confirmed are protogynous.

The evolution of bidirectional sex change could be prevented by distinct sex-based differences, such as body coloration and general morphology (except urogenital papilla), because those differences would increase the morphological changes necessary to shift from one sexual phenotype to the other. Of 69 species in which bidirectional sex change is confirmed, 62 species lack distinct sex-based differences. In contrast, bidirectional sex change is reported in at least five sexually dimorphic species; three species exhibit sexual differences in body color (e.g.,

Table 5.1 List of teleost fish species confirmed to exhibit bidirectional sex change

Family	Species	Length (mm)	Sexual dimorphism	Sexual pattern	Evidence	Mating system	References	Remarks
Gobiidae	*Eviota epiphanes*	14 SL	N	PG (1), BS (2)	Histology (1, 2), aquarium (1, 2)	Unknown	(1) Cole (1990), (2) Maxfield and Cole (2019a)	
	Gobiodon erythrospilus	54 TL	N	BS (1, 2, 3, 4)	Field (1, 2, 3, 4), aquarium (1)	SA monogamy (1)	(1) Nakashima et al. (1996), (2) Munday (2002), (3) Munday and Molony (2002), (4) Kroon et al. (2003)	*G. rivulatus rivulatus* (1)
	Gobiodon histrio	35 TL	N	PG, BS (1, 2)	Field (1, 2)	SA monogamy (1)	(1) Munday et al. (1998), (2) Munday (2002)	
	Gobiodon micropus	35 TL	N	BS	Aquarium	SA monogamy	Nakashima et al. (1996)	
	Gobiodon oculolineatus	35 TL	N	BS	Aquarium	SA monogamy	Nakashima et al. (1996)	
	Gobiodon quinquestrigatus	45 SL	N	PG (1), BS *(1)	Field, aquarium (1), aquarium* (1)	SA monogamy (1, 2)	(1) Nakashima et al. (1996), (2) Thompson et al. (2007)	*BS was confirmed by an aquarium observation
	Lythrypnus dalli	64 TL	Y (fin length)	PG (1, 2, 3, 4, 5, 7, 8), BS* (1, 2, 6, 8)	Field (1, 4), aquarium (2, 3, 5, 7, 8), aquarium* (1, 2, 6, 8), histology (9)	MTV polygamy (1)	(1) St. Mary (1994), (2) Reavis and Grober (1999), (3) Black et al. (2004), (4) Black et al. (2005a), (5) Black et al. (2005b), (6) Rodgers et al. (2005), (7) Lorenzi et al. (2006), (8) Rodgers et al. (2007), (9) Maxfield and Cole (2019b)	*BS was confirmed by aquarium observations
	Lythrypnus pulchellus	45 TL	Y (fin length)	BS	Aquarium, histology	Unknown	Muñoz-Arroyo et al. (2019)	
	Lythrypnus zebra	57 TL	N	BS	Aquarium	MTV polygamy	St. Mary (1996)	

(continued)

Table 5.1 (continued)

Family	Species	Length (mm)	Sexual dimorphism	Sexual pattern	Evidence	Mating system	References	Remarks
	Paragobiodon echinocephalus	40 TL	N	PG, BS (1, 2)	Field (1, 2), aquarium (2)	SA monogamy (3, 4, 5)	(1) Kuwamura et al. (1994a), (2) Nakashima et al. (1995), (3) Lassig (1976), (4) Lassig (1977), (5) Kuwamura et al. (1993)	
	Priolepis akihitoi	53 SL	N	BS (1)	Aquarium (1)	SA monogamy (2)	(1) Manabe et al. (2013), (2) Fukuda and Sunobe (2020)	
	Priolepis borea	24 SL	N	BS	Histology	Unknown	Manabe et al. (2013)	
	Priolepis cincta	70 FL	N	BS (1, 2)	Aquarium (1), histology (2)	SA monogamy (1, 2)	(1) Manabe et al. (2013), (2) Sunobe and Nakazono (1999)	
	Priolepis eugenius	56 SL	N	PG, BS	Histology	Unknown	Cole (1990)	
	Priolepis fallacincta	32 TL	N	BS	Histology	Unknown	Manabe et al. (2013)	
	Priolepis hipoliti	40 TL	N	PG, BS	Histology	Unknown	Cole (1990)	
	Priolepis inhaca	40 TL	N	BS	Histology	Unknown	Manabe et al. (2013)	
	Priolepis latifascima	21 SL	N	BS	Aquarium	Unknown	Manabe et al. (2013)	
	Priolepis semidoliata	24 SL	N	BS	Aquarium	SA monogamy	Manabe et al. (2013)	
	Trimma annosum	28 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma benjamini	30 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma caesiura	35 SL	N	BS	Histology, aquarium	Unknown	Sunobe et al. (2017)	
	Trimma cana	25 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	

	Trimma caudomaculatum	27 SL	N	BS	Histology (1), aquarium (2)	MTV polygamy (1)	(1) Sunobe et al. (2017), (2) Tomatsu et al. (2018)	
	Trimma emeryi	25 TL	N	BS	Histology (1)	Harem (2)	(1) Sunobe et al. (2017), (2) Fukuda and Sunobe (2020)	
	Trimma fangi	21	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma flammeum	22 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma flavatram	23 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma fucatum	20 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma gigantum	30 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma grammistes	30 SL	N	BS	Aquarium (1), field (2)	Harem (2)	(1) Shiobara (2000), (2) Fukuda et al. (2017)	
	Trimma hayashii	30 TL	N	BS	Histology (1)	Harem (2)	(1) Sunobe et al. (2017), (2) Fukuda and Sunobe (2020)	
	Trimma kudoi	25 SL	N	BS	Aquarium	Unknown	Manabe et al. (2008)	*Trimma* sp.
	Trimma lantana	29 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma macrophthalma	25 TL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma maiandros	27 SL	N	BS	Histology, aquarium	Unknown	Sunobe et al. (2017)	
	Trimma marinae	20 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma milta	30 TL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma nasa	23 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma naudei	35 SL	N	BS	Histology, aquarium	Unknown	Sunobe et al. (2017)	
	Trimma necopinum	40 TL	N	BS	Histology	Unknown	Sunobe et al. (2017)	

(continued)

Table 5.1 (continued)

Family	Species	Length (mm)	Sexual dimorphism	Sexual pattern	Evidence	Mating system	References	Remarks
	Trimma okinawae	35 SL	N	PG (1, 2, 3, 4, 5), BS (2, 3, 5)	Filed (1, 4, 5), aquarium (2, 3)	Harem (1)	(1) Sunobe and Nakazono (1990), (2) Sunobe and Nakazono (1993), (3) Sunobe et al. (2005), (4) Manabe et al. (2007a), (5) Manabe et al. (2007b)	
	Trimma preclarum	20 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma rubromaculatum	35 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma sheppardi	19 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma stobbsi	25 TL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma striatum	30 TL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma tauroculum	19 SL	N	BS	Histology	Unknown	Sunobe et al. (2017)	
	Trimma taylori	35 SL	N	BS	Histology (1, 2)	Unknown* (2)	(1) Sunobe et al. (2017), (2) Oyama et al. (2022)	*Monogamy in aquarium
	Trimma unisquamis	26	N	BS	Histology	Unknown	Cole (1990)	
	Trimma yanagitai	37 SL	N	BS	Aquarium	Unknown	Sakurai et al. (2009)	
Pomacentridae	*Dascyllus aruanus*	100 TL	N	PG (1, 2*, 3, 4), G (5), BS (7)	Histology (1, 3, 4, 5), field (2*, 7)	Harem, MTV polygamy (1–7)	(1) Fricke and Holzberg (1974), (2) Coates (1982), (3) Shpigel and Fishelson (1986), (4) Cole (2002), (5) Asoh (2003), (6) Wong et al. (2012), (7) Kuwamura et al. (2016a)	*Weak evidence

	Dascyllus reticulatus	90 TL	N	PG (1, 4), G (2), BS (4)	Histology (1, 2), field (4)	Harem, MTV polygamy (2, 3)	(1) Schwarz and Smith (1990), (2) Asoh (2005), (3) Sakanoue and Sakai (2019), (4) Sakanoue and Sakai (2022)	
Pseudochromidae	*Pseudochromis aldabraensis*	100 TL	N	BS	Histology, aquarium	Unknown	Wittenrich and Munday (2005)	
	Pseudochromis cyanotaenia	62 TL	Y (color)	BS	Histology, aquarium	Unknown	Wittenrich and Munday (2005)	
	Pseudochromis flavivertex	72 TL	N	BS	Histology, aquarium	Unknown	Wittenrich and Munday (2005)	
	Pictichromis porphyrea	60 TL	N	BS	Field	Unknown	Kuwamura et al. (2015)	
Labridae	*Halichoeres trimaculatus*	270 TL	Y (color)	PG, BS (1)	Field, aquarium (1)	MTV polygamy, GSP (2, 3)	(1) Kuwamura et al. (2007), (2) Suzuki et al. (2008), (3) Suzuki et al. (2010)	
	Labroides dimidiatus	140 TL	N	PG (1), BS (2, 3, 4)	Field (1, 3, 4), aquarium (2)	Harem (1–4)	(1) Robertson (1972), (2) Kuwamura et al. (2002), (3) Kuwamura et al. (2011), (4) Kuwamura et al. (2014)	
Serranidae (Epinephelinae)	*Cephalopholis boenak*	300 TL	N	PG (1), BS (2)	Histology (1), aquarium (2)	Harem (3)	(1) Liu and Sadovy (2004a), (2) Liu and Sadovy (2004b), (3) Liu and Sadovy (2005)	
	Epinephelus akaara	580 TL	N	PG, BS (1, 2)	Histology, aquarium (1, 2)	Unknown	(1) Tanaka et al. (1990), (2) Okumura (2001)	
	Epinephelus coioides	1200 TL	?	PG (1, 2, 4, 5), BS (3)	Histology (1), aquarium (2, 3, 4,5)	Unknown	(1) Liu and Sadovy de Mitcheson (2011), (2) Quinitio et al. (1997), (3) Chen et al. (2019), (4) Chen et al. (2020), (5) Chen et al. (2021)	

(continued)

Table 5.1 (continued)

Family	Species	Length (mm)	Sexual dimorphism	Sexual pattern	Evidence	Mating system	References	Remarks
	Epinephelus bruneus	1360 TL	?	PG, BS	Aquarium	Unknown	Oh et al. (2013)	
Pomacanthidae	*Centropyge acanthops*	80 TL	N	PG, BS	Aquarium	Unknown	Hioki and Suzuki (1996)	
	Centropyge ferrugata	100 TL	Y (color)	PG (1), BS (2, 3)	Field (1, 3), aquarium (2)	Harem (4)	(1) Sakai (1997), (2) Sakai et al. (2003), (3) Kuwamura et al. (2011), (4) Sakai and Kohda (1997)	
	Centropyge fisheri	84 TL	N	PG, BS	Aquarium, histology	Unknown	Hioki and Suzuki (1996)	
	Centropyge flavissimus	140 TL	N	BS (1)	Aquarium (1)	Harem (2)	(1) Hioki and Suzuki (1996), (2) Thresher (1982)	
Cirrhitidae	*Cirrhitichthys aureus*	140 TL	N	PG, BS	Aquarium, histology	Unknown	Kobayashi and Suzuki (1992)	
	Cirrhitichthys falco	70 TL	N	PG (1, 2, 3), BS (3)	Histology (1, 2)*, field (3)	Harem (4, 5)	(1) Sadovy and Donaldson (1995), (2) Kobayashi and Suzuki (1992), (3) Kadota et al. (2012), (4) Donaldson (1987), (5) Kadota et al. (2011)	*Small sample size

Order and family names are arranged following Nelson et al. (2016) and genus and species in alphabetical order within each family and genus, respectively. Length is based on FishBase (https://www.fishbase.in) resource

For evidence to confirm functional hermaphroditism, *histology* by the examination of gonad histology, *field* and *aquarium* by field and aquarium observations, respectively, of identified individuals. When evidence seems very weak (e.g., small sample size for gonad histology), a note is given in remarks

SL standard length, *TL* total length, *N* not reported, *?* unclear, *Y* yes, *BS* bidirectional sex change, *PG* protogyny, *SA* size-assortative, *MTV* male-territory-visiting, *GSP* group spawning

Pseudochromis cyanotaenia), and two species in dorsal fin length (e.g., *Lythrypnus pulchellus*) (Table 5.1). Thus, at a minimum, dichromatism and minor dimorphism (such as fin length) would not always play a critical role in preventing the evolution of bidirectional sex change. In addition, body size would not become a critical factor for the deterrence. Most species (84%) exhibiting bidirectional sex change achieve sizes smaller than 10 cm in total length (TL) (e.g., Gobiidae), although bidirectional sex change was recently confirmed in *Epinephelus bruneus* and *E. coioides* which can attain more than 1 m TL (Table 5.1). The number of fish species confirmed to undergo bidirectional sex change is increasing, and future research will no doubt confirm bidirectional sex change in other protogynous species of Percomorpha.

5.3 Bidirectional Sex Change Recorded in Aquaria

Aquarium experiments have been important to the study of bidirectional sex change, especially research in the 1990s–2000s. In these experiments, two or more individuals of the same sex are housed together, and any change in behavior and/or in the gonad is observed. These experiments have confirmed bidirectional sex change in 34 species (Table 5.1), which accounts for 49% of all species so far reported to exhibit bidirectional sex change.

Aquarium experiments (and some field studies) have also revealed that bidirectional sex change can be socially controlled (see Chap. 1). For instance, Sunobe and Nakazono (1993) reared multiple females of *Trimma okinawae* in a tank and then moved any sex-changed individuals to another tank where a larger male was kept. As a result, the largest female that had changed sex to male while in the first tank changed sex back to female and spawned with the larger male in the second tank. Furthermore, Kuwamura et al. (2002) confirmed that the smaller individuals of *Labroides dimidiatus* behaved as female and released eggs in tanks where two males were kept. These studies show that individuals would change sex as a consequence of their position in a social hierarchy based on relative body size. Of 32 species exhibiting bidirectional sex change, the same rule of larger individuals being males and smaller individuals being females is known for at least 27 species (Table 5.2). However, this rule does not apply to *Trimma kudoi*: in this species, the smaller female in groups of two females, and the middle-sized female in groups of three females, change sex to male (Manabe et al. 2008). Furthermore, larger males change sex to female in groups of two males. A new version of the SA model (Muñoz and Warner 2003, 2004; see Chap. 4) predicts that the largest female does not necessary change sex to male if the largest female's fecundity is markedly higher than the combined fecundity of all other females in the group (meaning her expected reproductive success after sex change). The patterns of sex change observed in *T. kudoi* could be explained by the new version of the SA model if the mating system and the social conditions associated with the sex change were clarified (Manabe et al. 2008).

Table 5.2 Gonad type, relative size of sex-changers, and time required for sex change in some bidirectional sex-changing fish species

Family/species	Gonad type	Female to male		Male to female		Ratio of mean time^c	References
		Relative size^a	Mean time^b	Relative size^a	Mean time^b		
Gobiidae							
Eviota epiphanes	Non-delimited	–	7*	–	5*	0.7	Maxfield and Cole (2019a)
Gobiodon erythrospilus	Non-delimited	L	–	S	–	–	Nakashima et al. (1996)
Gobiodon histrio^d	Non-delimited	L	–	S	–	–	Munday (2002)
Gobiodon micropus	–	L	–	S	–	–	Nakashima et al. (1996)
Gobiodon oculolineatus	–	L	–	L	–	–	Nakashima et al. (1996)
Gobiodon quinquestrigatus	Non-delimited	L	–	S	–	–	Nakashima et al. (1996)
Lythrypnus dalli	Delimited	L	16.5	S	17.2	1.0	Rodgers et al. (2007)
Lythrypnus pulchellus	Delimited	L	11.3	S	12.0	1.1	Muñoz-Arroyo et al. (2019)
Paragobiodon echinocephalus	Non-delimited	L	–	S	–	–	Nakashima et al. (1995)
Priolepis akihitoi	Delimited	L	25	S	27.5	1.1	Manabe et al. (2013)
Priolepis cincta	Delimited	L	10	S	–	–	Manabe et al. (2013)
Priolepis latifascima	Delimited	L	35	S	48	1.4	Manabe et al. (2013)
Priolepis semidoliata	Delimited	L	21	S	–	–	Manabe et al. (2013)
Trimma caesiura	Delimited	L	6	S	21	3.5	Sunobe et al. (2017)
Trimma caudomaculatum	Delimited	L	14	S	67	4.8	Tomatsu et al. (2018)
Trimma grammistes	Delimited	L	11.5	S	15.5	1.3	Shiobara (2000)
Trimma kudoi	Delimited	Female–female pair: S three-female group: M	Female–female pair: 22.3 three-female group: 16.6	L	15.9	0.7	Manabe et al. (2008)
Trimma maiandros	Delimited	L	3	S	8	2.7	Sunobe et al. (2017)
Trimma naudei	Delimited	L	3	S	19	6.3	Sunobe et al. (2017)
Trimma okinawae	Delimited	L	9.8	S	8.5	0.9	Sunobe and Nakazono (1993)

Trimma yanagitai	Delimited	L	21.5	S	23.5	1.1	Sakurai et al. (2009)
Pseudochromidae							
Pseudochromis flavivertex	Non-delimited	L	28*	S	52*	1.9	Wittenrich and Munday (2005)
Pseudochromis aldabraensis	Non-delimited	L	18*	S	64*	3.6	Wittenrich and Munday (2005)
Pseudochromis cyanotaenia	Non-delimited	L	23*	S	67*	2.9	Wittenrich and Munday (2005)
Labridae							
Labroides dimidiatus	Non-delimited	L	17	S	64	3.8	Nakashima et al. (2000) and Kuwamura et al. (2002)
Serranidae							
Cephalopholis boenak	Non-delimited	L	–	S	–	–	Liu and Sadovy (2004b)
Pomacanthidae							
Centropyge acanthops	Non-delimited	L	8	S	–	–	Hioki and Suzuki (1996)
Centropyge ferrugata	Non-delimited	L	15*	S	47*	3.1	Sakai et al. (2003)
Centropyge fisheri	Non-delimited	L	6	S	–	–	Hioki and Suzuki (1996)
Centropyge flavissimus	Non-delimited?	–	–	S	81	–	Hioki and Suzuki (1996)
Cirrhitidae							
Cirrhitichthys aureus[e]	Non-delimited	L	231	L	55	0.2	Kobayashi and Suzuki (1992)
Cirrhitichthys falco	Non-delimited?	L	–	S	–	–	Kadota et al. (2012)

[a] Relative size of individuals that changed sex compared with individuals that did not change sex: *L* larger, *M* middle, *S* smaller

[b] Mean time (days) to complete change sex in each direction. In cases that mean time cannot be calculated (asterisks), the minimum time is indicated

[c] Ratio of mean time = mean time for male to female/mean time for female to male

[d] Data in *G histrio* include those in *G. erythrospilus*

[e] Data were removed from analysis for Ts because this experiment would be conducted across the non-reproductive season

Furthermore, aquarium experiments (and a few field studies) have revealed the time required for bidirectional sex change (Ts). Although Ts varies with species, Ts for male-to-female sex change (median 23.5 days, range 5–81 days, $n = 21$ species) tends to be longer than Ts for female-to-male sex change (median 14.5 days, range 3–35, $n = 22$ species; Mann–Whitney U test, $P < 0.05$). Of the 18 species for which aquarium experiments and/or field studies confirmed the Ts for both directions, 15 species required longer Ts for male-to-female sex change (Table 5.2). When looking at variation among species, species of *Trimma*, *Priolepis*, and *Lythrypnus* have a shorter Ts in male-to-female sex change (median 18.1 days, range 8–67, $n = 14$) compared with other species (64.0 days, range 5–81, $n = 7$, Mann–Whitney U test, $P < 0.05$), although no significant difference in Ts for female-to-male sex change was detected between the former group (median 12.8 days, range 3–35, $n = 14$) and the others (median 16 days, range 6–28, $n = 8$; Mann–Whitney U test, $P > 0.05$). These differences in Ts are suggested to be affected by gonad types (Munday et al. 2010). *Trimma*, *Priolepis*, and *Lythrypnus* retain the gonad of a delimited type (Table 5.2), wherein ovarian and testis tissues are separated by a thin cellular wall. The ovarian and testis tissues proliferate or regress, depending on the functional sex of the individual. The delimited type of gonad, which retains a regressed gonad region of either male or female tissue, is considered an adaptation to reduce the amount of gonad to be newly produced, hence shortening the Ts. Body size or metabolic rate has recently been suggested to also affect Ts (Tokunaga et al. 2022); however, it is unknown which factor most strongly affects the Ts because of multicollinearity between gonad type and body mass in the species for which Ts has been confirmed. Additional sex-change experiments, particularly with small-sized species having non-delimited gonads or with large-sized species having delimited gonads, are required to fill these data gaps and so inform our understanding of how Ts is determined in fishes.

Aquarium experiments have helped to reveal a species' ability to undergo bidirectional sex change, including the proximate cues and the time required for the sex change. However, the adaptive significance of bidirectional sex change cannot be wholly understood based on aquarium experiments only, since the frequency and process of bidirectional sex change by fish in aquaria will not necessarily reflect those under natural conditions. For instance, subordinate males might be obligated to change sex when held in an aquarium because these males cannot escape interference by the dominant males, whereas subordinate males could adopt alternative tactics under natural conditions. Munday et al. (2010) state the need to prioritize studies of bidirectional sex change under natural conditions in the field, to document the occurrence of this sexual pattern and better understand its adaptive significance. Therefore, we need to observe the process of bidirectional sex change under natural conditions to discern especially the social context.

Fig. 5.2 *Paragobiodon echinocephalus*: a monogamous fish with bidirectional sex change (photo by T. Kuwamura)

5.4 Bidirectional Sex Change in Monogamous Fish

Bidirectional sex change in monogamy has been revealed in detail in *Paragobiodon echinocephalus* (Fig. 5.2; Kuwamura et al. 1994a), a goby that lives among branches of the coral *Stylophora pistillata*. Although two or more fish often inhabit a large coral, only the largest two fish in the coral consistently breed monogamously. Though the size of mature individuals is about 2–4 cm TL, the sizes of a male and female in a breeding pair are approximately the same (i.e., size-assortative monogamy). Pairs usually spawn in the afternoon, and the eggs hatch around sunset about 5 days afterward (at a water temperature of 25 °C). Until hatching, the male guards the eggs against predators such as crabs cohabiting the host coral.

Kuwamura et al. (1994a) investigated *P. echinocephalus* associated with corals within a 20 m × 20 m area on the fringing reef of Sesoko Island, Okinawa, Japan, for 3 years, and confirmed 48 cases of female-to-male sex change and 24 cases of male-to-female sex change under natural conditions. Of these transitions, the social context was revealed in 24 cases of the former and 10 cases of the latter. Both directions of sex change occurred when a new same-sex pair formed by movement between host corals after mate loss. The larger individual changed sex in most female–female pairs, whereas the smaller individual underwent sex change in most male–male pairs. In addition, female-to-male sex change occurred when a female–juvenile pair formed. In all cases, the sex change resulted in the formation of pairs consisting of a larger male and a smaller female. The reproductive success of *P. echinocephalus* pairs is limited by the smaller individual because the female's fecundity is limited by her body size and the male can guard no more than one clutch spawned by the female of similar body size (Kuwamura et al. 1993). In addition, females grow much faster than their mates in the nonbreeding season (growth-rate advantage) (Kuwamura et al. 1994a). Thus, the smaller individual in new pairs ought to be female to catch up with body size of the larger individual and increase the

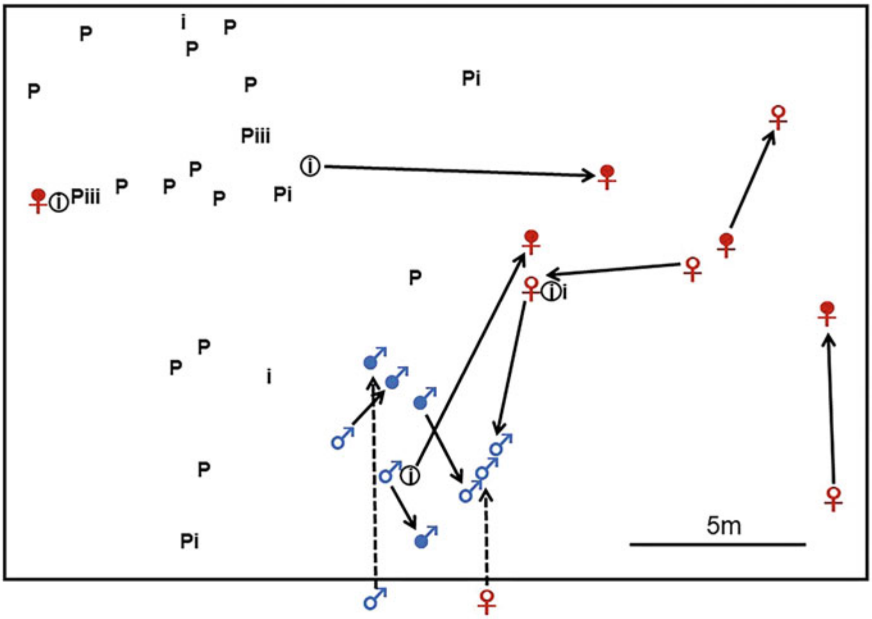

Fig. 5.3 Sex change and movements of *Paragobiodon echinocephalus* between host corals in a field experiment. The symbols represent nine males and nine females that belonged to pairs from which one partner was removed. The arrows connect the new pairs formed by the end of the experiment. The direction of the arrow indicates which individual left its host coral (base of the arrow) to form the new pair (end of the arrow). Filled symbols represent the original sex of individuals that changed sex after the formation of a new pair. *P* unmanipulated pairs, *i* immature fish, four of which (encircled i) later matured and bred with the unmated fish. A male and a female (symbols with broken arrows) came from outside the experimental area and bred with the experimental fish. (Modified from Nakashima et al. 1995)

reproductive success after their own or their partner's sex change. Bidirectional sex change is also confirmed under social conditions similar to that of *P. echinocephalus* in other size-assortatively monogamous gobies, such as *Gobiodon* spp. (Nakashima et al. 1996; Munday et al. 1998).

Nakashima et al. (1995) conducted a field experiment to reveal the adaptive significance of bidirectional sex change in *P. echinocephalus* (Fig. 5.3). The researchers removed either males or females in existing pairs, creating two adjoining areas inhabited by only males and only females. Thus, the "widowed" individuals, which had lost their immediate mating opportunity, were forced to choose to pair with an opposite-sex individual following long-distance movement or else to pair with a same-sex individual after short-distance movement. As a result, five of nine bachelor females and four of nine bachelor males changed sex after pairing with nearby same-sex individuals. Because predation risk is relatively high for small coral reef fishes, individuals would be particularly vulnerable to predation during movements outside the host coral. In addition, nearly all suitable host coral colonies were occupied by a *P. echinocephalus* breeding pair, with very few single mature individuals in the population (Kuwamura et al. 1994b). Therefore, bidirectional sex change enables this goby species to pair with close-neighboring individuals regardless of their sex when individuals lose their mating opportunities, which would increase their reproductive value (i.e., the expected future reproductive success, taking into account the effects of growth and mortality: Munday et al. 2006) by reducing the risk of movement to seek a new mate (risk-of-movement hypothesis: Nakashima et al. 1995). The same advantage of bidirectional sex change (decreased risk of movement to seek a mate) was also shown by field experiments in another size-assortatively monogamous goby inhabiting corals, *Gobiodon histrio* (Munday et al. 1998). Bidirectional sex change with the same suggested advantage was further observed in a size-assortatively monogamous goby inhabiting rocky reefs, *Priolepis akihitoi* (Manabe et al. 2013; Fukuda and Sunobe 2020).

Which factors (growth-rate advantage for females during the non-breeding season or risk of movement to seek a mate) are more strongly attributed to bidirectional sex change in coral-dwelling gobies? A field experiment to answer this question has been conducted in *G. histrio*. Munday (2002) created four social conditions: (1) female–female pairs; (2) male–male pairs; (3) heterosexual pairs where the male is larger than the female; (4) heterosexual pairs where the female is larger than the male. If the growth-rate advantage is the primary factor driving bidirectional sex change, the larger individual, smaller individual, and both individuals are predicted to change sex in the first, second, and fourth social conditions, respectively. In addition, neither individual should change sex in the third social condition. However, only the first three (1–3) of the predicted outcomes were observed in the experiment. Even in field studies in *P. echinocephalus*, simultaneous sex change of both mates did not occur when a larger female and a smaller male formed a new pair or when a female became larger than her mate (Kuwamura et al. 1994a). These studies show the risk of moving among spatially isolated habitat patches and the low probability of finding a mate have been more important than sex-specific differences in growth rates to the evolution of bidirectional sex change in coral-dwelling gobies. In short, risk-of-movement hypothesis can explain why bidirectional sex change occurs in the coral-dwelling gobies, whereas growth-rate advantage can explain which individual should change sex in homosexual pairs.

5.5 Reversed Sex Change in Haremic Fish

5.5.1 Social Conditions and Adaptive Significance of Bidirectional Sex Change in Haremic Fish

Bidirectional sex change in polygynous fish under natural conditions was first confirmed in *Trimma okinawae* (Fig. 5.4a; Manabe et al. 2007a). This small goby (<30 mm standard length) inhabits cave ceilings, rock slopes, holes, or the underside

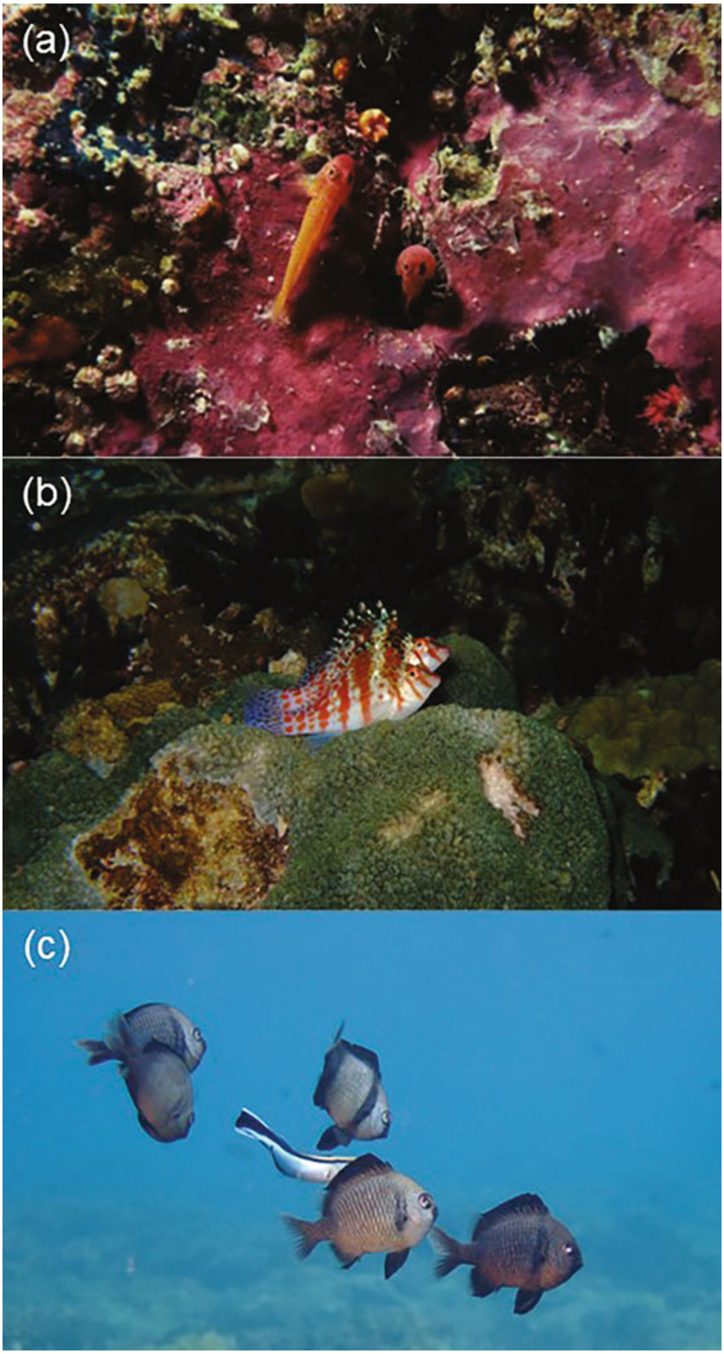

Fig. 5.4 Haremic fishes with reversed sex change; *Trimma okinawae* (**a**) (photo by T. Sunobe), *Cirrhitichthys falco* (**b**), and *Dascyllus reticulatus* (**c**)

of table corals, where they feed on planktonic copepods. The mating system of this species is polygyny, consisting of a single dominant male and one to six females. In this system, the larger males tend to have larger mating groups. Males maintain a spawning site within their territories, and females visit there to spawn in the morning. After spawning, males stay within the spawning site and guard the eggs, while females return to their respective home ranges (Sunobe and Nakazono 1990). As predicted by the SA model, protogyny would be favored in *T. okinawae* because the mating system of this species is polygyny, where larger males monopolize the mating opportunities, like in other haremic protogynous fishes.

Manabe et al. (2007a) conducted scuba observations of *T. okinawae* at Kagoshima Prefecture, Japan, for 16 months. They set two study areas along a cliff face at a depth of 4–7 m and investigated changes in spatial distribution and sex. As a result, 22 instances of female-to-male sex change and three instances of male-to-female sex change were observed. Of these instances, the social context was revealed in 14 instances of the former, and in all three instances of the latter. The most typical pattern of female-to-male sex change involved the largest female in a mating group changing sex after the disappearance of males. Sex change under this social context is called "takeover sex change," and it has been confirmed in a range of haremic protogynous fishes, including *Labroides dimidiatus* and *Centropyge ferrugata* (see Chap. 4).

Manabe et al. (2007a) reported that all three observed instances of male-to-female sex change occurred in widowed males. In the first case (Fig. 5.5a), a male became widowed after the only female in his group disappeared, and 7 days after the mate loss, the male moved to a neighboring polygynous group whose male was larger than it and the widowed male then changed sex. In the second case (Fig. 5.5b), a female became solitary by moving from a harem to a vacant site and thereafter changed sex; later, it returned to the original group and changed back to female. In the third case (Fig. 5.5c), a female changed sex to become a solitary male after all members of her group disappeared. Thereafter, that solitary male changed sex back to female following the immigration of a larger male and two females.

Male-to-female sex change in *T. okinawae* appears to be consistent with the SA model (Manabe et al. 2007a; Munday et al. 2010). This model predicts that an individual should change sex when the reproductive value of the other sex exceeds that of its present sex. Given this, it is thought that bidirectional sex change will likewise be favored if the reproductive value between the sexes changes more than once during a lifetime (Fig. 5.6; Nakashima et al. 1995). In *T. okinawae*, male reproductive success is generally higher than that of a female when the body size is larger, because of polygynous mating whereby larger males monopolize mating opportunities to the detriment of smaller ones (Fig. 5.6). However, the reproductive success of a male decreases to zero if it immigrates into a mating group with a larger male after the loss of its mate or if a larger male immigrates into its mating group. In those situations, the larger dominant male would exclude the smaller male from reproducing as a male in the new group, but the smaller male could reproduce as a female. In other words, reproductive success as a female is expected to be greater than that as a male. Thus, reversed sex change would be one tactic used by widowed

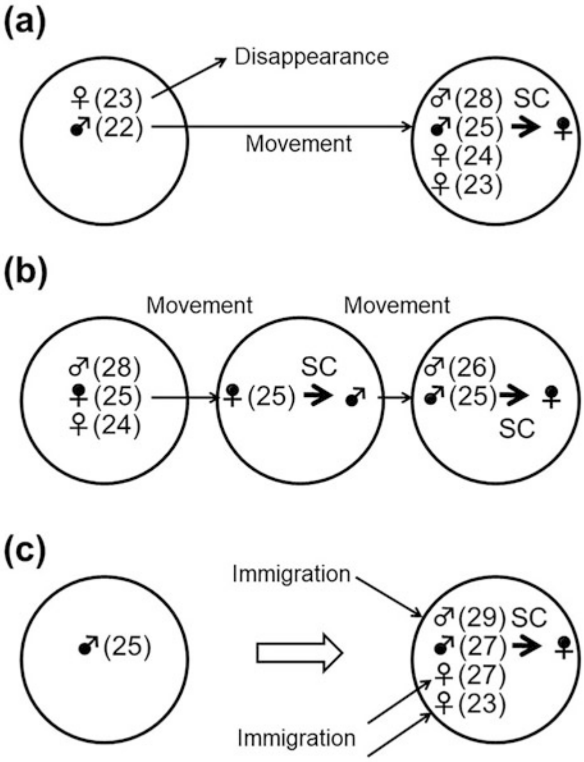

Fig. 5.5 Social conditions of reversed sex change in a natural population of *Trimma okinawae*. Three cases (**a**, **b**, **c**) are shown. Filled symbols show sex-changed individuals. Circles indicate caves, rock slopes, holes, or the underside of table corals. The standard length (mm) of each individual is given in parentheses. *SC* sex change. (Modified from Manabe et al. 2007a)

males to improve their mating success. Recently, reversed sex change was likewise observed in a similar social context in the closely related *Trimma grammistes* (Fukuda et al. 2017).

Can reversed-sex-changed individuals really acquire mating opportunities? In *Trimma*, it is difficult to directly observe spawning behavior because the species spawn in holes on rocky reefs, but sex in these species can be determined by the shape of the urogenital papilla. Thus, whether the reversed-sex-changed individuals get mating opportunities was not exactly confirmed in *T. okinawae* and *T. grammistes* (Manabe et al. 2007a; Fukuda et al. 2017). Nonetheless, the question can be answered by studies of fish that produce pelagic eggs, which allows confirmation of functional sex by collection of gametes in the water (Shapiro et al. 1994). Hawkfish are pelagic spawners that inhabit coral and rocky reefs, and at least two species, *Cirrhitichthys aureus* and *C. falco*, were shown to undergo bidirectional sex change, in aquarium experiments and field observations, respectively (Kobayashi and Suzuki 1992; Kadota et al. 2012).

Cirrhitichthys falco is one of the smallest cirrhitids (max. 6 cm SL) and is widely distributed on coral reefs in the Pacific Ocean, from the Philippines to Hawaii. The mating system of this species is harem polygyny, consisting of a single dominant male and one to seven females (Donaldson 1987). Females maintain territories

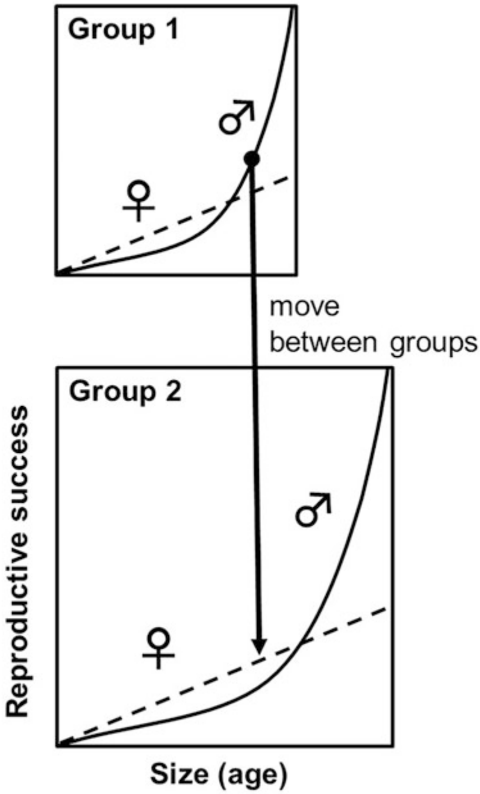

Fig. 5.6 Conditions for the evolution of reversed sex change, associated with relationships between body size (or age) and reproductive success in males and females. Groups 1 and 2 show the relationship before and after movements, respectively; if a male moves to a new group dominated by a larger male, its reproductive success will be improved by changing sex back to female. (Modified from Nakashima et al. 1995)

against adjacent females for food resources (Kadota et al. 2011). Males often visit female territories to court, and spawning occurs after sunset (Donaldson 1987; Kadota et al. 2011). Kadota et al. (2012) conducted a 3-year demographic survey of a population of *C. falco* at Kuchierabu Island, southern Japan, and observed reversed sex change in two instances. In both cases, all the females disappeared from the harem and the neighboring males expanded their territories to encompass the territories of the widowed males, which changed sex (Fig. 5.7). The sex changers spawned with the neighboring males, with the release of eggs being confirmed by egg collection. The sex changers spawned almost every day, and their frequency of spawning was not significantly different from that of other females. Field experiments have also confirmed eggs produced by a reversed sex changer in other pelagic spawners (e.g., *L. dimidiatus* and *C. ferrugata*: Kuwamura et al. 2011, 2014). Thus, reversed sex change was confirmed under natural conditions as a tactic to improve reproductive success for widowed males, as predicted by the SA model (Fig. 5.6).

The risk-of-movement hypothesis would apply to small haremic fish as well. In *C. falco*, the reversed sex changers did not alter the location of their territories to any large degree after the sex change (Fig. 5.8; Kadota et al. 2012). This means that reversed-sex-changed individuals can acquire mating opportunities without any

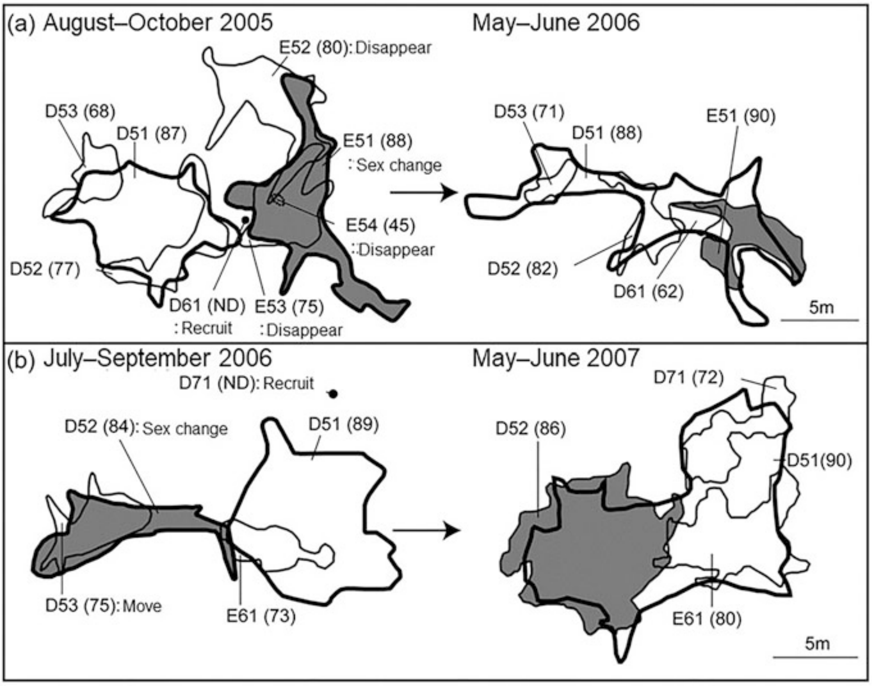

Fig. 5.7 Reversed sex change in *Cirrhitichthys falco* observed on a reef. Thick, thin, and broken lines represent male territories, female territories, and juvenile home ranges, respectively. The shading represents the territory of sex changers. The total length (mm) of each individual is given in parentheses. *ND* no data. (Modified from Kadota et al. 2012)

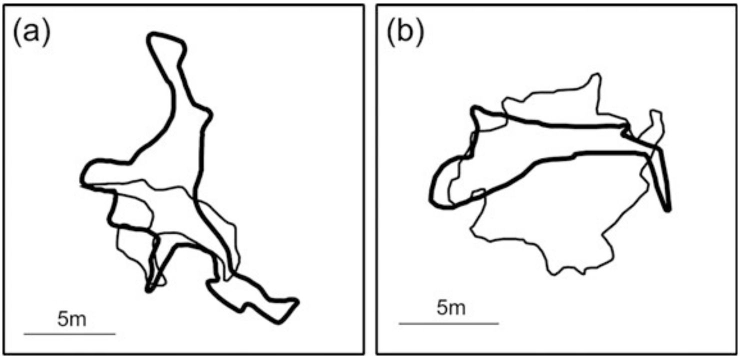

Fig. 5.8 Position of territories before and after reversed sex change in *Cirrhitichthys falco*, as observed on a reef. Panels (**a**) and (**b**) represent the individuals shown in Fig. 5.7a and b, respectively. Thick and thin lines represent territories before (when male) and after (female) sex change, respectively. (Modified from Kadota et al. 2012)

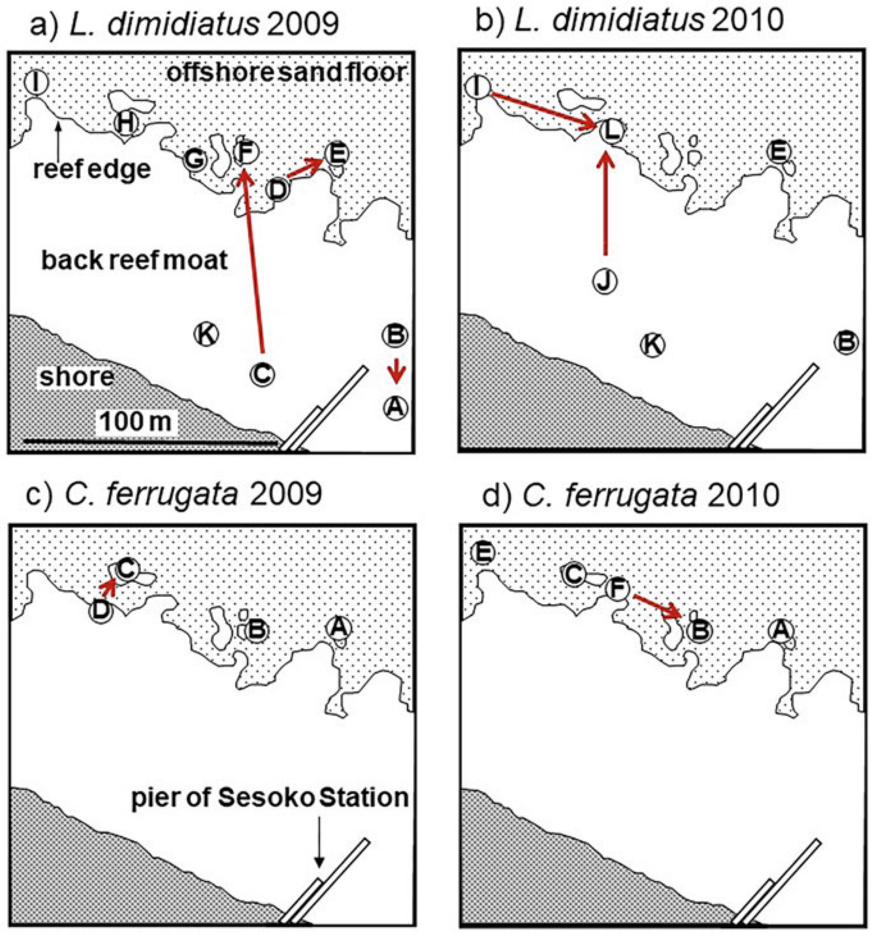

Fig. 5.9 Original sites and the emigration of widowed males in female-removal experiments on coral reefs; site names are designated with capital letters; arrows indicate the movements of the males in the field experiments. *Labroides dimidiatus* in 2009 (**a**) and 2010 (**b**); *Centropyge ferrugata* in 2009 (**c**) and 2010 (**d**). (Modified from Kuwamura et al. 2011)

movements. Kuwamura et al. (2011) conducted female removal experiments in *L. dimidiatus* and *C. ferrugata* and revealed the process of pair formations between widowed males. Four and two male–male pairs in the field experiments were confirmed in *L. dimidiatus* and *C. ferrugata*, respectively. These new male–male pairs were formed with the nearest or second-nearest male in both species (Fig. 5.9). These studies indicate that, in haremic fish, the risk of predation that is associated with searching for a new mate of the opposite sex is reduced by changing sex.

5.5.2 Low-Density Hypothesis for Reversed Sex Change

Reversed sex change has been identified in at least 11 haremic fishes including fish whose mating system changes between harem polygyny and MTV polygamy. However, the reversed sex change was confirmed under natural conditions in only four of the species: *T. okinawae*, *T. grammistes*, *Dascyllus reticulatus*, and *C. falco*. In the other species, reversed sex change was recorded based on field/aquarium experiments or histological evaluation of the gonads. Considering the numerous field studies that have been conducted on sex change in haremic protogynous fish (see Chap. 4), reversed sex change seems to have been too rarely confirmed. In fact, although reversed sex change was shown through field/aquarium experiments, it was never observed under natural conditions in some species for which long-term field experiments have been conducted—such as in field studies of *L. dimidiatus* conducted for approximately 2 years at Heron Island, Great Barrier Reef (Robertson 1972), and at Funakoshi Canal, Shikoku Island, Japan (Sakai et al. 2001), and for 5 years at Shirahama, Honshu Island, Japan (Kuwamura 1984).

The rare occurrence of reversed sex change could be attributable to the densities of studied populations (Kuwamura et al. 2002). Because these population densities are often relatively high, with the number of females in a harem therefore comparatively large, then widowed males would rarely occur, and reversed sex change would consequently not be present to observe. However, facultative monogamy may occur in low-density populations of haremic species (Moyer et al. 1983; Barlow 1984; Petersen 2006). Thus, it is predicted that reversed sex change would happen in low-density populations because widowed males are likely to occur (i.e., low-density hypothesis for reversed sex change: Kuwamura et al. 2002, 2011, 2014). In addition, the theoretical model indicates that not only risk of movement but also the number of females in harems (population density) will influence decision-making by widowed males in favor of reversed sex change, because the benefit of being male is reduced under small harem size (Sawada et al. 2017).

Of the four studies where reversed sex change was confirmed in the wild, at least that of *C. falco* supports the low-density hypothesis. In the study site at Kuchierabu Island, which is located near the northern distributional limit of *C. falco*, recruitments of small individuals including juveniles were not abundant (Kadota et al. 2012). Furthermore, the mean number of females within harems was maintained at around just 2.2 individuals, as harem-fission sex change (see Chap. 4) occurred when the number increased to 4 or more females. A survey of the mating system of this species in several locations in the Pacific (e.g., Guam, Miyake-jima, Lizard Island) reported the mean number of females in a harem at 2.9 individuals (Donaldson 1987); thus, the number recorded at Kuchierabu Island is smaller than that at other areas studied. In addition, the harem sizes of *C. falco* appear to be somewhat smaller in comparison to other haremic and protogynous fish in which reversed sex change has not been observed in nature despite long-term studies. For example, the mean harem size was 2.5–6.0 in *L. dimidiatus* (Robertson 1974; Kuwamura 1984; Sakai et al. 2001) and 2.3–3.0 in *Centropyge* angelfishes (Moyer and Nakazono 1978; Aldenhoven 1986; Sakai and Kohda 1997).

The low-density hypothesis for the reversed sex change in protogynous species predicts the following process of how reversed sex change occurs (Kuwamura et al. 2014): (1) females will sometimes disappear from monogamous pairs, and males will become single; (2) widowed males will wait or move to search for a new mate if no migration of females into their territories occurs, whereas they need not move if migration occurs; (3) moving males will choose a new mate from among the nearest individuals, whether male or females because of the cost or risk of father movement; and (4) when two males form a pair, the smaller will change sex to female according to the rule of social control. To confirm these predictions, Kuwamura et al. (2014) repeatedly removed some or all females from the harems in the study area and created 48 pairs and 56 widowed males in *L. dimidiatus*. The disappearance of females from monogamous pairs was observed, and the disappearance rates did not differ between sexes in the monogamous pairs. In addition, the widowed males moved to form pairs with nearby single fish only when no immigration occurred. Afterward, when two males formed a pair, the smaller changed sex to female. This process supports the predictions of the low-density hypothesis for reversed sex change.

Another interesting field experiment supporting the low-density hypothesis is that of *Dascyllus aruanus* (Kuwamura et al. 2016a). This coral-dwelling damselfish exhibits protogynous sex change in harems on isolated corals, as the SA model predicts. In contrast, sex change rarely occurs (i.e., gonochorism) in high-density populations inhabiting continuous coral-covered habitat (Cole 2002; Asoh 2003; Kuwamura et al. 2016a), where females can choose mates with low risk of movement. So far, reversed sex change has been confirmed by mate-removal experiments on isolated coral heads under low-density conditions only (Kuwamura et al. 2016a).

Furthermore, these studies indicate reversed sex change is unlikely to be the best tactic for widowed males to regain mating opportunities. In field experiments involving *L. dimidiatus* (Kuwamura et al. 2014), of 56 widowed males that were created by female removals, 36 males did not move when females and/or juveniles immigrated into their territories (Fig. 5.10); moreover, 13 males did not move despite no such immigration occurring. Only six males moved or expanded their territories when no immigration occurred; of these six, three males behaved as females, and two of them completed sex change. In the study of *C. falco*, a dominant male was observed to experience widowed status twice, in addition to the cases mentioned above (Kadota et al. 2012). This male regained mating opportunities following the immigration of a female into his territory or by taking a female from a neighboring harem. These studies show that widowed males use reversed sex change as a last resort when they cannot gain new mating opportunities by the immigration of females into their territories or by winning new females from another male's harem.

Not all instances of reserved sex change in *T. okinawae* appear to correspond to the low-density hypothesis for reversed sex change. Of the three instances (Manabe et al. 2007a), a male changed sex to female after mate loss (Fig. 5.4a), while another male changed sex after undergoing early sex change (Fig. 5.4b). In the third case, it was not understandable why the widowed female changed to male (Fig. 5.4c). The

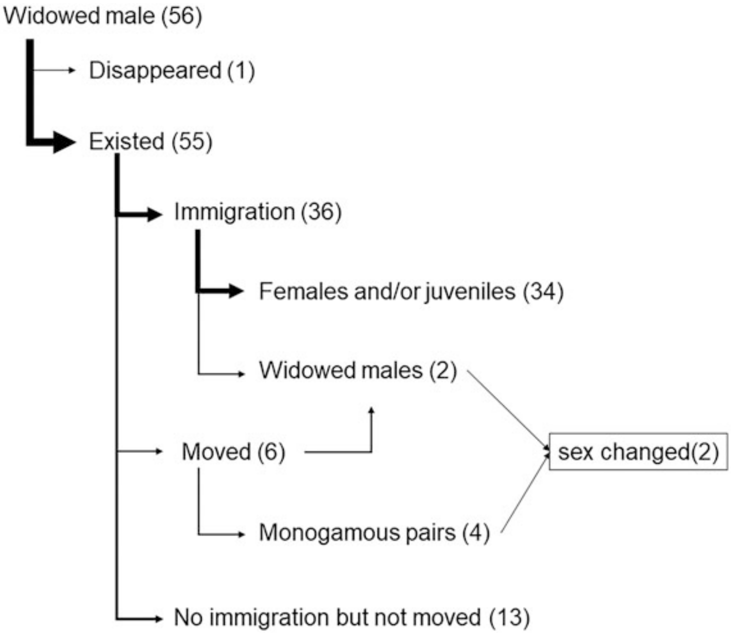

Fig. 5.10 Summary of female-removal experiments on a coral reef to create low-density conditions for the haremic *Labroides dimidiatus*. Numbers in parentheses indicate the number of cases observed. (Drawn from the data of Kuwamura et al. 2014)

first case corresponds to the low-density hypothesis, but the second case does not. Some studies have suggested early sex change is favored in populations characterized by a large harem size and high density (see Chap. 4). This social condition favoring early sex change would be opposed to that favoring reversed sex change. Therefore, the case of reversed sex change in males derived from early sex change can be explained by the low-density hypothesis if the population density drastically changes from high to low.

Ecological conditions driving bidirectional sex change might differ somewhat between small haremic gobies like *Trimma* and other haremic fishes. Ts (time required for sex change; Table 5.2) is considerably shorter in *Trimma* compared with in labroids and pomacanthids, and the relatively short time means higher sexual flexibility in *Trimma*. Sexual flexibility is suggested to be affected by reliability in male reproduction by a comparative study between the gobies *Lythrypnus dalli* and *L. zebra* (St. Mary 1996). *Lythrypnus zebra*, which has a shorter Ts, has shorter nest longevities of the males than those of *L. dalli*, although reproduction as a male is equally advantageous relative to adopting the female role in both species (i.e., the rates of spawning by males to females are similar). Thus, reversed sex change in small haremic gobies with the gonad of delimited type might be a tactic more adapted in response to greater temporal fluctuations in population densities, while in other protogynous fishes with the gonad of non-delimited type, the reversed sex change would be a tactic for low-density populations with more peripherally distributed individuals. Interestingly, reversed sex change in *Trimma* is suggested to evolve from gonochoristic ancestors through evolution of bidirectional sex change in monogamous species (Sunobe et al. 2017), while reversed sex change in the other groups is suggested to evolve from protogynous ancestors (Kuwamura et al. 2014, 2016a), which can reflect difference of primary factor driving bidirectional sex change.

Recently, a new pattern of reversed sex change was reported in *D. reticulatus* (Fig. 5.4c; Sakanoue and Sakai 2022). The mating system of this damselfish is MTV polygamy in short-branching corals (short-branch group) but becomes haremic in long-branching corals (long-branch group) (Sakanoue and Sakai 2019). Sakanoue and Sakai (2022) suggest that moving from a short-branching coral to a long-branching coral would be a particularly important life-history strategy in this damselfish because the spawning frequency of females utilizing the long-branch coral group is approximately three-times as high as females using the short-branch coral group. Moreover, the species' survival rate tends to be higher when occupying a coral of the long-branch group as opposed to the short-branch group. Interestingly, a female could conduct cryptic bachelor sex change, promoting her rapid growth (see Chap. 4), when in a short-branch coral, and then acquired mating status as a female again in a long-branch coral via the sequential processes of group migration and reversed sex change. This reversed sex change is beyond what could be predicated by the low-density hypothesis and indicates the possible existence of a greater variety of reversed sex change patterns than we have previously expected.

In general, reversed sex change occur in low-density condition in haremic fish and risk-of-movement to seek a new mate is important in the evolution. These points are very similar to bidirectional sex change in monogamous fish. However, haremic fish tend to avoid conducting reversed sex change as much as possible (i.e., widowed males use reversed sex change as a last resort when they cannot gain new mating opportunities in any other way). Furthermore, some social conditions of reversed sex change in haremic fish have not been observed in monogamous fish. Males derived from early sex change or cryptic bachelor sex change have been observed to change back to female only in haremic fish. Although we have not known enough about these new types of reversed sex change, these differences could be derived by the difference between mating systems because male reproductive success relative to female in haremic fish is considerably higher and more variable than that in monogamous fish.

5.6 Bidirectional Sex Change in Male-Territory-Visiting (MTV) Polygamy

Bidirectional sex change in MTV polygamy has been reported in the threespot wrasse *Halichoeres trimaculatus* (Fig. 5.11; Kuwamura et al. 2007). Two types of males have been identified among many hermaphroditic labrids, including

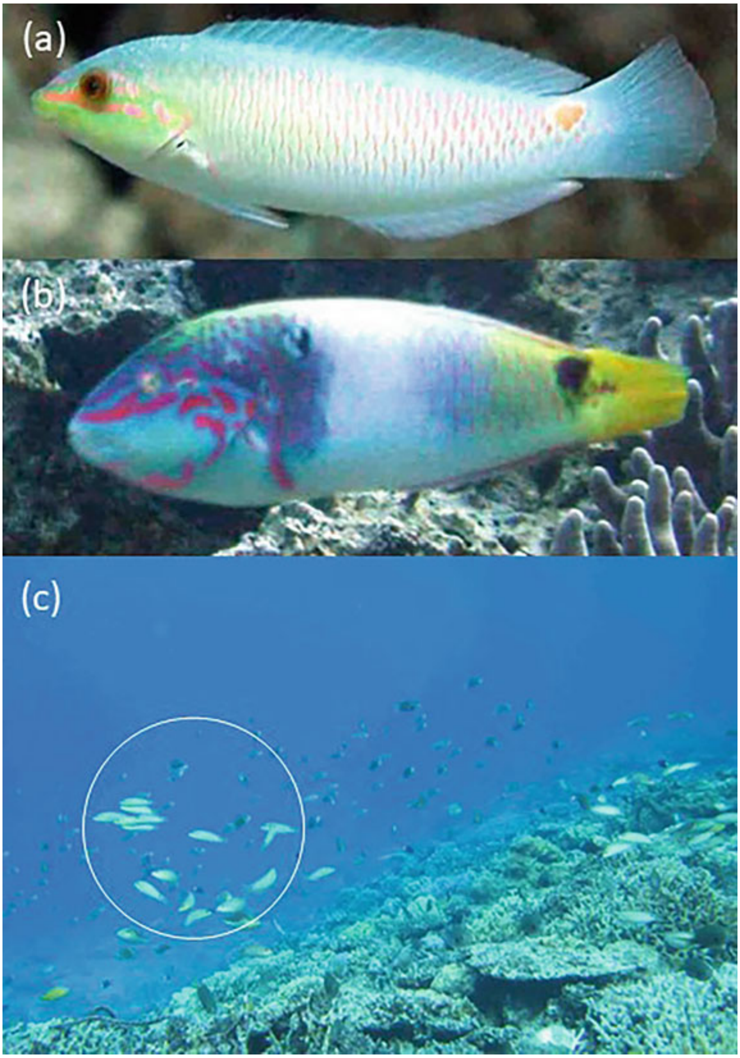

Fig. 5.11 *Halichoeres trimaculatus*: a MTV polygamous fish with bidirectional sex change (photo by T. Kuwamura). Its body coloration changes from initial phase (**a**) to terminal phase (**b**) with the increase of body size. Group spawning (**c**) is one of alternative tactics in *H. trimaculatus*

H. trimaculatus, wherein primary males function as male for their entire lives, and secondary males derive from females through sex change (diandry; Suzuki et al. 2008, 2010; Kuwamura et al. 2016b). In this species, coloration of the small primary male is similar to that of females (i.e., drab; initial phase or IP; Fig. 5.11a), whereas large males, either primary or secondary, assume bright coloration (terminal phase or TP; Fig. 5.11b). Small IP males are non-territorial and participate in group spawning involving multiple IP males and a single female (Fig. 5.11c), streaking by rushing into a spawning pair at the moment of gamete release or sneaking (pair spawning) with a female around the territories of TP males. Large TP males establish mating territories and pair-spawn with visiting females.

Mark-recapture research on *H. trimaculatus* was conducted on the fringing reef of Sesoko Island for 18 months, and sex change of a primary IP male was observed (Kuwamura et al. 2007). This male performed group spawning, streaking, and sneaking during summer in the first year. In the next spring, however, the shape of its urogenital papilla changed to female, and the fish performed pair spawning with a TP male. A gamete cloud was visible at the spawning rush and the abdomen of the IP fish became slender, indicating it had completed the male-to-female sex change. Furthermore, five and one instances of sex change to females were confirmed by aquarium experiments in IP and TP males, respectively (Kuwamura et al. 2007).

Sex change of an IP male is suggested to be affected by population density (Kuwamura et al. 2007). Generally, in the major mating sites on larger reefs, group spawning is predominant by mating groups composed of multiple IP and TP males, because TP males cannot drive out IP males that invade their territories. In contrast, on smaller reefs, pair spawning by TP males becomes predominant, as IP males have few mating opportunities. The proportion of IP males is reported to increase with the local population size or reef size (Warner and Hoffman 1980; Suzuki et al. 2010). Kuwamura et al. (2007) infer the population density would have decreased because the mortality of the studied fish was extremely high before sex change of the IP male. This may have resulted in large territorial TP males successfully excluding small IP males from mating. The IP male can change sex to female due to a loss of mating opportunities as a male. Reversed sex change would be a tactic to adapt to changing reproductive success of alternative tactics according to population density.

5.7 Future Research Directions

Reversed sex change has been reported in species with size-assortative monogamy, harem polygyny, and MTV polygamy. In these mating systems, protogyny is predicted to be favored by the SA model or the growth-rate advantage model. In monogamous fishes and haremic fishes, widowed males change back to female to regain mating opportunities and increase reproductive value through decreasing the risk of movement to seek new mates. In the monogamous gobies, nearly all suitable coral colonies are occupied by a breeding pair and there are few single mature individuals (Kuwamura et al. 1994b; Nakashima et al. 1995; Munday 2002). This situation indicates that mating opportunities for widowed individuals are considerably restricted, which would be similar to the situation in a low-density population of haremic species. Even in haremic fish, reversed sex change would occur in low-density populations where facultative monogamy is likely to occur (Kuwamura et al. 2002, 2014; Kadota et al. 2012; Sawada et al. 2017). Furthermore, low-density condition can drive male-to-female sex change of primary male in MTV polygamous fish by decreasing reproductive success of alternative tactics (Kuwamura et al. 2007). The low-density conditions, where few mating opportunities are expected and simultaneous hermaphrodites are favored (see Chap. 2), would also influence sexual flexibility in sequential hermaphroditism (Kuwamura et al. 2020). The list of species in which reversed sex change can occur has been growing as a result of aquarium and field experiments. However, evidence of reversed sex change under natural conditions has been limited to the Gobiidae (Kuwamura et al. 1994a; Manabe et al. 2007a; Fukuda et al. 2017), Pomacentridae (Sakanoue and Sakai 2022), and Cirrhitidae (Kadota et al. 2012). Field studies of species under low-density conditions can be expected to recognize sexual flexibility in sequential hermaphroditism and reveal the missing link between simultaneous hermaphrodites and sequential hermaphrodites.

The process and advantage of reversed sex change in teleosts has been studied by focusing on changes in the social condition to which the sex changer belonged. However, to clarify the relationship between reversed sex change and other mating tactics, it will be necessary to direct our attention to the social conditions of new groups to which sex changers move and to their surroundings (e.g., number of females in new groups, distance between the groups). Although reversed sex change is a tactic to regain mating opportunity when males have lost all their mates, widowed males do not always change back to female (Kadota et al. 2012; Kuwamura et al. 2014). In addition, the variation in time required for widowed males to form new pairs with other males is reported to be considerably large in *Labroides dimidiatus* and *Centropyge ferrugata* (Kuwamura et al. 2011). These studies suggest that the loss of mating opportunities for males is not the only factor driving reversed sex change but that other factors must be considered. Furthermore, males derived from early sex change or cryptic bachelor sex change have been confirmed to conduct reversed sex change (Manabe et al. 2007a; Sakanoue and Sakai 2022). The study of reversed sex change now merits elucidation of the decision-making of widowed males. Aquarium experiments using small gobies such as *Trimma* could be effective in clarifying this, as a first step. In *Trimma* and related genera, the Ts for male-to-female sex change is considerably shorter when compared with that of other fish with non-delimited gonads. In addition, these gobies display various patterns of the mating system and sexual pattern (Sunobe et al. 2017). Furthermore, not only reversed sex change after the disappearance of all females in a mating group but also early sex changers were observed under natural conditions (Manabe et al. 2007a).

In MTV polygamy, a small male, which had performed alternative mating tactics like group spawning, changed sex and performed pair spawning with a TP male. This sex change would be derived from a decreased advantage of alternative tactics because of a decrease in the population density (Kuwamura et al. 2007). Notably, a similar explanation of reversed sex change could also be applied to larger-sized fish like groupers, to which the risk-of-movement hypothesis would not apply. Continuing research on this topic is expected because the number of reports on reversed sex change in MTV polygamy is currently limited.

5.8 Conclusions

This chapter introduced the following topics related to bidirectional sex change in fish

1. The ability to undergo bidirectional sex change has been confirmed in 7 families, 15 genera, and 69 species (14% of 481 hermaphroditic species), through aquarium experiments, field studies, and histological analyses. Confirmations of bidirectional sex change are most abundant in the Gobiidae (51 species), followed by in the Pomacanthidae (4 species) and Pseudochromidae (4 species). All these families belong to the clade Percomorpha.
2. Aquarium experiments have revealed that bidirectional sex change is socially controlled. In many of these experiments in which two or more individuals of the same sex are held in a tank, larger females change sex to males while smaller males change back to females, according to their position in a social hierarchy based on relative body size.
3. In size-assortative monogamous fish, bidirectional sex change occurs when new same-sex pairs are formed after movements between social groups following mate loss. Widowed individuals tend to prefer pairing with a nearby individual of the same-sex rather than undertaking long-distance movement to pair with an opposite-sex individual. The ability of bidirectional sex change would increase their reproductive value by reducing the risk of movement to seek a new mate.
4. In haremic fish, in which protogyny is predicted by the SA model, males change back to females when all females disappear from the mating group, and they then move to a mating group dominated by a larger male. However, widowed males do not conduct reversed sex change when females or juveniles immigrate into their mating group or when they can take a female from a neighboring harem. Thus, widowed males use reversed sex change as a last resort when they cannot gain new mating opportunities in any other way, which is more likely to occur in low-density populations, because the number of females in a mating group tends to become small and immigrations rarely occur, as shown by some field studies.
5. In MTV polygamous fish, a small male, which has performed alternative mating tactics like group spawning, changes sex to perform pair spawning with a TP male. This may have resulted in large territorial TP males successfully excluding small IP males from mating owing to the decrease in population density. Reversed sex change would be a tactic to adapt to changing reproductive success of alternative tactics according to the population density.
6. The low-density conditions, where few mating opportunities are expected and simultaneous hermaphrodites are favored would also influence sexual flexibility in sequential hermaphroditism. However, research observations of reversed sex change under natural conditions are limited to the Gobiidae, Pomacentridae, and Cirrhitidae. Field studies of populations under low-density conditions are expected to recognize sexual flexibility in sequential hermaphroditism and to inform the link between simultaneous hermaphrodites and sequential hermaphrodites.

Acknowledgements I thank Tetsuo Kuwamura, Yoichi Sakai, Kota Sawada, and Tomoki Sunobe for helpful comments to improve the manuscript. I also thank Cynthia Kulongowski with Edanz (jp.edanz.com) for the English language review. Thanks also due to Tomonobu Uryu (Marin Life Navigation) for giving the opportunity to take pictures of *Cirrhitichthys aureus*.

References

Aldenhoven JM (1986) Different reproductive strategies in a sex-changing coral reef fish *Centropyge bicolor* (Pomacanthidae). Aust J Mar Freshw Res 37:353–360

Asoh K (2003) Gonadal development and infrequent sex change in a population of the humbug damselfish, *Dascyllus aruanus* in continuous coral-cover habitat. Mar Biol 142:1207–1218

Asoh K (2005) Gonadal development and diandric protogyny in two populations of *Dascyllus reticulatus* from Madang, Papua New Guinea. J Fish Biol 66:1127–1148

Barlow GW (1984) Patterns of monogamy among teleost fishes. Arch FischWiss 35:75–123

Black MP, Reavis RH, Grober MS (2004) Socially induced sex change regulates forebrain isotocin in *Lythrypnus dalli*. Neuroreport 15:185–189

Black MP, Balthazart J, Baillien M, Grober MS (2005a) Socially induced and rapid increases in aggression are inversely related to brain aromatase activity in a sex-changing fish, *Lythrypnus dalli*. Proc R Soc B Biol Sci 272:2435–2440

Black MP, Moore B, Canario AVM, Ford D, Reavis RH, Grober MS (2005b) Reproduction in context: field testing a laboratory model of socially controlled sex change in *Lythrypnus dalli* (Gilbert). J Exp Mar Biol Ecol 318:127–143

Chen J, Xiao L, Peng C, Ye Z, Wang D, Yang Y, Zhang H, Zhao M, Li S, Lin H, Zhang Y (2019) Socially controlled male-to-female sex reversal in the protogynous orange-spotted grouper, *Epinephelus coioides*. J Fish Biol 94:414–421

Chen J, Chen H, Peng C, Ye Z, Zhao M, Xiao L, Zhang H, Li S, Lin H, Zhang Y (2020) A highly efficient method of inducing sex change using social control in the protogynous orange-spotted grouper (*Epinephelus coioides*). Aquaculture 517:734787

Chen J, Peng C, Huang J, Shi H, Xiao L, Tang L, Lin H, Li S, Zhang Y (2021) Physical interactions facilitate sex change in the protogynous orange-spotted grouper, *Epinephelus coioides*. J Fish Biol 98:1308–1320

Coates D (1982) Some observations on the sexuality of humbug damselfish, *Dascyllus aruanus* (Pisces, Pomacentridae) in the field. Z Tierpsychol 59:7–18

Cole KS (1990) Patterns of gonad structure in hermaphroditic gobies (Teleostei, Gobiidae). Environ Biol Fishes 28:125–142

Cole KS (2002) Gonad morphology, sexual development, and colony composition in the obligate coral-dwelling damselfish *Dascyllus aruanus*. Mar Biol 140:151–163

Donaldson TJ (1987) Social organization and reproductive behavior of the hawkfish *Cirrhitichthys falco* (Cirrhitidae). Bull Mar Sci 41:531–540

Fricke HW, Holzberg S (1974) Social units and hermaphroditism in a pomacentrid fish. Naturwissenschaften 61:367–368

Fukuda K, Sunobe T (2020) Group structure and putative mating system of three hermaphrodite gobiid fish, *Priolepis akihitoi*, *Trimma emeryi*, and *Trimma hayashii* (Actinopterygii: Gobiiformes). Ichthyol Res 67:552–558

Fukuda K, Tanazawa T, Sunobe T (2017) Polygynous mating system and field evidence for bidirectional sex change in the gobiid fish *Trimma grammistes*. Int J Pure Appl Zool 5:92–99

Ghiselin MT (1969) The evolution of hermaphroditism among animals. Q Rev Biol 44:189–208

Hioki S, Suzuki K (1996) Sex changing from male to female on the way of protogynous process in three Centropyge angelfishes (Pomacanthidae: Teleostei). Bull Inst Oceanic Res Dev Tokai Univ 17:27–34

Iwasa Y (1991) Sex change evolution and cost of reproduction. Behav Ecol 2:56–68

Kadota T, Osato J, Hashimoto H, Sakai Y (2011) Harem structure and female territoriality in the dwarf hawkfish *Cirrhitichthys falco* (Cirrhitidae). Environ Biol Fishes 92:79–88

Kadota T, Osato J, Nagata K, Sakai Y (2012) Reversed sex change in the haremic protogynous hawkfish *Cirrhitichthys falco* in natural conditions. Ethology 118:226–234

Kobayashi K, Suzuki K (1992) Hermaphroditism and sexual function in *Cirrhitichthys aureus* and other Japanese hawkfishes (Cirrhitidae: Teleostei). Jpn J Ichthyol 38:397–410

Kroon FJ, Munday PL, Pankhurst NW (2003) Steroid hormone levels and bi-directional sex change in *Gobiodon histrio*. J Fish Biol 62:153–167

Kuwamura T (1984) Social structure of the protogynous fish *Labroides dimidiatus*. Publ Seto Mar Biol Lab 29:117–177

Kuwamura T, Nakashima Y (1998) New aspects of sex change among reef fishes: recent studies in Japan. Environ Biol Fishes 52:125–135

Kuwamura T, Yogo Y, Nakashima Y (1993) Size-assortative monogamy and paternal egg care in a coral goby *Paragobiodon echinocephalus*. Ethology 95:65–75

Kuwamura T, Nakashima Y, Yogo Y (1994a) Sex change in either direction by growth-rate advantage in the monogamous coral goby, *Paragobiodon echinocephalus*. Behav Ecol 5:434–438

Kuwamura T, Yogo Y, Nakashima Y (1994b) Population dynamics of goby *Paragobiodon echinocephalus* and host coral *Stylophora pistillata*. Mar Ecol Prog Ser 103:17–23

Kuwamura T, Tanaka N, Nakashima Y, Karino K, Sakai Y (2002) Reversed sex-change in the protogynous reef fish *Labroides dimidiatus*. Ethology 108:443–450

Kuwamura T, Suzuki S, Tanaka N, Ouchi E, Karino K, Nakashima Y (2007) Sex change of primary males in a diandric labrid *Halichoeres trimaculatus*: coexistence of protandry and protogyny within a species. J Fish Biol 70:1898–1906

Kuwamura T, Suzuki S, Kadota T (2011) Reversed sex change by widowed males in polygynous and protogynous fishes: female removal experiments in the field. Naturwissenschaften 98:1041–1048

Kuwamura T, Kadota T, Suzuki S (2014) Testing the low-density hypothesis for reversed sex change in polygynous fish: experiments in *Labroides dimidiatus*. Sci Rep 4:4369

Kuwamura T, Kadota T, Suzuki S (2015) Bidirectional sex change in the magenta dottyback *Pictichromis porphyrea*: first evidence from the field in Pseudochromidae. Environ Biol Fishes 98:201–207

Kuwamura T, Suzuki S, Kadota T (2016a) Male-to-female sex change in widowed males of the protogynous damselfish *Dascyllus aruanus*. J Ethol 34:85–88

Kuwamura T, Suzuki S, Kadota T (2016b) Interspecific variation in the spawning time of labrid fish on a fringing reef at Iriomote Island, Okinawa. Ichthyol Res 63:460–469

Kuwamura T, Sunobe T, Sakai Y, Kadota T, Sawada K (2020) Hermaphroditism in fishes: an annotated list of species, phylogeny, and mating system. Ichthyol Res 67:341–360

Lassig BR (1976) Field observations on the reproductive behaviour of *Paragobiodon* spp. (Osteichthyes: Gobiidae) at Heron Island Great Barrier Reef. Mar Behav Physiol 3:283–293

Lassig BR (1977) Socioecological strategies adopted by obligate coral dwelling fishes. In: Proceedings of 3rd International Coral Reef Symposium. University of Miami, Miami, pp 565–570

Liu M, Sadovy Y (2004a) Early gonadal development and primary males in the protogynous epinepheline, *Cephalopholis boenak*. J Fish Biol 65:987–1002

Liu M, Sadovy Y (2004b) The influence of social factors on adult sex change and juvenile sexual differentiation in a diandric, protogynous epinepheline, *Cephalopholis boenak* (Pisces, Serranidae). J Zool 264:239–248

Liu M, Sadovy Y (2005) Habitat association and social structure of the chocolate hind, *Cephalopholis boenak* (Pisces: Serranidae: Epinephelinae), at Ping Chau Island, northeastern Hong Kong waters. Environ Biol Fishes 74:9–18

Liu M, Sadovy de Mitcheson Y (2011) The influence of social factors on juvenile sexual differentiation in a diandric, protogynous grouper *Epinephelus coioides*. Ichthyol Res 58:84–89

Lorenzi V, Earley RL, Grober MS (2006) Preventing behavioural interactions with a male facilitates sex change in female bluebanded gobies, *Lythrypnus dalli*. Behav Ecol Sociobiol 59:715–722

Manabe H, Ishimura M, Shinomiya A, Sunobe T (2007a) Field evidence for bi-directional sex change in the polygynous gobiid fish *Trimma okinawae*. J Fish Biol 70:600–609

Manabe H, Ishimura M, Shinomiya A, Sunobe T (2007b) Inter-group movement of females of the polygynous gobiid fish *Trimma okinawae* in relation to timing of protogynous sex change. J Ethol 25:133–137

Manabe H, Matsuoka M, Goto K, Dewa S, Shinomiya A, Sakurai M, Sunobe T (2008) Bi-directional sex change in the gobiid fish *Trimma* sp.: does size-advantage exist? Behaviour 145:99–113

Manabe H, Toyoda K, Nagamoto K, Dewa S, Sakurai M, Hagiwara K, Shinomiya A, Sunobe T (2013) Bidirectional sex change in seven species of *Priolepis* (Actinopterygii: Gobiidae). Bull Mar Sci 89:635–642

Maxfield JM, Cole KS (2019a) Patterns of structural change in gonads of the divine dwarfgoby *Eviota epiphanes* as they sexually transition. J Fish Biol 94:142–153

Maxfield JM, Cole KS (2019b) Structural changes in the ovotestis of the bidirectional hermaphrodite, the blue-banded goby (*Lythrypnus dalli*), during transition from ova production to sperm production. Environ Biol Fishes 102:1393–1404

Moyer JT, Nakazono A (1978) Population structure, reproductive behavior and protogynous hermaphroditism in angelfish *Centropyge interruptus* at Miyake-jima, Japan. Jpn J Ichthyol 25:25–39

Moyer JT, Thresher RE, Colin PL (1983) Courtship, spawning and inferred social organization of American angelfishes (Genera *Pomacanhthus*, *Holacanthus* and *Centropyge*; Pomacanthidae). Environ Biol Fish 9:25–39

Munday PL (2002) Bi-directional sex change: testing the growth-rate advantage model. Behav Ecol Sociobiol 52:247–254

Munday PL, Molony BW (2002) The energetic cost of protogynous versus protandrous sex change in the bi-directional sex-changing fish *Gobiodon histrio*. Mar Biol 141:1011–1017

Munday PL, Caley MJ, Jones GP (1998) Bi-directional sex change in a coral-dwelling goby. Behav Ecol Sociobiol 43:371–377

Munday PL, Buston PM, Warner RR (2006) Diversity and flexibility of sex-change strategies in animals. Trends Ecol Evol 21:89–95

Munday PL, Kuwamura T, Kroon FJ (2010) Bidirectional sex change in marine fishes. In: Cole KS (ed) Reproduction and sexuality in marine fishes: patterns and processes. University of California Press, Berkeley, pp 241–271

Muñoz RC, Warner RR (2003) Alternative contexts of sex change with social control in the bucktooth parrotfish, *Sparisoma radians*. Environ Biol Fishes 68:307–319

Muñoz RC, Warner RR (2004) Testing a new version of the size-advantage hypothesis for sex change: sperm competition and size-skew effects in the bucktooth parrotfish, *Sparisoma radians*. Behav Ecol 15:129–136

Muñoz-Arroyo S, Rodríguez-Jaramillo C, Balart EF (2019) The goby *Lythrypnus pulchellus* is a bi-directional sex changer. Environ Biol Fishes 102:1377–1391

Nakashima Y, Kuwamura T, Yogo Y (1995) Why be a both-ways sex changer? Ethology 101:301–307

Nakashima Y, Kuwamura T, Yogo Y (1996) Both-ways sex change in monogamous coral gobies, *Gobiodon* spp. Environ Biol Fishes 46:281–288

Nakashima Y, Sakai Y, Karino K, Kuwamura T (2000) Female-female spawning and sex change in a haremic coral-reef fish, *Labroides dimidiatus*. Zool Sci 17:967–970

Nakazono A, Kuwamura T (eds) (1987) Sex change in fishes. Tokai University Press, Tokyo

Nelson JS, Grande TC, Wilson MVH (2016) Fishes of the world, 5th edn. John Wiley & Sons, New Jersey

Oh SR, Kang HC, Lee CH, Hur SW, Lee YD (2013) Sex reversal and masculinization according to growth in longtooth grouper *Epinephelus bruneus*. Dev Reprod 17:79–85

Okumura S (2001) Evidence of sex reversal towards both directions in reared red spotted grouper *Epinephelus akaara*. Fish Sci 67:535–537

Oyama T, Tomatsu S, Manabe H, Sakurai M, Matsuoka M, Shinomiya A, Dewa S, Sunobe T (2022) Monogamous mating system and protandrous-like sexuality in the goby *Trimma taylori*. Ichthyol Res 70. https://doi.org/10.1007/s10228-022-00876-z

Petersen CW (2006) Sexual selection and reproductive success in hermaphroditic seabasses. Integr Comp Biol 46:439–448

Quinitio GF, Caberoy NB, Reyes DM (1997) Induction of sex change in female *Epinephelus coioides* by social control. Isr J Aquac 49:77–83

Reavis RH, Grober MS (1999) An integrative approach to sex change: social, behavioural and neurochemical changes in *Lythrypnus dalli* (Pisces). Acta Ethol 2:51–60

Robertson DR (1972) Social control of sex reversal in a coral reef fish. Science 177:1007

Robertson DR (1974) A study of the ethology and reproductive biology of the labrid fish, *Labroides dimidiatus*, at Heron Island, Great Barrier Reef. Ph. D. Thesis. University of Queensland, Brisbane

Rodgers EW, Drane S, Grober MS (2005) Sex reversal in pairs of *Lythrypnus dalli*: behavioral and morphological changes. Biol Bull 208:120–126

Rodgers EW, Earley RL, Grober MS (2007) Social status determines sexual phenotype in the bi-directional sex changing bluebanded goby *Lythrypnus dalli*. J Fish Biol 70:1660–1668

Sadovy Y, Donaldson TJ (1995) Sexual pattern of *Neocirrhites armatus* (Cirrhitidae) with notes on other hawkfish species. Environ Biol Fishes 42:143–150

Sakai Y (1997) Alternative spawning tactics of female angelfish according to two different contexts of sex change. Behav Ecol 8:372–377

Sakai Y, Kohda M (1997) Harem structure of the protogynous angelfish, *Centropyge ferrugatus* (Pomacanthidae). Environ Biol Fishes 49:333–339

Sakai Y, Kohda M, Kuwamura T (2001) Effect of changing harem on timing of sex change in female cleaner fish *Labroides dimidiatus*. Anim Behav 62:251–257

Sakai Y, Karino K, Kuwamura T, Nakashima Y, Maruo Y (2003) Sexually dichromatic protogynous angelfish *Centropyge ferrugata* (Pomacanthidae) males can change back to females. Zool Sci 20:627–633

Sakanoue R, Sakai Y (2019) Dual social structures in harem-like colony groups of the coral-dwelling damselfish *Dascyllus reticulatus* depending on body size and sheltering coral structures. J Ethol 37:175–186

Sakanoue R, Sakai Y (2022) Cryptic bachelor sex change in harem colonial groups of the coral-dwelling damselfish *Dascyllus reticulatus*. J Ethol 40:181–192

Sakurai M, Nakakoji S, Manabe H, Dewa S, Shinomiya A, Sunobe T (2009) Bi-directional sex change and gonad structure in the gobiid fish *Trimma yanagitai*. Ichthyol Res 56:82–86

Sawada K, Yamaguchi S, Iwasa Y (2017) Be a good loser: a theoretical model for subordinate decision-making on bi-directional sex change in haremic fishes. J Theor Biol 421:127–135

Schwarz AL, Smith CL (1990) Sex change in the damselfish *Dascyllus reticulatus* (Richardson) (Perciformes: Pomacentridae). Bull Mar Sci 46:790–798

Shapiro DY, Marconato A, Yoshikawa T (1994) Sperm economy in a coral reef fish, *Thalassemia bifasciatum*. Ecology 75:1334–1344

Shiobara Y (2000) Reproduction and hermaphroditism of the gobiid fish, *Trimma grammistes*, from Suruga Bay, central Japan. Sci Rep Mus Tokai Univ 2:19–30

Shpigel M, Fishelson L (1986) Behavior and physiology of coexistence in two species of *Dascyllus* (Pomacentridae, Teleostei). Environ Biol Fishes 17:253–265

St. Mary CM (1994) Sex allocation in a simultaneous hermaphrodite, the blue-banded goby (*Lythrypnus dalli*): the effect of body size and behavioral gender and the consequences for reproduction. Behav Ecol 5:304–313

St. Mary CM (1996) Sex allocation in a simultaneous hermaphrodite, the zebra goby *Lythrypnus zebra*: insights gained through a comparison with its sympatric congener, *Lythrypnus dalli*. Environ Biol Fishes 45:177–190

Sunobe T, Nakazono A (1990) Polygynous mating system of *Trimma okinawae* (Pisces, Gobiidae) at Kagoshima, Japan with a note on sex change. Ethology 84:133–143

Sunobe T, Nakazono A (1993) Sex change in both directions by alteration of social dominance in *Trimma okinawae* (Pisces: Gobiidae). Ethology 94:339–345

Sunobe T, Nakazono A (1999) Mating system and hermaphroditism in the gobiid fish, *Priolepis cincta*, at Kagoshima, Japan. Ichthyol Res 46:103–105

Sunobe T, Nakamura M, Kobayashi Y, Kobayashi T, Nagahama Y (2005) Aromatase immunoreactivity and the role of enzymes in steroid pathways for inducing sex change in the hermaphrodite gobiid fish *Trimma okinawae*. Comp Biochem Phys A 141:54–59

Sunobe T, Sado T, Hagiwara K, Manabe H, Suzuki T, Kobayashi Y, Sakurai M, Dewa S, Matsuoka M, Shinomiya A, Fukuda K, Miya M (2017) Evolution of bidirectional sex change and gonochorism in fishes of the gobiid genera *Trimma, Priolepis*, and *Trimmatom*. Sci Nat 104: 15

Suzuki S, Toguchi K, Makino Y, Kuwamura T, Nakashima Y, Karino K (2008) Group spawning results from the streaking of small males into a sneaking pair: male alternative reproductive tactics in the threespot wrasse *Halichoeres trimaculatus*. J Ethol 26:397–404

Suzuki S, Kuwamura T, Nakashima Y, Karino K, Kohda M (2010) Social factors of group spawning as an alternative mating tactic in the territorial males of the threespot wrasse *Halichoeres trimaculatus*. Environ Biol Fishes 89:71–77

Tanaka H, Hirose K, Nogami K, Hattori K, Ishibashi N (1990) Sexual maturation and sex reversal in red spotted grouper, *Epinephelus akaara*. Bull Natl Res Inst Aquac 17:1–15

Thompson VJ, Munday PL, Jones GP (2007) Habitat patch size and mating system as determinants of social group size in coral-dwelling fishes. Coral Reefs 26:165–174

Thresher RE (1982) Courtship and spawning in the emperor angelfish *Pomacanthus imperator*, with comments on reproduction by other pomacanthid fishes. Mar Biol 70:149–156

Tokunaga S, Kadota T, Watanabe YY, Kuwamura T, Kawabata Y (2022) Idea paper: effects of gonad type and body mass on the time required for sex change in fishes. Ecol Res 37:490–494

Tomatsu S, Ogiso K, Fukuda K, Deki M, Dewa S, Manabe H, Sakurai M, Shinomiya A, Sunobe T (2018) Multi-male group and bidirectional sex change in the gobiid fish, *Trimma caudomaculatum*. Ichthyol Res 65:502–506

Warner RR (1975) The adaptive significance of sequential hermaphroditism in animals. Am Nat 109:61–82

Warner RR (1984) Mating behavior and hermaphroditism in coral reef fishes. Am Sci 72:128–136

Warner RR, Hoffman SG (1980) Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.). Evolution 34:508–518

Wittenrich ML, Munday PL (2005) Bi-directional sex change in coral reef fishes from the family Pseudochromidae: an experimental evaluation. Zool Sci 22:797–803

Wong MYL, Fauvelot C, Planes S, Buston PM (2012) Discrete and continuous reproductive tactics in a hermaphroditic society. Anim Behav 84:897–906

Chapter 6
Database of Hermaphroditic Fish Species and References

Tetsuo Kuwamura, Kota Sawada, Tomoki Sunobe, Yoichi Sakai, and Tatsuru Kadota

Abstract This chapter provides a database of hermaphroditic fishes and references. The database includes, for each species, the type of hermaphroditism, method of confirmation (evidence), mating system, habitat, references, and remarks. Kuwamura et al. (2020) reported 461 species as functional hermaphroditic fishes; 21 species were added, and one species was deleted in this database.

Keywords Bidirectional sex change · Functional hermaphroditism · Protandry · Protogyny · Reversed sex change · Simultaneous hermaphroditism · Teleost fish

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T. Kuwamura et al. (eds.), *Hermaphroditism and Mating Systems in Fish*,
https://doi.org/10.1007/978-981-19-6095-6_6

As explained in Kuwamura et al. (2020), 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, the type of hermaphroditism, method of confirmation (evidence), mating system, habitat, references, and remarks were recorded.

A database of hermaphroditic fish species is presented in Appendix. Order and family names are arranged following Nelson et al. (2016) and genus and species in alphabetical order within each family and genus, respectively. Species name and habitat are based on FishBase (https://www.fishbase.in). When a different genus or species name was used in the reference, it is shown in the Remarks. 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 or macroscopic observation of eggs and sperm is also useful to confirm sexual maturation. For species for which functional hermaphroditism has been suggested by weak evidence, the type of hermaphroditism is marked with a question mark and the rationale is noted in the Remarks. The database has been modified from Table S1 of Kuwamura et al. (2020) by adding 23 species (2 with question marks) and deleting 1 species.

Appendix Database of Hermaphroditic Fish Species

(Modified from Table S1 of Kuwamura et al. 2020)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Anguilliformes							
Muraenidae	*Echidna nebulosa*	Protogyny?	Histology*	Unknown	Coral reef	Fishelson 1992	*small sample size
Muraenidae	*Gymnothorax gracilicauda*	Protogyny?	Histology*	Unknown	Coral reef	Fishelson 1992	*small sample size
Muraenidae	*Gymnothorax griseus*	Simultaneous	Histology	Unknown	Coral reef	Fishelson 1992	*Siderea grisea*
Muraenidae	*Gymnothorax fimbriatus*	Protogyny?	Histology*	Unknown	Coral reef	Fishelson 1992	*small sample size
Muraenidae	*Gymnothorax flavimarginatus*	Protogyny?	Histology*	Unknown	Coral reef	Fishelson 1992	*small sample size
Muraenidae	*Gymnothorax margaritophorus*	Protogyny?	Histology*	Unknown	Coral reef	Fishelson 1992	*small sample size
Muraenidae	*Gymnothorax pictus*	Simultaneous	Histology	Unknown	Coral reef	Fishelson 1992	*Siderea picta*
Muraenidae	*Gymnothorax thyrsoideus*	Simultaneous	Histology	Unknown	Coral reef	Fishelson 1992	*Siderea thyrzoidea*
Muraenidae	*Gymnomuraena zebra*	Protogyny?	Histology*	Unknown	Coral reef	Fishelson 1992	*small sample size
Muraenidae	*Muraena pavonina*	Protogyny?	Histology*	Unknown	Coral reef	Fishelson 1992	*small sample size
Muraenidae	*Rhinomuraena quaesita*	Protandry	Histology (1, 2), aquarium (1)*	Unknown	Coral reef	(1) Shen et al. 1979, (2) Fishelson 1990	*color change only
Muraenidae	*Uropterygius fasciolatus*	Protogyny?	Histology*	Unknown	Coral reef	Fishelson 1992	*small sample size
Muraenidae	*Uropterygius polyspilus*	Protogyny?	Histology*	Unknown	Coral reef	Fishelson 1992	*small sample size
Clupeiformes							
Clupeidae	*Tenualosa macrura*	Protandry	Histology (1, 2)	Unknown	Tropical estuaries and coastal	(1) Blaber et al. 1999, (2) Blaber et al. 2005	
Clupeidae	*Tenualosa toli*	Protandry	Histology	Unknown	Tropical estuaries and coastal	Blaber et al. 1996	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Cypriniformes							
Cobitidae	*Cobitis taenia*	Protandry (1), gonochorism (2, 3)	Histology (1, 2, 3)	Unknown	Freshwater	(1) Lodi 1967, (2) Lodi 1980a, (3) Rasotto 1992	
Stomiiformes							
Gonostomatidae	*Cyclothone atraria*	Protandry	Microscopic, histology (1, 2)	Unknown	Deep sea	(1) Miya & Nemoto 1985, (2) Miya & Nemoto 1987	
Gonostomatidae	*Cyclothone microdon*	Protandry	Microscopic, histology	Unknown	Deep sea	Badcock & Merrett 1976	
Gonostomatidae	*Gonostoma elongatum*	Protandry	Microscopic, histology	Unknown	Deep sea	Fisher 1983	
Gonostomatidae	*Sigmops bathyphilum*	Protandry	Microscopic, histology	Unknown	Deep sea	Badcock 1986	*Gonostoma*
Gonostomatidae	*Sigmops gracile*	Protandry	Microscopic, histology	Unknown	Deep sea	Kawaguchi & Marumo 1967	*Gonostoma*
Aulopiformes							
Ipnopidae	*Bathymicrops brevianalis*	Simultaneous	Histology	Unknown	Deep sea	Nielsen 1966	
Ipnopidae	*Bathymicrops regis*	Simultaneous	Histology	Unknown	Deep sea	Nielsen 1966	
Ipnopidae	*Bathypterois grallator*	Simultaneous	Histology	Unknown	Deep sea	Mead 1960	*Benthosaurus*
Ipnopidae	*Bathypterois mediterraneus*	Simultaneous	Histology (1, 2)	Unknown	Deep sea	(1) Fishelson & Galil 2001, (2) Porcu et al. 2010	
Ipnopidae	*Bathypterois quadrifilis*	Simultaneous	Histology	Unknown	Deep sea	Mead 1960	
Ipnopidae	*Bathypterois viridensis*	Simultaneous	Histology	Unknown	Deep sea	Mead 1960	

Ipnopidae	*Bathytyphlops marionae*	Simultaneous	Histology	Unknown	Deep sea	Nielsen 1966	
Ipnopidae	*Bathytyphlops sewelli*	Simultaneous?	Histology*	Unknown	Deep sea	Merrett 1980	*male function not confirmed
Ipnopidae	*Ipnops agassizii*	Simultaneous	Histology	Unknown	Deep sea	Nielsen 1966	
Ipnopidae	*Ipnops meadi*	Simultaneous	Histology	Unknown	Deep sea	Nielsen 1966	
Giganturidae	*Gigantura chuni*	Simultaneous	Histology	Pair-bonding? (2)	Deep sea	(1) Johnson & Bertelsen 1991, (2) Kupchik et al. 2018	
Giganturidae	*Gigantura indica*	Gonochorism? (1), simultaneous (2)	Microscopic* (1), histology (2)	Pair-bonding? (3)	Deep sea	(1) Clarke & Wagner 1976, (2) Johnson & Bertelsen 1991, (3) Kupchik et al. 2018	*Bathyleptus lisae* (1), *only one matured specimen
Bathysauridae	*Bathysaurus ferox*	Simultaneous	Histology	Unknown	Deep sea	Sulak et al. 1985	
Bathysauridae	*Bathysaurus mollis*	Simultaneous	Histology	Unknown	Deep sea	Sulak et al. 1985	
Chlorophthalmidae	*Chlorophthalmus agassizi*	Simultaneous	Histology	Unknown	Deep sea	Cabiddu et al. 2010	
Chlorophthalmidae	*Chlorophthalmus brasiliensis*	Simultaneous	Histology	Unknown	Deep sea	Mead 1960	
Chlorophthalmidae	*Parasudis truculenta*	Simultaneous	Histology	Unknown	Deep sea	Mead 1960	*P. truculentus*
Notosudidae	*Ahliesaurus brevis*	Simultaneous	Histology	Unknown	Deep sea	Bertelsen et al. 1976	
Scopelarchidae	*Benthalbella infans*	Simultaneous	Histology	Unknown	Deep sea	Merrett et al. 1973	
Scopelarchidae	*Scopelarchus guentheri*	Simultaneous	Histology	Unknown	Deep sea	Merrett et al. 1973	
Paralepididae	*Arctozenus risso*	Simultaneous	Histology	Unknown	Deep sea	Devine & Guelpen 2021	
Paralepididae	*Lestidium pseudosphyraenoides*	Simultaneous	Histology	Unknown	Deep sea	Mead 1960	
Alepisauridae	*Alepisaurus brevirostris*	Simultaneous?	Histology*	Unknown	Deep sea	Gibbs 1960	*poor fixation
Alepisauridae	*Alepisaurus ferox*	Simultaneous?	Histology*	Unknown	Deep sea	Gibbs 1960	*poor fixation

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Alepisauridae	*Omosudis lowii*	Simultaneous	Histology (1, 2)	Unknown	Deep sea	(1) Smith & Atz 1973, (2) Merrett et al. 1973	*O. lowei*
Gobiiformes							
Gobiidae	*Bryaninops yongei*	Bidirectional?	Histology*	Monogamy	Coral reef	Munday et al. 2002	*suggested from gonadal structure
Gobiidae	*Coryphopterus alloides*	Protogyny	Histology	Unknown	Coral reef	Cole & Shapiro 1990	
Gobiidae	*Coryphopterus dicrus*	Protogyny	Histology, aquarium	Unknown	Coral reef	Cole & Shapiro 1990	
Gobiidae	*Coryphopterus eidolon*	Protogyny	Histology	Unknown	Coral reef	Cole & Shapiro 1990	
Gobiidae	*Coryphopterus glaucofraenum*	Protogyny	Histology (1), aquarium (1, 2)	MTV polygamy (3)	Coral reef	(1) Cole & Shapiro 1992, (2) Cole & Shapiro 1995, (3) Forrester et al. 2011, (4) Baldwin et al. 2009, (5) Kramer et al. 2009	Including *C. tortugae* and *C. venezuelae*? (4, 5)
Gobiidae	*Coryphopterus hyalinus*	Protogyny	Histology, aquarium	Unknown	Coral reef	Cole & Shapiro 1990	
Gobiidae	*Coryphopterus lipernes*	Protogyny	Histology, aquarium	Unknown	Coral reef	Cole & Shapiro 1990	
Gobiidae	*Coryphopterus personatus*	Protogyny	Histology (1, 2), aquarium (1, 2, 3)	Unknown	Coral reef	(1) Robertson & Justines 1982, (2) Cole & Robertson 1988, (3) Allsop & West 2004	
Gobiidae	*Coryphopterus thrix*	Protogyny	Histology	Unknown	Coral reef	Cole & Shapiro 1990	
Gobiidae	*Coryphopterus urospilus*	Protogyny	Histology	Unknown	Coral reef	Cole & Shapiro 1990	
Gobiidae	*Eviota epiphanes*	Protogyny (1), bidirectional (2)	Histology (1, 2), aquarium (1, 2)	Unknown	Coral reef	(1) Cole 1990, (2) Maxfield & Cole 2019a	

Gobiidae	*Fusigobius neophytus*	Protogyny	Field	MTV polygamy	Coral reef	Tsuboi & Sakai 2016	
Gobiidae	*Gobiodon erythrospilus*	Bidirectional (1, 2, 3, 4)	Field (1, 2, 3, 4), aquarium (1)	Size-assortative monogamy (1)	Coral reef	(1) Nakashima et al. 1996, (2) Munday 2002, (3) Munday & Molony 2002, (4) Kroon et al. 2003	*G. rivulatus rivulatus* (1)
Gobiidae	*Gobiodon histrio*	Protogyny, bidirectional (1, 2)	Field (1, 2)	Size-assortative monogamy (1)	Coral reef	(1) Munday et al. 1998, (2) Munday 2002	
Gobiidae	*Gobiodon micropus*	Bidirectional	Aquarium	Size-assortative monogamy	Coral reef	Nakashima et al. 1996	
Gobiidae	*Gobiodon oculolineatus*	Bidirectional	Aquarium	Size-assortative monogamy	Coral reef	Nakashima et al. 1996	
Gobiidae	*Gobiodon okinawae*	Protogyny, bidirectional*?	Field, *aquarium	Size-assortative monogamy	Coral reef	Cole & Hoese 2001	*bidirectional was reported from aquarium with weak evidence
Gobiidae	*Gobiodon quinquestrigatus*	Protogyny (1), bidirectional* (1)	Field, aquarium (1), *aquarium (1)	Size-assortative monogamy (1, 2)	Coral reef	(1) Nakashima et al. 1996, (2) Thompson et al. 2007	*bidirectional was observed in aquarium
Gobiidae	*Lythrypnus dalli*	Protogyny (1, 2, 3, 4, 5, 7, 8), bidirectional* (1, 2, 6, 8)	Field (1, 4), aquarium (2, 3, 5, 7, 8), *aquarium (1, 6, 8), histology (9)	Male polygamy (1)	Temperate rocky reef (1)	(1) St. Mary 1994, (2) Reavis & Grober 1999, (3) Black et al. 2004, (4) Black et al. 2005a, (5) Black et al. 2005b, (6) Rodgers et al. 2005, (7) Lorenzi et al. 2006, (8) Rodgers et al. 2007, (9) Maxfield & Cole 2019b	*bidirectional was observed in aquarium
Gobiidae	*Lythrypnus nesiotes*	Protogyny	Histology (1, 2)	Unknown	Coral reef	(1) Cole 1988, (2) St. Mary 2000	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Gobiidae	*Lythrypnus phorellus*	Protogyny	Histology	Unknown	Temperate rocky reef	St. Mary 2000	
Gobiidae	*Lythrypnus pulchellus*	Bidirectional	Aquarium, histology	Harem polygyny?*	Temperate rocky reef	Muñoz-Arroyo et al. 2019	*weak evidence
Gobiidae	*Lythrypnus spilus*	Protogyny	Histology	Unknown	Temperate rocky reef	St. Mary 2000	
Gobiidae	*Lythrypnus zebra*	Bidirectional	Aquarium	Male polygamy	Temperate rocky reef	St. Mary 1996	
Gobiidae	*Paragobiodon echinocephalus*	Protogyny, bidirectional (1, 2)	Field (1, 2), aquarium (2)	Size-assortative monogamy (3, 4, 5)	Coral reef	(1) Kuwamura et al. 1994, (2) Nakashima et al. 1995, (3) Lassig 1976, (4) Lassig 1977, (5) Kuwamura et al. 1993	
Gobiidae	*Paragobiodon xanthosomus*	Protogyny (1, 2)	Field (1), histology (1, 2)	Size-assortative monogamy (3)	Coral reef	(1) Lassig 1977, (2) Fishelson 1989, (3) Wong et al. 2008	
Gobiidae	*Priolepis akihitoi*	Bidirectional (1)	Aquarium (1)	Size-assortative monogamy (2)	Cave or rocky crevice	(1) Manabe et al. 2013, (2) Fukuda & Sunobe 2020	
Gobiidae	*Priolepis borea*	Bidirectional	Histology	Unknown	Cave or rocky crevice	Manabe et al. 2013	
Gobiidae	*Priolepis cincta*	Bidirectional (1, 2)	Aquarium (1), histology (2)	Size-assortative monogamy (1, 2)	Tide pool (2), caves or rocky crevices (1)	(1) Manabe et al. 2013, (2) Sunobe & Nakazono 1999	
Gobiidae	*Priolepis eugenius*	Protogyny, bidirectional	Histology	Unknown	Coral reef	Cole 1990	
Gobiidae	*Priolepis fallacincta*	Bidirectional	Histology	Unknown	Cave or rocky crevice	Manabe et al. 2013	

Gobiidae	*Priolepis hipoliti*	Protogyny, bidirectional	Histology	Unknown	Coral reef	Cole 1990	
Gobiidae	*Priolepis inhaca*	Bidirectional	Histology	Unknown	Cave or rocky crevice	Manabe et al. 2013	
Gobiidae	*Priolepis latifascima*	Bidirectional	Aquarium	Unknown	Cave or rocky crevice	Manabe et al. 2013	
Gobiidae	*Priolepis semidoliata*	Bidirectional	Aquarium	Size-assortative monogamy	Cave or rocky crevice	Manabe et al. 2013	
Gobiidae	*Rhinogobiops nicholsii*	Protogyny	Aquarium, histology	Unknown	Rock rubble area	Cole 1983	*Coryphopterus*
Gobiidae	*Tigrigobius multifasciatus*	Protogyny?	Aquarium*	Unknown	Coral reef	Robertson & Justines 1982	*Gobiosoma*, *change of papillae morphology incomplete
Gobiidae	*Trimma annosum*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma benjamini*	Bidirectional	Histology	Unknown	Cave or rocky crevice	Sunobe et al. 2017	
Gobiidae	*Trimma caesiura*	Bidirectional	Histology, aquarium	Unknown	Cave or rocky crevice	Sunobe et al. 2017	
Gobiidae	*Trimma cana*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma caudomaculatum*	Bidirectional	Histology (1), aquarium (2)	Multi-male group (2)	Cave or rocky crevice	(1) Sunobe et al. 2017, (2) Tomatsu et al. 2018	
Gobiidae	*Trimma emeryi*	Bidirectional (1)	Histology (1)	Harem (2)	Coral reef	(1) Sunobe et al. 2017, (2) Fukuda & Sunobe 2020	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Gobiidae	*Trimma fangi*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma flammeum*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma flavatrum*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	*T. flavatram*
Gobiidae	*Trimma fucatum*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma gigantum*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma grammistes*	Bidirectional (1, 2)	Aquarium (1), field (2)	Harem (2)	Rocky shore	(1) Shiobara 2000, (2) Fukuda et al. 2017	
Gobiidae	*Trimma hayashii*	Bidirectional (1)	Histology (1)	Harem (2)	Coral reef	(1) Sunobe et al. 2017, (2) Fukuda & Sunobe 2020	
Gobiidae	*Trimma kudoi*	Bidirectional	Aquarium	Harem?	Rocky slope, cave ceiling, hole	Manabe et al. 2008	*Trimma* sp.
Gobiidae	*Trimma lantana*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma macrophthalma*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma maiandros*	Bidirectional	Histology, aquarium	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma marinae*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma milta*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma nasa*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma naudei*	Bidirectional	Histology, aquarium	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma necopinum*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	

Gobiidae	*Trimma okinawae*	Protogyny (1, 2, 3, 4, 5), bidirectional (2, 3, 5)	Field (1, 4, 5), aquarium (2, 3)	Harem (1)	Rocky slope, coral reef	(1) Sunobe & Nakazono 1990, (2) Sunobe & Nakazono 1993, (3) Sunobe et al. 2005, (4) Manabe et al. 2007a, (5) Manabe et al. 2007b	
Gobiidae	*Trimma preclarum*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma rubromaculatum*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma sheppardi*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma stobbsi*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma striatum*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma tauroculum*	Bidirectional	Histology	Unknown	Coral reef	Sunobe et al. 2017	
Gobiidae	*Trimma taylori*	Bidirectional	Histology (1, 2)	Monogamy in aquarium (2)	Coral reef	(1) Sunobe et al. 2017, (2) Oyama et al. 2022	
Gobiidae	*Trimma unisquamis*	Bidirectional	Histology	Unknown	Coral reef	Cole 1990	
Gobiidae	*Trimma yanagitai*	Bidirectional	Aquarium	Unknown	Rock slope	Sakurai et al. 2009	
Uncertain orders in Ovalentaria							
Pomacentridae	*Amphiprion akallopisos*	Protandry	Aquarium (1, 3), histology (2, 3)	Monogamy (1, 2, 3)	Coral reef	(1) Fricke & Fricke 1977, (2) Fricke 1979, (3) Casadevall et al. 2009	
Pomacentridae	*Amphiprion bicinctus*	Protandry	Field (1, 2), histology (1)	Monogamy (1)	Coral reef	(1) Fricke & Fricke 1977, (2) Fricke 1983	No reversed sex change (1)
Pomacentridae	*Amphiprion clarkii*	Protandry	Field (1, 2, 3, 4), histology (1, 3)	Monogamy(1, 2, 3, 4)	Coral reef	(1) Moyer & Nakazono 1978b, (2) Ochi 1989, (3) Hattori & Yanagisawa 1991a, (4) Hattori & Yanagisawa 1991b	
Pomacentridae	*Amphiprion frenatus*	Protandry	Histology (1, 2), field (2)	Monogamy (1, 2)	Coral reef	(1) Moyer & Nakazono 1978b, (2) Hattori 1991	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Pomacentridae	*Amphiprion melanopus*	Protandry	Histology (1, 2), field (2, 3)	Monogamy (1, 2, 3, 4)	Coral reef	(1) Shapiro 1992, (2) Godwin 1994a, (3) Godwin 1994b, (4) Ross 1978	
Pomacentridae	*Amphiprion ocellaris*	Protandry	Histology (1), aquarium (2)	Monogamy (1)	Coral reef	(1) Moyer & Nakazono 1978b, (2) Madhu et al. 2010	
Pomacentridae	*Amphiprion percula*	Protandry	Histology	Monogamy	Coral reef	Madhu & Madhu 2006	
Pomacentridae	*Amphiprion perideraion*	Protandry	Histology (1, 2), field (2)	Monogamy (1, 2)	Coral reef	(1) Moyer & Nakazono 1978b, (2) Hattori 2000	
Pomacentridae	*Amphiprion polymnus*	Protandry	Histology (1, 2)	Monogamy (1)	Coral reef	(1) Moyer & Nakazono 1978b, (2) Rattanayuvakorn et al. 2006	
Pomacentridae	*Amphiprion sandaracinos*	Protandry	Histology	Monogamy	Coral reef	Moyer & Nakazono 1978b	
Pomacentridae	*Dascyllus aruanus*	Protogyny (1, 2*, 3, 4), juvenile hermaphroditism (5), reversed sex change (7)	Histology (1, 3, 4, 5), field (2*, 7)	Harem, multi-male group (1–7)	Coral reef	(1) Fricke & Holzberg 1974, (2) Coates 1981, (3) Shpigel & Fishelson 1986, (4) Cole 2002, (5) Asoh 2003, (6) Wong et al. 2012, (7) Kuwamura et al. 2016a	*weak evidence
Pomacentridae	*Dascyllus carneus*	Protogyny	Histology	Harem, multi-male group	Coral reef	Asoh & Yoshikawa 2003	
Pomacentridae	*Dascyllus flavicaudus*	Protogyny (1, 2), juvenile hermaphroditism (1)	Histology (1, 2)	Harem, multi-male group (1, 2)	Coral reef	(1) Asoh 2004, (2) Godwin 1995	
Pomacentridae	*Dascyllus marginatus*	Protogyny	Histology (1)	Harem (1, 2), multi-male group (2)	Coral reef	(1) Shpigel & Fishelson 1986, (2) Fricke 1980	

Pomacentridae	*Dascyllus melanurus*	Protogyny, juvenile hermaphroditism	Histology	Harem, multi-male group	Coral reef	Asoh 2005a	
Pomacentridae	*Dascyllus reticulatus*	Protogyny (1, 2, 4), juvenile hermaphroditism (3), reversed sex change (4)	Histology (1, 3), aquarium (2), field (4)	Harem, multi-male group (2, 4)	Coral reef	(1) Schwarz & Smith 1990, (2) Tanaka 1999, (3) Asoh 2005b, (4) Sakanoue & Sakai 2022	
Pseudochromidae	*Anisochromis straussi*	Protogyny	Histology	Unknown	Coral reef	Springer et al. 1977	
Pseudochromidae	*Ogilbyina queenslandiae*	Protogyny, reversed sex change*?	Histology, *field	Male egg care	Coral reef	Ferrell 1987	*Pseudochromis queenslandica*, *color change only
Pseudochromidae	*Pseudochromis aldabraensis*	Bidirectional	Histology, aquarium	Male egg care	Coral reef	Wittenrich & Munday 2005	
Pseudochromidae	*Pseudochromis cyanotaenia*	Bidirectional	Histology, aquarium	Male egg care	Coral reef	Wittenrich & Munday 2005	
Pseudochromidae	*Pseudochromis flavivertex*	Bidirectional	Histology, aquarium	Male egg care	Coral reef	Wittenrich & Munday 2005	
Pseudochromidae	*Pseudoplesiops howensis*	Simultaneous?	Histology*	Unknown	Coral reef	Cole & Gill 2000	*function unconfirmed
Pseudochromidae	*Pictichromis porphyrea*	Bidirectional	Field	Polygyny?	Coral reef	Kuwamura et al. 2015	
Cichliformes							
Cichlidae	*Metriaclima* cf. *livingstoni*	Protogyny	Aquarium	Male territory, maternal mouthbrooder	Freshwater (shell-dwelling)	Stauffer & Ruffing 2008	
Cichlidae	*Satanoperca jurupari*	Simultaneous	Histology (1)	Internal self-fertilization (1), biparental mouthbrooder (2)	Estuarine	(1) Matos et al. 2002, (2) Reid & Atz 1958	*Geophagus* (2)

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Cyprinodontiformes							
Rivulidae	*Kryptolebias hermaphroditus*	Simultaneous (2), androdioecy? (3)	Histology (2), external morphology (3)	Internal self-fertilizing (1, 2)	Freshwater and brackish	(1) Tatarenkov et al. 2009, (2) Costa et al. 2010, (3) Berbel-Filho et al. 2016	*K. ocellatus* (see Costa 2011)
Rivulidae	*Kryptolebias marmoratus*	Simultaneous (1, 4–6), androdioecy (males primary (2, 4, 6) or derived from hermaphrodites (3, 6)	Histology (1–6)	Internal self-fertilization (2, 7), external outcrossing between hermaphrodites and males (8)	Freshwater and brackish	(1) Harrington 1961, (2) Harrington 1967, (3) Harrington 1971, (4) Soto et al. 1992, (5) Sakakura & Noakes 2000, (6) Sakakura et al. 2006, (7) Tatarenkov et al. 2009, (8) Furness et al. 2015	*Rivulus*
Rivulidae	*Kryptolebias ocellatus*	Simultaneous, androdioecy (1)	Histology	Predominantly outcrossing (2, 3)	Freshwater	(1) Costa et al. 2010, (2) Tatarenkov et al. 2009, (3) Berbel-Filho et al. 2020	*K. caudomarginatus* (see Costa 2011)
Poeciliidae	*Xiphophorus helleri*	Protogyny, gonochorism	Histology (1, 2), aquarium (2)	Unknown	Freshwater	(1) Lodi 1979, (2) Lodi 1980b	
Synbranchiformes							
Synbranchidae	*Monopterus albus*	Protogyny	Histology (1–4), aquarium (5)	MTV-polygamy (6)	Freshwater and brackish	(1) Liem 1963, (2) Okada 1966b, (3) Chan & Phillips 1967, (4) Liem 1968, (5) Chan et al. 1972, (6) Matsumoto et al. 2011	*Fluta*
Synbranchidae	*Monopterus boueti*	Protogyny	Histology	Unknown	Freshwater	Liem 1968	*Typhlosynbranchus*

Synbranchidae	*Ophisternon bengalense*	Protogyny	Histology	Unknown	Freshwater and brackish	Liem 1968	*Synbranchus bengalensis*
Synbranchidae	*Synbranchus marmoratus*	Protogyny	Histology (1, 2)	Unknown	Freshwater and brackish	(1) Liem 1968, (2) Lo Nostro & Guerrero 1996	
Trachiniformes							
Pinguipedidae	*Parapercis clathrata*	Protogyny	Histology	Unknown	Coral reef	Stroud 1982	
Pinguipedidae	*Parapercis colias*	Protogyny	Histology (1, 2)	Harem? (3)	Temperate reef	(1) Blackwell 1998, (2) Carbines 2004, (3) Beentjes & Carbines 2005	
Pinguipedidae	*Parapercis cylindrica*	Protogyny	Histology (1, 2), field (1, 3), aquarium (3, 4)	Harem (1, 3)	Coral reef	(1) Stroud 1982, (2) Walker & McCormick 2004, (3) Walker & McCormick 2009, (4) Sprenger et al. 2012	
Pinguipedidae	*Parapercis hexophtalma*	Protogyny	Histology (1)	Harem (2)	Coral reef	(1) Stroud 1982, (2) Clark et al. 1991	
Pinguipedidae	*Parapercis nebulosa*	Protogyny	Histology	Unknown	Coral reef	Stroud 1982	
Pinguipedidae	*Parapercis snyderi*	Protogyny	Histology (1, 2, 6), aquarium (1, 3), field (1, 5)	Harem (1, 2, 4)	Coral reef	(1) Nakazono et al. 1985, (2) Ohta 1987, (3) Kobayashi et al. 1993, (4) Ohnishi et al. 1997, (5) Ohnishi 1998, (6) Walker et al. 2007	
Pinguipedidae	*Parapercis xanthozona*	Protogyny	Histology	Unknown	Coral reef	Stroud 1982	
Trichonotidae	*Trichonotus filamentosus*	Protogyny	Histology	Harem?	Temperate reef	Kusen et al. 1991	
Creediidae	*Crystallodytes cookei*	Protandry	Histology, aquarium	Unknown	Coral reef	Langston 2004	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Creediidae	*Limnichthys fasciatus*	Protandry	Histology	Unknown	Temperate reef	Shitamitsu & Sunobe 2017	
Creediidae	*Limnichthys nitidus*	Protandry	Histology (1, 2), aquarium (1)	Unknown	Coral reef	(1) Langston 2004, (2) Shitamitsu & Sunobe 2017	*L. donaldsoni* (1)
Percophidae	*Matsubaraea fusiforme*	Protogyny?	Macroscopic*	Unknown	Temperate reef	Noichi et al. 1991	*weak evidence
Labriformes							
Labridae	*Achoerodus gouldii*	Protogyny	Histology	Unknown	Temperate reef	Coulson et al. 2009	
Labridae	*Achoerodus viridis*	Protogyny	Histology (1)	Unknown; no movement between reefs (2)	Temperate reef	(1) Gillanders 1995, (2) Lee et al. 2014	
Labridae	*Anampses geographicus*	Protogyny	Histology (1, 2)	Unknown	Coral reef	(1) Choat 1969, (2) Leem et al. 1998	*A. pterophthalmus* (1)
Labridae	*Bodianus axillaris*	Protogyny	Histology	Unknown	Coral reef	Hubble 2003	
Labridae	*Bodianus diplotaenia*	Protogyny	Histology (1)	MTV polygamy (2)	Temperate reef	(1) Hoffman 1980, (2) Hoffman 1985	
Labridae	*Bodianus eclancheri*	Protogyny, prematurational sex change (3)	Histology (1, 2)	Group spawning (3)	Temperate reef	(1) Warner 1978, (2) Hoffman 1980, (3) Hoffman 1985	
Labridae	*Bodianus frenchii*	Protogyny	Histology	Unknown	Temperate reef	Cossington et al. 2010	
Labridae	*Bodianus mesothorax*	Protogyny	Histology (1)	Spawning aggregation (2)	Coral reef	(1) Hubble 2003, (2) Claydon 2005	
Labridae	*Bodianus rufus*	Protogyny	Histology (1, 2), field (4)	Harem (3)	Coral reef	(1) Warner & Robertson 1978, (2) Hoffman 1980, (3) Hoffman 1985, (4) Hoffman et al. 1985	
Labridae	*Cheilinus chlorurus*	Protogyny	Histology	Unknown	Coral reef	Choat 1969	

Labridae	*Cheilinus fasciatus*	Protogyny	Histology (1, 3)	Harem (2)	Coral reef	(1) Hubble 2003, (2) Donaldson 1995b, (3) Lowe et al. 2021	
Labridae	*Cheilinus trilobatus*	Protogyny	Histology (1)	Harem (2), MTV polygamy (3)	Coral reef	(1) Choat 1969, (2) Colin & Bell 1991, (3) Claydon 2005	
Labridae	*Cheilinus undulatus*	Protogyny	Histology (1)	MTV polygamy (2)	Coral reef	(1) Sadovy de Mitcheson et al. 2010, (2) Colin 2010	
Labridae	*Choerodon anchorago*	Protogyny?	Macroscopic*	Unknown	Temperate reef	Tuwo et al. 2020	*weak evidence
Labridae	*Choerodon azurio*	Protogyny	Histology	Unknown	Temperate reef	Nakazono & Kusen 1991	
Labridae	*Choerodon cauteroma*	Protogyny	Histology	Unknown	Coral reef	Fairclough 2005	
Labridae	*Choerodon cyanodus*	Protogyny	Histology (1, 2)	Unknown	Coral reef	(1) Choat 1969, (2) Fairclough 2005	*C. albigena* (1)
Labridae	*Choerodon fasciatus*	Protogyny	Histology (1)	Facultative monogamy? (2)	Coral reef	(1) Hubble 2003, (2) Donaldson 1995b	
Labridae	*Choerodon graphicus*	Protogyny	Histology	Unknown	Coral reef	Choat 1969	*C. transversalis*
Labridae	*Choerodon rubescens*	Protogyny	Histology	Unknown	Coral reef	Fairclough 2005	
Labridae	*Choerodon schoenleinii*	Protogyny	Histology (1, 2), aquarium (3)	Unknown	Coral reef	(1) Ebisawa et al. 1995, (2) Fairclough 2005, (3) Sato et al. 2018	
Labridae	*Choerodon venustus*	Protogyny	Histology	Unknown	Coral reef	Platten et al. 2002	
Labridae	*Cirrhilabrus temmincki*	Protogyny	Histology (1)	MTV polygamy (2, 3)	Temperate reef	(1) Kobayashi & Suzuki 1990, (2) Bell 1983, (3) Kohda et al. 2005	
Labridae	*Clepticus parrae*	Protogyny	Histology (1)	Non-territorial, lekking, pair spawning (1, 2)	Coral reef	(1) Warner & Robertson 1978, (2) Robertson & Hoffman 1977	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Labridae	*Coris auricularis*	Protogyny	Histology	Unknown	Temperate reef	Lek 2011	
Labridae	*Coris dorsomacula*	Protogyny	Microscopic	Harem	Temperate reef	Tribble 1982	
Labridae	*Coris gaimard*	Protogyny	Histology (1)	MTV polygamy (2)	Coral reef	(1) Choat 1969, (2) Sancho et al. 2000	
Labridae	*Coris julis*	Protogyny	Histology (1, 2)	MTV polygamy (3)	Temperate reef	(1) Reinboth 1975, (2) Brusléa 1987, (3) Lejeune 1987	
Labridae	*Coris variegata*	Protogyny	Histology	Unknown	Coral reef	Choat 1969	
Labridae	*Decodon melasma*	Protogyny	Histology	Unknown	Temperate reef	Diener 1977	
Labridae	*Epibulus insidiator*	Protogyny	Histology (1, 2, 3)	Haremic (4), MTV polygamy (5)	Coral reef	(1) Choat 1969, (2) Leem et al.1998, (3) Hubble 2003, (4) Colin & Bell 1991, (5) Kuwamura et al. 2016b	
Labridae	*Gomphosus varius*	Protogyny	Histology (1)	MTV polygamy (2, 3)	Coral reef	(1) Choat 1969, (2) Colin & Bell 1991, (3) Kuwamura et al. 2016b	
Labridae	*Halichoeres bivittatus*	Protogyny	Histology (1, 2)	MTV polygamy (2, 3), group spawning (3)	Coral reef	(1) Reinboth 1975, (2) Warner & Robertson 1978, (3) Clavijo & Donaldson 1994	
Labridae	*Halichoeres garnoti*	Protogyny	Histology (1)	MTV polygamy (2)	Coral reef	(1) Warner & Robertson 1978, (2) Robertson 1981	
Labridae	*Halichoeres maculipinna*	Protogyny	Histology (1)	MTV polygamy (2)	Coral reef	(1) Warner & Robertson 1978, (2) Robertson 1981	

Labridae	*Halichoeres margaritaceus*	Protogyny	Histology (1)	Harem (2)	Coral reef	(1) Choat 1969, (2) Walker & Ryen 2007	
Labridae	*Halichoeres marginatus*	Protogyny	Histology (1, 2)	MTV polygamy, group spawning (2, 3)	Coral reef	(1) Choat 1969, (2) Shibuno et al. 1993a, (3) Shibuno et al. 1993b	
Labridae	*Halichoeres melanochir*	Protogyny	Histology (1, 2)	MTV polygamy (1, 2)	Rocky reef	(1) Moyer & Yogo 1982, (2) Yogo 1985	
Labridae	*Halichoeres melanurus*	Protogyny	Field (1), histology (2)	MTV polygamy (3)	Coral reef	(1) Sakai et al. 2002, (2) Hubble 2003, (3) Kuwamura et al. 2000	
Labridae	*Halichoeres miniatus*	Protogyny	Field	Harem	Coral reef	Munday et al. 2009	
Labridae	*Halichoeres nebulosus*	Protogyny	Histology	Unknown	Coral reef	Choat 1969	
Labridae	*Halichoeres pictus*	Protogyny	Histology	Pair spawning	Coral reef	Warner & Robertson 1978	
Labridae	*Halichoeres poeyi*	Protogyny	Histology	Pair spawning	Coral reef	Warner & Robertson 1978	
Labridae	*Halichoeres radiatus*	Protogyny	Histology	Unknown	Coral reef	Warner & Robertson 1978	
Labridae	*Halichoeres scapularis*	Protogyny	Histology	Unknown	Coral reef	Leem et al. 1998	
Labridae	*Halichoeres semicinctus*	Protogyny	Histology	MTV polygamy, group spawning	Coral reef	Adreani & Allen 2008	
Labridae	*Halichoeres tenuispinnis*	Protogyny	Histology	MTV polygamy	Temperate reef	Nakazono 1979	
Labridae	*Halichoeres trimaculatus*	Protogyny, reversed sex change	Field, aquarium (1)	MTV polygamy, group spawning (2, 3)	Coral reef	(1) Kuwamura et al. 2007, (2) Suzuki et al. 2008, (3) Suzuki et al. 2010	
Labridae	*Hemigymnus fasciatus*	Protogyny	Histology	Unknown	Coral reef	Lowe et al. 2021	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Labridae	*Hemigymnus melapterus*	Protogyny	Histology (1, 2)	Unknown	Coral reef	(1) Hubble 2003, (2) Lowe et al. 2021	
Labridae	*Hologymnosus annulatus*	Protogyny	Histology (1, 2)	Unknown	Coral reef	(1) Choat 1969, (2) Leem et al. 1998	*H. semidiscus* (1)
Labridae	*Iniistius dea*	Protogyny	Histology	Unknown	Temperate Sea	Leem et al. 1998	*Xyrichtys*
Labridae	*Iniistius geisha*	Protogyny	Histology	Unknown	Temperate Sea	Leem et al. 1998	*Xyrichtys*
Labridae	*Iniistius pentadactylus*	Protogyny	Histology, field, aquarium	Harem	Tropicale Sea	Nemtzov 1985	*Xyrichtys*
Labridae	*Labrichthys unilineatus*	Protogyny	Histology (1)	Harem (2)	Coral reef	(1) Choat 1969, (2) Colin & Bell 1991	
Labridae	*Labroides dimidiatus*	Protogyny (1), reversed sex change (2, 3, 4)	Field (1, 3, 4), aquarium (2)	Harem (1, 2, 3, 4)	Coral reef	(1) Robertson 1972, (2) Kuwamura et al. 2002, (3) Kuwamura et al. 2011, (4) Kuwamura et al. 2014	
Labridae	*Labrus bergylta*	Protogyny	Histology (1, 2)	Unknown	Temperate reef	(1) Dipper & Pullin 1979, (2) Muncaster et al. 2013	
Labridae	*Labrus merula*	Protogyny	Histology	Unknown	Temperate reef	Sordi 1962	
Labridae	*Labrus mixtus*	Protogyny	Histology (1, 2)	Unknown	Temperate reef	(1) Sordi 1964, (2) Dipper & Pullin 1979	*L. bimaculatus* (1), *L. ossifagus* (2)
Labridae	*Labrus viridis*	Protogyny	Histology	Unknown	Temperate reef	Sordi 1962	*L. turdus*
Labridae	*Lachnolaimus maximus*	Protogyny	Histology	Harem	Coral reef	McBride & Johnson 2007	

Labridae	*Macropharyngodon moyeri*	Protogyny	Field	Harem	Temperate reef	Moyer 1991	
Labridae	*Notolabrus celidotus*	Protogyny, prematurational sex change (1)	Histology	Pair spawing, MTV polygamy (2)	Temperate reef	(1) Jones 1980a, (2) Jones 1981	*Pseudolabrus* (1, 2)
Labridae	*Notolabrus gymnogenis*	Protogyny	Histology (1), microscopic (2)	Unknown	Temperate reef	(1) McPherson 1977, (2) Morton et al. 2008	*Pseudolabrus* (1)
Labridae	*Notolabrus parilus*	Protogyny	Histology	Unknown	Temperate reef	Lek 2011	
Labridae	*Notolabrus tetricus*	Protogyny	Histology	Male territory	Temperate reef	Barrett 1995	
Labridae	*Ophthalmolepis lineolatus*	Protogyny	Microscopic (1), histology (2)	Unknown	Temperate reef	(1) Morton et al. 2008, (2) Lek 2011	
Labridae	*Oxycheilinus digramma*	Protogyny	Histology	Unknown	Coral reef	(1) Choat 1969, (2) Lowe et al. 2021	*Cheilinus diagrammus* (1)
Labridae	*Parajulis poecilepterus*	Protogyny	Histology (1, 2, 3), aquarium (4)	Group spawning (2)	Temperate reef	(1) Okada 1962, (2) Fukui et al.1991, (3) Kobayashi & Suzuki 1994, (4) Miyake et al. 2012	*Halichoeres* (1, 2, 3)
Labridae	*Pictilabrus laticlavius*	Protogyny	Histology (1), microscopic (2)	Pair spawning, male territory (1)	Temperate reef	(1) Barrett 1995, (2) Morton et al. 2008	
Labridae	*Pseudocheilinops ataenia*	Protogyny	Histology	Unknown	Coral reef	Hubble 2003	
Labridae	*Pseudocheilinus evanidus*	Protogyny	Histology	Unknown	Coral reef	Hubble 2003	
Labridae	*Pseudocheilinus hexataenia*	Protogyny	Histology (1)	Harem (2)	Coral reef	(1) Hubble 2003, (2) Colin & Bell 1991	
Labridae	*Pseudolabrus guentheri*	Protogyny	Histology	Unknown	Coral reef	Choat 1969	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Labridae	*Pseudolabrus rubicundus*	Protogyny	Histology	Male territory	Rocky reef	Barrett 1995	*P. psittaculus*
Labridae	*Pseudolabrus sieboldi*	Protogyny (1), reversed sex change? (2)	Histology (1), aquarium (2)	MTV polygamy (1)	Temperate reef	(1) Nakazono 1979, (2) Ohta et al. 2003	*P. japonicus* (1), *color change only (2)
Labridae	*Pteragogus aurigarius*	Protogyny	Histology (1, 3), aquarium (3)	MTV polygamy (1, 2)	Temperate reef	(1) Nakazono 1979, (2) Moyer 1991, (3) Shimizu et al. 2022	*Duymaeria flagellifera* (1)
Labridae	*Semicossyphus darwini*	Protogyny	Histology	Unknown	Temperate reef	Warner 1978	*Pimelometopon*
Labridae	*Semicossyphus pulcher*	Protogyny	Histology (1, 2)	MTV polygamy (3)	Temperate reef	(1) Warner 1975, (2) Cowen 1990, (3) Adreani et al. 2004	*Pimelometopon pulchrum* (1)
Labridae	*Semicossyphus reticulatus*	Protogyny	Histology	Harem?*	Temperate reef	Ochi et al. 2017	*personal communication
Labridae	*Stethojulis balteata*	Protogyny	Histology	Unknown	Coral reef	Choat 1969	*S. axillaris*
Labridae	*Stethojulis interrupta*	Protogyny	Histology	MTV polygamy	Temperate reef	Nakazono 1979	
Labridae	*Stethojulis strigiventer*	Protogyny	Histology	Unknown	Coral reef	Choat 1969	
Labridae	*Stethojulis trilineata*	Protogyny	Histology (1)	MTV polygamy (2)	Coral reef	(1) Leem et al.1998, (2) Kuwamura et al. 2016b	
Labridae	*Suezichthys ornatus*	Protogyny	Histology	MTV polygamy	Temperate reef	Andrew et al. 1996	*Nelabrichthys*
Labridae	*Symphodus melanocercus*	Protogyny	Histology	MTV polygamy	Temperate reef	Warner & Lejeune 1985	
Labridae	*Symphodus tinca*	Protogyny* or gonochorism	Histology	MTV polygamy	Temperate reef	Warner & Lejeune 1985	*rare or absent

Labridae	*Thalassoma bifasciatum*	Protogyny	Histology (1, 2), field (4)	MTV polygamy, group spawning (1, 3)	Coral reef	(1) Warner & Robertson 1978, (2) Shapiro & Rasotto 1993, (3) Reinboth 1973, (4) Warner & Swearer 1991	
Labridae	*Thalassoma cupido*	Protogyny	Histology	MTV polygamy, group spawning	Temperate reef	Meyer 1977	
Labridae	*Thalassoma duperrey*	Protogyny	Aquarium (1, 2, 3), histology (2, 4)	MTV polygamy, group spawning (2)	Coral reef	(1) Ross 1981, (2) Ross 1982, (3) Ross et al. 1983, (4) Nakamura et al. 1989	
Labridae	*Thalassoma hardwicke*	Protogyny	Histology (1)	MTV polygamy (4), group spawning (2, 3, 4)	Coral reef	(1) Choat 1969, (2) Robertson & Choat 1974, (3) Craig 1998, (4) Kuwamura et al. 2016b	
Labridae	*Thalassoma jansenii*	Protogyny	Histology (1)	MTV polygamy, group spawning (2)	Coral reef	(1) Choat 1969, (2) Kuwamura et al. 2016b	
Labridae	*Thalassoma lucasanum*	Protogyny	Histology, aquarium	MTV polygamy, group spawning	Coral reef	Warner 1982	
Labridae	*Thalassoma lunare*	Protogyny	Histology	MTV polygamy, group spawning	Coral reef	Robertson & Choat 1974	
Labridae	*Thalassoma lutescens*	Protogyny	Histology (1)	MTV polygamy (1, 2), group spawning (2)	Coral reef	(1) Shibuno et al. 1994a, (2) Kuwamura et al. 2016b	
Labridae	*Thalassoma pavo*	Protogyny	Histology	MTV polygamy, group spawning	Temperate reef	Wernerus & Tessari 1991	
Labridae	*Thalassoma purpureum*	Protogyny	Histology	Unknown	Coral reef	Leem et al. 1998	
Labridae	*Thalassoma quinquevittatum*	Protogyny	Histology (1)	MTV polygamy (3), group spawning (2, 3)	Coral reef	(1) Leem et al.1998, (2) Craig 1998, (3) Kuwamura et al. 2016b	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Labridae	*Xyrichtys martinicensis*	Protogyny	Histology (1), field (2)	Harem (2)	Coral reef	(1) Roede 1972, (2) Victor 1987	*Hemipteronotus*
Labridae	*Xyrichtys novacula*	Protogyny	Histology (1, 2)	Harem (3)	Temperate reef	(1) Bentivegna & Rasotto 1987, (2) Candi et al. 2004, (3) Marconato et al. 1995	
Odacidae	*Odax pullus*	Protogyny	Histology	Unknown	Temperate reef	Trip et al. 2011	
Scaridae	*Calotomus carolinus*	Protogyny	Histology	Pair spawning, male territory	Coral reef	Robertson et al. 1982	
Scaridae	*Calotomus japonicus*	Protogyny	Histology (1, 2)	MTV polygamy (3)	Rocky reef	(1) Kusen & Nakazono 1991, (2) Kume et al. 2010, (3) Shibuno et al. 1994b	
Scaridae	*Calotomus spinidens*	Protogyny	Histology	Pair spawning, male territory	Tropical seagrass beds	Robertson et al. 1982	
Scaridae	*Cetoscarus bicolor*	Protogyny	Histology (1)	Haremic? (2)	Coral reef	(1) Taylor & Choat 2014, (2) Colin & Bell 1991	
Scaridae	*Chlorurus sordidus*	Protogyny	Histology (1, 2, 3, 4)	MTV polygamy, group spawning (2)	Coral reef	(1) Choat & Robertson 1975, (2) Yogo et al. 1980, (3) Gust 2004, (4) El-Sayed Ali et al. 2011	*Scarus* (1, 2)
Scaridae	*Chlorurus spilurus*	Protogyny	Histology	Unknown	Coral reef	Taylor 2014	
Scaridae	*Cryptotomus roseus*	Protogyny	Histology	MTV polygamy	Coral reef	Robertson & Warner 1978	
Scaridae	*Hipposcarus harid*	Protogyny	Histology	Unknown	Coral reef	El-Sayed Ali et al. 2011	

Scaridae	*Hipposcarus longiceps*	Protogyny	Histology (1, 2)	Unknown	Coral reef	(1) Taylor & Cruz 2017, (2) Moore 2022	
Scaridae	*Nicholsina denticulata*	Protogyny?	Histology*	Unknown	Rocky reef	Reinboth 1968	*small sample size
Scaridae	*Scarus coeruleus*	Protogyny?	Histology*	Unknown	Rocky reef	Reinboth 1968	*small sample size
Scaridae	*Scarus ferrugineus*	Protogyny	Histology (1, 2)	Unknown	Coral reef	(1) El-Sayed Ali et al. 2011, (2) Abdel-Aziz et al. 2012	
Scaridae	*Scarus festivus*	Protogyny	Histology	Unknown	Coral reef	Choat & Robertson 1975	*S. lunula*
Scaridae	*Scarus forsteni*	Protogyny	Histology (1)	MTV polygamy (2, 3)	Coral reef	(1) Choat & Robertson 1975, (2) Colin & Bell 1991, (3) Kuwamura et al. 2009	
Scaridae	*Scarus frenatus*	Protogyny	Histology (1, 2)	Harem (2)	Coral reef	(1) Choat & Robertson 1975, (2) Gust 2004	*S. sexvittatus* (1)
Scaridae	*Scarus ghobban*	Protogyny	Histology (1)	Unknown	Coral reef	(1) Choat & Robertson 1975, (2) Grandcourt 2002	
Scaridae	*Scarus globiceps*	Protogyny	Histology (1)	MTV polygamy (2), group spawning (1)	Coral reef	(1) Choat & Robertson 1975, (2) Kuwamura et al. 2009	
Scaridae	*Scarus iseri*	Protogyny	Histology (1)	Harem (1), group spawning (1, 2)	Coral reef	(1) Robertson & Warner 1978, (2) Colin 1978	*S. croicensis* (1, 2)
Scaridae	*Scarus niger*	Protogyny	Histology (1)	MTV polygamy, group spawning (2)	Coral reef	(1) Choat & Robertson 1975, (2) Kuwamura et al. 2009	
Scaridae	*Scarus oviceps*	Protogyny	Histology (1)	MTV polygamy (2)	Coral reef	(1) Choat & Robertson 1975, (2) Claydon 2005	
Scaridae	*Scarus psittacus*	Protogyny	Histology (1)	MTV polygamy (2, 3, 4)	Coral reef	(1) Choat & Robertson 1975, (2) Colin & Bell 1991, (3) Claydon 2005, (4) Kuwamura et al. 2009	*S. venosus* (1)

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Scaridae	*Scarus rivulatus*	Protogyny	Histology (1, 2)	MTV polygamy, group spawning (1, 3)	Coral reef	(1) Choat & Robertson 1975, (2) Lou 1992, (3) Kuwamura et al. 2009	*S. fasciatus* (1)
Scaridae	*Scarus rubroviolaceus*	Protogyny	Histology (1), macrscopic? (2)	Pair spawning (1, 3)	Coral reef	(1) Randall & Bruce 1983, (2) Grandcourt 2002, (3) Colin & Bell 1991	
Scaridae	*Scarus russelii*	Protogyny	Histology	Unknown	Coral reef	Randall & Bruce 1983	
Scaridae	*Scarus scaber*	Protogyny	Histology	Pair spawning	Coral reef	Randall & Bruce 1983	
Scaridae	*Scarus schlegeli*	Protogyny	Histology (1)	MTV polygamy, group spawning (2, 3)	Coral reef	(1) Lou 1992, (2) Colin & Bell 1991, (3) Kuwamura et al. 2009	
Scaridae	*Scarus spinus*	Protogyny	Histology	Unknown	Coral reef	Choat & Robertson 1975	*S. formosus*
Scaridae	*Scarus taeniopterus*	Protogyny	Histology (1)	Harem? (1), pair spawning (2)	Coral reef	(1) Robertson & Warner 1978, (2) Colin & Clavijo 1988	
Scaridae	*Scarus tricolor*	Protogyny	Histology	Pair spawning	Coral reef	Randall & Bruce 1983	
Scaridae	*Scarus vetula*	Protogyny	Histology (1)	MTV polygamy, harem (2)	Coral reef	(1) Robertson & Warner 1978, (2) Clavijo 1983	
Scaridae	*Scarus viridifucatus*	Protogyny	Histology	Unknown	Coral reef	Randall & Bruce 1983	
Scaridae	*Sparisoma atomarium*	Protogyny	Histology	Harem	Coral reef	Robertson & Warner 1978	
Scaridae	*Sparisoma aurofrenatum*	Protogyny	Histology	Harem	Coral reef	Robertson & Warner 1978	
Scaridae	*Sparisoma chrysopterum*	Protogyny	Histology	MTV polygamy	Coral reef	Robertson & Warner 1978	
Scaridae	*Sparisoma cretense*	Protogyny, mostly prematurational sex change	Histology	Harem	Temperate reef	De Girolamo et al. 1999	

Scaridae	*Sparisoma radians*	Protogyny	Histology (1), field (2, 3)	MTV polygamy, group spawning (1), harem (2, 3)	Coral reef	(1) Robertson & Warner 1978, (2) Muñoz & Warner 2003, (3) Muñoz & Warner 2004	
Scaridae	*Sparisoma rubripinne*	Protogyny	Histology	MTV polygamy, group spawning	Coral reef	Robertson & Warner 1978	
Scaridae	*Sparisoma viride*	Protogyny	Histology	MTV polygamy	Coral reef	Robertson & Warner 1978	
Perciformes							
Centropomidae	*Centropomus parallelus*	Protandry	Histology	Unknown	Tropical Sea and esturaries	Costa e Silva et al. 2021	
Centropomidae	*Centropomus undecimalis*	Protandry	Histology (1, 2), aquarium (1)	Unknown	Tropical Sea and esturaries	(1) Taylor et al. 2000, (2) Young et al. (2020)	
Latidae	*Lates calcarifer*	Protandry	Histology (1, 2)	Unknown	Tropical Sea and esturies	(1) Guiguen et al. 1994, (2) Roberts et al. 2021	
Polynemidae	*Eleutheronema tetradactylum*	Protandry	Histology (1, 2)	Unknown	Tropical Sea	(1) Shihab et al. 2017, (2) Junnan et al. 2020	
Polynemidae	*Filimanus heptadactyla*	Trioecy (partially simultaneous)	Histology (1, 2)	Unknown	Tropical Sea	(1) Nayak 1959, (2) Kagwade 1967	*Polynemus heptadactylus* (1, 2)
Polynemidae	*Galeoides decadactylus*	Protandry	Microscopic	Unknown	Tropical Sea	Longhurst 1965	
Polynemidae	*Polydactylus macrochir*	Protandry	Microscopic	Unknown	Tropical Sea	Moore et al. 2017	
Polynemidae	*Polydactylus microstomus*	Trioecy (partially simultaneous)	Histology	Unknown	Tropical Sea	Dorairaj 1973	*Polynemus microstoma*
Polynemidae	*Polydactylus quadrifilis*	Protandry	Microscopic (1)	Unknown	Tropical Sea	(1) Lawson & Olagundoye 2011, (2) Butler et al. 2021	

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Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Terapontidae	*Bidyanus bidyanus*	Protandry	Histology	Unknown	Freshwater	Moiseeva et al. 2001	
Terapontidae	*Mesopristes cancellatus*	Protandry	Ocular	Unknown	Freshwater	Barazona et al. 2015	
Serranidae (Epinephelinae)	*Alphestes afer*	Protogyny?	Histology*	Unknown	Coral reef	Smith 1959	*small sample size
Serranidae (Epinephelinae)	*Cephalopholis argus*	Protogyny	Histology	Harem	Coral reef	Shpigel & Fishelson 1991	
Serranidae (Epinephelinae)	*Cephalopholis boenak*	Protogyny (1), reversed sex change (2)	Histology (1), aquarium (2)	Harem (3)	Coral reef	(1) Liu & Sadovy 2004a, (2) Liu & Sadovy 2004b, (3) Liu & Sadovy 2005	
Serranidae (Epinephelinae)	*Cephalopholis cruentata*	Protogyny	Histology (1–3)	Harem (4)	Coral reef	(1) Smith 1959, (2) Smith 1965, (3) Nagelkerken 1979, (4) Sadovy et al. 1994	*Epinephelus cruentatus, Petrometopon cruentatus*
Serranidae (Epinephelinae)	*Cephalopholis cyanostigma*	Protogyny	Histology	Harem (1)	Coral reef	Mosse et al. 2002	
Serranidae (Epinephelinae)	*Cephalopholis fulva*	Protogyny	Histology (1, 2)	Harem (3)	Coral reef	(1) Smith 1959, (2) Smith 1965, (3) Sadovy et al. 1994	*Epinepherus fulvus*
Serranidae (Epinephelinae)	*Cephalopholis hemistiktos*	Protogyny	Histology	Monogamy, harem (1)	Coral reef	Shpigel & Fishelson 1991	
Serranidae (Epinephelinae)	*Cephalopholis miniata*	Protogyny	Histology	Harem (1)	Coral reef	Shpigel & Fishelson 1991	
Serranidae (Epinephelinae)	*Cephalopholis panamensis*	Protogyny	Histology	Harem (1)	Coral reef	Erisman et al. 2010	
Serranidae (Epinephelinae)	*Cephalopholis taeniops*	Protogyny	Histology	Unknown	Coral reef	Siau 1994	
Serranidae (Epinephelinae)	*Cephalopholis urodeta*	Protogyny	Histology (1)	Harem? (2)	Coral reef	(1) Nakai & Sano 2002, (2) Donaldson 1995a	

Serranidae (Epinephelinae)	*Epinephelus adscensionis*	Protogyny	Histology, aquarium (1)	Harem (1)	Coral reef	Kline et al. 2011	
Serranidae (Epinephelinae)	*Epinephelus aeneus*	Protogyny	Histology	Unknown	Coral reef	Bruslé amd Bruslé 1975	
Serranidae (Epinephelinae)	*Epinephelus akaara*	Protogyny, reversed sex change	Histology, aquarium (1, 2)	Pair spawning (aquarium:3)	Coral reef	(1) Tanaka et al. 1990, (2) Okumura 2001, (3) Okumura et al. 2002	
Serranidae (Epinephelinae)	*Epinephelus andersoni*	Protogyny	Histology	Unknown	Coral reef	Fennessy & Sadovy 2002	
Serranidae (Epinephelinae)	*Epinephelus areolatus*	Protogyny	Histology	Unknown	Coral reef	Boddington et al. 2021	
Serranidae (Epinephelinae)	*Epinephelus bruneus*	Protogyny, reversed sex change	Aquarium	Unknown	Coral reef	Oh et al. 2013	
Serranidae (Epinephelinae)	*Epinephelus chlorostigma*	Protogyny	Histology	Unknown	Coral reef	Moussac 1986	
Serranidae (Epinephelinae)	*Epinephelus coioides*	Protogyny (1, 2, 4, 5), reversed sex change (3)	Histology (1), aquarium (2, 3, 4, 5)	Unknown	Coral reef	(1) Liu & Sadovy de Mitcheson 2011, (2) Quinitio et al. 1997, (3) Chen et al. 2019, (4) Chen et al. 2020, (5) Chen et al. 2021	
Serranidae (Epinephelinae)	*Epinephelus diacanthus*	Protogyny	Histology	Unknown	Coral reef	Chen et al. 1980	
Serranidae (Epinephelinae)	*Epinephelus drummondhayi*	Protogyny	Histology	Unknown	Coral reef	Brulé et al. 2000	
Serranidae (Epinephelinae)	*Epinephelus fasciatus*	Protogyny	Histology	Unknown	Coral reef	Vadiya 1984	*E alexandrinus*
Serranidae (Epinephelinae)	*Epinephelus fuscoguttatus*	Protogyny	Histology	Spawning aggregation	Coral reef	Pears et al. 2007	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Serranidae (Epinephelinae)	*Epinephelus guttatus*	Protogyny	Histology (1–4)	Spawning aggregation (4, 5)	Coral reef	(1) Smith 1959, (2) Bruslé & Bruslé 1975, (3) Shapiro et al. 1993, (4) Sadovy et al. 1994, (5) Nemeth et al. 2007	*E. guaza*
Serranidae (Epinephelinae)	*Epinephelus labriformis*	Protogyny	Histology	Unknown	Coral reef	Erisman 2008	
Serranidae (Epinephelinae)	*Epinephelus malabaricus*	Protogyny	Histology	Unknown	Coral reef	Sheaves 1995	
Serranidae (Epinephelinae)	*Epinephelus marginatus*	Protogyny	Histology (1)	MTV polygamy (2, 3)	Temperate Sea	(1) Reñones et al. 2010, (2) Zabala et al. 1997a, (3) Zabala et al. 1997b	
Serranidae (Epinephelinae)	*Epinephelus merra*	Protogyny	Histology (1)	Spawning aggregation (2)	Coral reef	(1) Bhandari et al. 2003, (2) Soyano et al. 2003	
Serranidae (Epinephelinae)	*Epinephelus morio*	Protogyny	Histology	Unknown	Temperate Sea	Burgos et al. 2007	
Serranidae (Epinephelinae)	*Epinephelus ongus*	Protogyny	Histology (1, 2)	Spawning aggregation, pair spawning (2, 3)	Coral reef	(1) Craig 2007, (2) Ohta & Ebisawa 2015, (3) Nanami et al. 2013	
Serranidae (Epinephelinae)	*Epinephelus rivulatus*	Protogyny	Histology, field (1)	Pair spwaning (2)	Coral reef	(1) Mackie 2003, (2) Mackie 2007	
Serranidae (Epinephelinae)	*Epinephelus striatus*	Protogyny (1), gonochorism (2)	Histology (1, 2)	Group spawning with spawning aggregation (2)	Coral reef	(1) Carter et al. 1994, (2) Sadovy & Eklund 1999	
Serranidae (Epinephelinae)	*Epinephelus summana*	Protogyny?	Macroscopic*	Unknown	Coral reef	Osman et al. 2021	*weak evidence
Serranidae (Epinephelinae)	*Epinephelus tauvina*	Protogyny	Histology (1)	Pair spwaning (2)	Coral reef	(1) Mathew & Mathew 2010, (2) Mathew 2010	
Serranidae (Epinephelinae)	*Hyporthodus flavolimbatus*	Protogyny	Histology	Unknown	Deep sea	Bullock et al. 1996	*Epinephelus*

Serranidae (Epinephelinae)	*Hyporthodus niveatus*	Protogyny	Histology	Unknown	Coral reef	Wyanski et al. 2000	
Serranidae (Epinephelinae)	*Hyporthodus quernus*	Protogyny	Histology	Unknown	Coral reef	DeMartini et al. 2011	
Serranidae (Epinephelinae)	*Mycteroperca bonaci*	Protogyny	Histology (1–3)	Unknown	Coral reef	(1) García-Cagide & García 1996, (2) Crabtree & Bullock 1998, (3) Brulé et al. 2003	
Serranidae (Epinephelinae)	*Mycteroperca interstitialis*	Protogyny	Histology	Unknown	Coral reef	Bullock & Murphy 1994	
Serranidae (Epinephelinae)	*Mycteroperca microlepis*	Protogyny	Histology (1)	Spawning aggregation (2)	Coral reef	(1) McErlean & Smith 1964, (2) Gilmore & Jones 1992	
Serranidae (Epinephelinae)	*Mycteroperca olfax*	Protogyny	Histology (1)	Spawning aggregation (2)	Coral reef	(1) Coello & Grimm 1993, (2) Salinas-de-León et al. 2015	
Serranidae (Epinephelinae)	*Mycteroperca phenax*	Protogyny	Histology (1)	Spawning aggregation (2)	Coral reef	(1) Harris et al. 2002, (2) Gilmore & Jones 1992	
Serranidae (Epinephelinae)	*Mycteroperca rubra*	Protogyny	Histology	Spawning aggregation	Coral reef	Aronov & Goren 2008	
Serranidae (Epinephelinae)	*Mycteroperca venenosa*	Protogyny	Histology (1)	Group spawning (2)	Coral reef	(1) García-Cagide & García 1996, (2) Schärer et al. 2012	
Serranidae (Epinephelinae)	*Plectropomus laevis*	Protogyny	Histology	Unknown	Coral reef	Adams 2003	
Serranidae (Epinephelinae)	*Plectropomus leopardus*	Protogyny	Histology (1, 2)	Pair spawning in spawning aggregation (3)	Coral reef	(1) Ferreira 1995, (2) Adams 2003, (3) Samoilys & Squire 1994	
Serranidae (Epinephelinae)	*Plectropomus maculatus*	Protogyny	Histology (1, 2)	Unknown	Coral reef	(1) Adams & Williams 2001, (2) Adams 2003	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Serranidae (Epinephelinae)	*Bullisichthys caribbaeus*	Simultaneous	Histology	Unknown	Coral reef	Smith & Erdman 1973	
Serranidae (Epinephelinae)	*Centropristis striata*	Protogyny	Histology	Unknown	Temperate Sea	Wenner et al. 1986	
Serranidae (Epinephelinae)	*Centropristis ocyurus*	Protogyny	Histology	Unknown	Temperate Sea	Bullock & Smith 1991	
Serranidae (Epinephelinae)	*Chelidoperca hirundinacea*	Protogyny	Histology	Unknown	Temperate Sea	Reinboth 1967	
Serranidae (Epinephelinae)	*Diplectrum bivittatum*	Simultaneous	Histology	Unknown	Temperate Sea	Touart & Bortone 1980	
Serranidae (Epinephelinae)	*Diplectrum formosum*	Simultaneous	Histology	Unknown	Temperate Sea	Bortone 1971	
Serranidae (Epinephelinae)	*Diplectrum macropoma*	Simultaneous	Histology	Unknown	Temperate Sea	Bortone 1977a	
Serranidae (Epinephelinae)	*Diplectrum pacificum*	Simultaneous	Histology	Unknown	Tropical Sea	Bortone 1977b	
Serranidae (Epinephelinae)	*Diplectrum rostrum*	Simultaneous	Histology	Unknown	Tropical Sea	Bortone 1974	
Serranidae (Epinephelinae)	*Hypoplectrus aberrans*	Simultaneous	Aquarium	Reciprocal pair spawning	Coral reef	Fischer 1981	
Serranidae (Epinephelinae)	*Hypoplectrus chlorurus*	Simultaneous	Field	Reciprocal pair spawning	Coral reef	Barlow 1975	
Serranidae (Epinephelinae)	*Hypoplectrus nigricans*	Simultaneous	Field (1), aquarium (2)	Reciprocal pair spawning (1), serial monogamy (2)	Coral reef	(1) Fischer 1980, (2) Petersen 1991	
Serranidae (Epinephelinae)	*Hypoplectrus puella*	Simultaneous	Field (1), aquarium (2)	Repeated pair spawning (1)	Coral reef	(1) Barlow 1975, (2) Fischer 1981	
Serranidae (Epinephelinae)	*Hypoplectrus unicolor*	Simultaneous	Field (1), aquarium (2)	Reciprocal pair spawning (2)	Coral reef	(1) Barlow 1975, (2) Fischer 1981	

Serranidae (Epinephelinae)	*Paralabrax maculatofasciatus*	Protogyny (1, 2), gonochorism (3)	Histology (1, 2, 3)	Unknown	Temperate Sea	(1) Hastings 1989, (2) Oda et al. 1993, (3) Sadovy & Domeier 2005	
Serranidae (Epinephelinae)	*Serraniculus pumilio*	Simultaneous	Histology	Unknown	Tropical Sea	Hastings 1973	
Serranidae (Epinephelinae)	*Serranus annularis*	Simultaneous	Histology	Unknown	Tropical Sea	Bullock & Smith 1991	
Serranidae (Epinephelinae)	*Serranus atricauda*	Simultaneous	Histology	Unknown	Temperate Sea	García-Díaz et al. 2002	
Serranidae (Epinephelinae)	*Serranus auriga*	Simultaneous	Histology	Unknown	Temperate Sea	Militelli & Rodrigues 2011	
Serranidae (Epinephelinae)	*Serranus baldwini*	Simultaneous, males derive from hermaprodites	Field (1), microscopic (2)	Harem (2)	Tropical Sea	(1) Fischer & Petersen 1986 (2) Petersen & Fischer 1986	
Serranidae (Epinephelinae)	*Serranus cabrilla*	Simultaneous	Histology	Unknown	Temperate Sea	García-Díaz et al. 1997	
Serranidae (Epinephelinae)	*Serranus hepatus*	Simultaneous	Histology	Unknown	Temperate Sea	Bruslé 1983	
Serranidae (Epinephelinae)	*Serranus phoebe*	Simultaneous	Histology	Unknown	Tropical Sea	Smith 1959	
Serranidae (Epinephelinae)	*Serranus psittacinus*	Simultaneous	Histology (1), field (2, 3, 4)	Harem (2, 3, 4), monogamy, complex harem (3)	Tropical Sea	(1) Hastings & Petersen 1986, (2) Petersen 1987, (3) Petersen 1990a, (4) Petersen 1990b	*S. fasciatus*
Serranidae (Epinephelinae)	*Serranus scriba*	Simultaneous	Histology (1, 2)	Unknown	Temperate Sea	(1) Tuset et al. 2005, (2) Zorica et al. 2005	
Serranidae (Epinephelinae)	*Serranus subligarius*	Simultaneous	Histology (1), field (2),	Reciprocal pair spawning, promiscuous (2)	Temperate Sea	(1) Hastings & Bortone 1980, (2) Oliver 1997	
Serranidae (Epinephelinae)	*Serranus tabacarius*	Simultaneous	Field	Reciprocal pair spawning, promiscuous	Coral reef	Petersen 1995	

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Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Serranidae (Epinephelinae)	*Serranus tigrinus*	Simultaneous	Field (1, 2)	Monogamy, pair spawning (1, 2)	Coral reef	(1) Pressley 1981, (2) Petersen 1991	
Serranidae (Epinephelinae)	*Serranus tortugarum*	Simultaneous	Field (1, 2, 3)	Reciprocal pair spawning (1), serial monogamy (3), monogamy (4)	Coral reef	(1) Fischer 1984, (2) Fischer & Hardison 1987, (3) Petersen 1991, (4) Hart et al. 2016	
Serranidae (Grammistini)	*Pseudogramma gregoryi*	Simultaneous	Histology	Unknown	Coral reef	Smith & Atz 1969	*P. bermudensis*
Serranidae (Grammistini)	*Rypticus saponaceus*	Protogyny	Histology	Unknown	Coral reef	Smith 1965	
Serranidae (Grammistini)	*Rypticus subbifrenatus*	Protogyny	Histology	Unknown	Coral reef	Smith 1965	*R. arenatus*
Serranidae (Anthiinae)	*Anthias anthias*	Protogyny	Histology	Unknown	Temperate Sea	Reinboth 1964	
Serranidae (Anthiinae)	*Anthias nicholsi*	Protogyny	Histology	Unknown	Tropical Sea	Bullock & Smith 1991	
Serranidae (Anthiinae)	*Anthias noeli*	Protogyny	Histology	Unknown	Tropical Sea	Anderson & Baldwin 2000	
Serranidae (Anthiinae)	*Baldwinella vivanus*	Protogyny	Histology	Unknown	Tropical Sea	Hastings 1981	*Hemanthias*
Serranidae (Anthiinae)	*Hemanthias leptus*	Protogyny	Histology	Unknown	Tropical Sea	Bullock & Smith 1991	
Serranidae (Anthiinae)	*Hemanthias peruanus*	Protogyny	Histology	Unknown	Tropical Sea	Coleman 1983	
Serranidae (Anthiinae)	*Hypoplectrodes huntii*	Protogyny	Histology	Unknown	Temperate Sea	Jones 1980b	*Ellerkeldia*
Serranidae (Anthiinae)	*Hypoplectrodes macculochi*	Protogyny	Histology	Unknown	Temperate Sea	Webb & Kingsford 1992	
Serranidae (Anthiinae)	*Pronotogrammus martinicensis*	Protogyny	Histology (1, 2)	Unknown	Tropical Sea	(1) Coleman 1981, (2) McBride et al. 2009	*Holanthias*

Serranidae (Anthiinae)	*Pseudanthias bicolor*	Protogyny?	Gonad*	Unknown	Tropical Sea	Howe 1996	*Anthias**weak evidence
Serranidae (Anthiinae)	*Pseudanthias conspicuus*	Protogyny	Histology	Unknown	Tropical Sea	Heemsta 1973	*Antias*
Serranidae (Anthiinae)	*Pseudanthias elongatus*	Protogyny	Histology	Unknown	Temperate Sea	Reinboth 1963	
Serranidae (Anthiinae)	*Pseudanthias pleurotaenia*	Protogyny	Aquarium, histology	Pair spawning	Tropical Sea	Hioki et al. 2001	
Serranidae (Anthiinae)	*Pseudanthias rubrizonatus*	Protogyny	Histology	Unknown	Temperate rocky reef	Hayasaka et al. 2019	
Serranidae (Anthiinae)	*Pseudanthias squamipinnis*	Protogyny	Aquarium (1), histology (2), field (3)	Pair spawning, multi-male group (3)	Coral reef	(1) Fishelson 1970, (2) Suzuki et al. 1978, (3) Yogo 1985	*Anthias, Franzia*
Serranidae (Anthiinae)	*Pseudanthias taeniatus*	Protogyny?	Microscopic*	Unknown	Tropical Sea	Katayama 1978	*weak evidence
Serranidae (Anthiinae)	*Sacura margaritacea*	Protogyny	Histology (1, 2, 3)	Unknown	Temperate Sea	(1) Reinboth 1963, (2) Okada 1965a, b, (3) Suzuki et al. 1974	
Pomacanthidae	*Apolemichthys trimaculatus*	Protogyny	Aquarium	Pair spawning	Coral reef	Hioki & Suzuki 1995	
Pomacanthidae	*Centropyge acanthops*	Protogyny, reversed sex change	Aquarium	Pair spawning	Coral reef	Hioki & Suzuki 1996	
Pomacanthidae	*Centropyge bicolor*	Protogyny	Field (1, 2)	Harem (1)	Coral reef	(1) Aldenhoven 1984, (2) Aldenhoven 1986	
Pomacanthidae	*Centropyge ferrugata*	Protogyny (1), reversed sex change (2, 3)	Field (1, 3), aquarium (2)	Harem (4)	Coral reef	(1) Sakai 1997, (2) Sakai et al. 2003a, (3) Kuwamura et al. 2011, (4) Sakai & Kohda 1997	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Pomacanthidae	*Centropyge fisheri*	Protogyny, reversed sex change	Aquarium, histology	Pair spawning	Coral reef	Hioki & Suzuki 1996	
Pomacanthidae	*Centropyge flavissimus*	Protogyny? Reversed sex change (1)	Aquarium (1)	Harem (2)	Coral reef	(1) Hioki & Suzuki 1996, (2) Thresher 1982	
Pomacanthidae	*Centropyge heraldi*	Protogyny	Aquarium (1)	Harem (2)	Coral reef	(1) Hioki 2002, (2) Thresher 1982	
Pomacanthidae	*Centropyge interruptus*	Protogyny	Field	Harem	Temperte reef	Moyer & Nakazono 1978a	
Pomacanthidae	*Centropyge multispinus*	Protogyny	Histology	Unknown	Coral reef	Bruce 1980	
Pomacanthidae	*Centropyge potteri*	Protogyny	Field (1, 2)	Harem (1, 2, 3)	Coral reef	(1) Lutnesky 1994, (2) Lutnesky 1996, (3) Lobel 1978	
Pomacanthidae	*Centropyge tibicen*	Protogyny	Field	Harem	Coral reef	Moyer & Zaiser 1984	
Pomacanthidae	*Centropyge vrolicki*	Protogyny	Field	Harem	Coral reef	Sakai et al. 2003b	
Pomacanthidae	*Chaetodontoplus septentrionalis*	Protogyny	Histology (1)	Harem (2)	Coral reef	(1) Chen & Tzeng 2009, (2) Leu et al. 2010	
Pomacanthidae	*Genicanthus bellus*	Protogyny	Aquarium	Pair spawning	Coral reef	Hioki et al. 1995	
Pomacanthidae	*Genicanthus caudovittatus*	Protogyny	Histology (1)	Harem (multi-male) (2)	Coral reef	(1) Bruce 1980, (2) Moyer 1990	
Pomacanthidae	*Genicanthus lamarck*	Protogyny	Histology (1), aquarium (1)	Harem (multi-male) (2)	Coral reef	(1) Suzuki et al. 1979, (2) Moyer 1984	
Pomacanthidae	*Genicanthus melanospilos*	Protogyny	Aquarium (1)	Harem (2, 3)	Coral reef	(1) Hioki et al. 1982, (2) Moyer 1987, (3) Moyer 1990	
Pomacanthidae	*Genicanthus personatus*	Protogyny	Aquarium (1)	Harem (multi-male) (2)	Coral reef	(1) Carlson 1982, (2) Pyle 1990 after Chung 1996	
Pomacanthidae	*Genicanthus semifasciatus*	Protogyny	Histology, aquarium (1, 2)	Harem (multi-male) (3, 4)	Coral reef	(1) Shen & Liu 1976, (2) Suzuki et al. 1979, (3) Moyer 1987, (4) Moyer 1990	

Pomacanthidae	*Genicanthus watanabei*	Protogyny	Aquarium	Pair spawning	Coral reef	Hioki et al. 1995	
Pomacanthidae	*Holacanthus passer*	Protogyny (1), gonochorism (2)	Histology (1, 2)	Monogamous, harem (multi-male?) (3)	Coral reef	(1) Arellano-Martínez 1997, (2) Arellano-Martínez et al. 1999, (3) Moyer et al. 1983	
Pomacanthidae	*Holacanthus tricolor*	Protogyny	Histology (1)	Harem (1, 2, 3)	Coral reef	(1) Hourigan & Kelley 1985, (2) Hourigan 1986, (3) Moyer et al. 1983	
Pomacanthidae	*Pomacanthus zonipectus*	Protogyny	Histology	Unknown	Coral reef	Arellano-Martínez 1997	
Malacanthidae	*Malacanthus plumieri*	Protogyny	Histology, field	Harem	Coral reef	Baird 1988	
Cirrhitidae	*Amblycirrhitus pinos*	Protogyny	Histology	Unknown	Coral reef	Sadovy & Donaldson 1995	
Cirrhitidae	*Cirrhitichthys aprinus*	Protogyny	Histology (1, 2)	Harem (3)	Coral reef	(1) Sadovy & Donaldson 1995, (2) Kobayashi & Suzuki 1992, (3) Donaldson 1990	
Cirrhitidae	*Cirrhitichthys aureus*	Protogyny, reversed sex change	Aquarium, histology	Pair spawning (aquarium)	Tropical-temperate reef	Kobayashi & Suzuki 1992	
Cirrhitidae	*Cirrhitichthys falco*	Protogyny (1, 2, 3), reversed sex change (3)	Histology (1, 2) *, field (3)	Harem (4, 5)	Coral reef	(1) Sadovy & Donaldson 1995, (2) Kobayashi & Suzuki 1992, (3) Kadota et al. 2012, (4) Donaldson 1987, (5) Kadota et al. 2011	*small sample size
Cirrhitidae	*Cirrhitichthys oxycephalus*	Protogyny	Histology (1)	Harem (2)	Coral reef	(1) Sadovy & Donaldson 1995, (2) Donaldson 1990	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Cirrhitidae	*Cirrhitops hubbardi*	Protogyny?	Histology*	Unknown	Coral reef	Kobayashi & Suzuki 1992	*small sample size
Cirrhitidae	*Cirrhitus pinnulatus*	Protogyny?	Histology (1)*	Harem (2)	Coral reef	(1) Sadovy & Donaldson 1995, (2) Donaldson 1990	*small sample size
Cirrhitidae	*Cyprinocirrhites polyactis*	Protogyny?	Histology*	Unknown	Coral reef	Kobayashi & Suzuki 1992	*small sample size
Cirrhitidae	*Neocirrhites armatus*	Protogyny	Histology (1)	Harem (1, 2, 3)	Coral reef	(1) Sadovy & Donaldson 1995, (2) Donaldson 1989, (3) Donaldson 1990	
Eleginopsidae	*Eleginops maclovinus*	Protandry	Histology (1, 2, 3)	Unknown	Temperate Sea	(1) Calvo et al. 1992, (2) Brickle et al. 2005, (3) Licandeo et al. 2006	
Scorpaeniformes							
Platycephalidae	*Cociella crocodila*	Protandry	Histology	Unknown	Temperate Sea	Aoyama et al. 1963	
Platycephalidae	*Inegocia japonica*	Protandry	Histology (1, 2), field (2)	Random mating (2)	Temperate Sea	(1) Fujii 1970, (2) Shinomiya et al. 2003	
Platycephalidae	*Kumococius rodericensis*	Protandry	Histology	Unknown	Temperate Sea	Fujii 1971	
Platycephalidae	*Onigocia macrolepis*	Protandry	Histology	Unknown	Temperate Sea	Fujii 1970	
Platycephalidae	*Platycephalus* sp.*	Protandry	Histology, aquarium	Random mating	Temperate Sea	Hara & Sunobe 2021	**Platycephalus* sp. 2 in Nakabo and Kai (2013)
Platycephalidae	*Suggrundus meerdervoorti*	Protandry	Histology (1, 2)	Unknown	Temperate Sea	(1) Okada 1966a, (2) Shitamitsu & Sunobe 2018	*Inegocia* (1)

Platycephalidae	*Thysanophrys celebica*	Protandry	Histology, field, aquarium	Random mating (1)	Temperate Sea	Sunobe et al. 2016	
Scorpaenidae	*Caracanthus unipinna*	Protogyny	Histology	Harem, facultative monogamy	Coral reef	Wong et al. 2005	
Moroniformes							
Moronidae	*Morone saxatilis*	Protandry	Histology	Unknown	Temperatel Sea and freshwater	Moser et al. 1983	
Spariformes							
Nemipteridae	*Scolopsis monogramma*	Protogyny	Histology (1, 2)	Unknown	Coral reef	(1) Young & Martin 1985, (2) Akita & Tachihara 2014	
Nemipteridae	*Scolopsis taenioptera*	Protogyny	Histology	Unknown	Coral reef	Young & Martin 1985	
Lethrinidae	*Lethrinus atkinsoni*	Protogyny	Histology	Unknown	Coral reef	Ebisawa 1999	
Lethrinidae	*Lethrinus genivittatus*	Protogyny	Histology	Unknown	Coral reef	Young & Martin 1982	*L. nematocanthus*
Lethrinidae	*Lethrinus harak*	Protogyny	Histology	Unknown	Coral reef	Ebisawa 2006	
Lethrinidae	*Lethrinus lentjan*	Protogyny	Histology	Unknown	Coral reef	Young & Martin 1982	
Lethrinidae	*Lethrinus miniatus*	Protogyny	Histology (1, 2, 3, 4)	Unknown	Coral reef	(1) Young & Martin 1982, (2) Sumpton & Brown 2004, (3) Bean et al. 2003, (4) Ebisawa 2006	*L. chrysostomus*
Lethrinidae	*Lethrinus nebulosus*	Protogyny (1), prematurational sex change (3, 4)	Histology (1, 3, 4)	Male territorial behavior, pair spawning, group spawning (2)	Coral reef	(1) Young & Martin 1982, (2) Akazaki et al. 1989, (3) Ebisawa 1990, (4) Marriott et al. 2010	*L. fraenatus*
Lethrinidae	*Lethrinus olivaceus*	Protogyny	Macroscopic (1), histology (2)	Spawning aggretation (1)	Coral reef	(1) Filous et al. 2022, (2) Shimose 2021	
Lethrinidae	*Lethrinus ornatus*	Protogyny	Histology	Unknown	Coral reef	Ebisawa 2006	
Lethrinidae	*Lethrinus ravus*	Protogyny	Histology	Unknown	Coral reef	Ebisawa 2006	
Lethrinidae	*Lethrinus rubrioperculatus*	Protogyny	Histology	Unknown	Coral reef	Ebisawa 1997	

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Lethrinidae	*Lethrinus variegatus*	Protogyny	Histology	Unknown	Coral reef	Young & Martin 1982	
Sparidae	*Acanthopagrus australis*	Protandry	Histology	Unknown	Temperate Sea	Pollock 1985	
Sparidae	*Acanthopagrus berda*	Protandry	Macroscopic (1)	Spawning aggregation (2)	Tropical and temperate sea	(1) Anam et al. 2019, (2) Garratt 1993	
Sparidae	*Acanthopagrus bifasciatus*	Protandry	Histology	Unknown	Temperate Sea	Etessami 1983	
Sparidae	*Acanthopagrus latus*	Protandry	Histology (1, 2)	Unknown	Temperate Sea	(1) Kinoshita 1939, (2) Akazaki 1962	
Sparidae	*Acanthopagrus morrisoni*	Protandry	Histology	Unknown	Temperate-Subtropical Sea	Hesp et al. 2004	*A. latus*
Sparidae	*Acanthopagrus pacificus*	Protandry	Histology	Unknown	Tropical and temperate sea	Tobin 1998	*A. berda*
Sparidae	*Acanthopagrus schlegelii*	Protandry	Histology (1, 2, 3, 4, 5), aquarium (3)	Unknown	Temperate Sea	(1) Kinoshita 1936, (2) Ohshima 1942, (3) Chang & Yueh 1990, (4) Lee et al. 2001, (5) Law & Sadovy de Mitcheson 2017	*Sparus longispinis* (1), *Sparus swinhonis* (2)
Sparidae	*Argyrops spinifer*	Protogyny (1), protogyny or rudimentary (2) hermaphroditism (2)	Macroscopic (1), histology (2)	Unknown	Temperate Sea	(1) El-Sayed & Abdel-Bary 1993, (2) Hamzeh et al. 2017	
Sparidae	*Boops boops*	Protogyny (2, 3), rudimentary hermaphroditism (1)	Microscopic (1, 2), macroscopic, histology (3)	Unknown	Temperate Sea	(1) D'Ancona 1949, (2) Monteiro et al. 2006, (3) Amira et al. 2019	

Sparidae	*Calamus leucosteus*	Protogyny	Histology	Unknown	Temperate Sea	Waltz et al. 1982	
Sparidae	*Calamus proridens*	Protogyny	Histology	Unknown	Tropical Sea	Tyler-Jedlund & Torres 2015	
Sparidae	*Chrysoblephus cristiceps*	Protogyny	Microscopic (1), histology (2)	Unknown	Temperate Sea	(1) Robinson 1976, (2) Buxton 1989	
Sparidae	*Chrysoblephus laticeps*	Protogyny	Microscopic (1), histology (2)	Pair spawning (3)	Temperate Sea	(1) Penrith 1972, (2) Buxton 1989, (3) Buxton 1990	
Sparidae	*Chrysoblephus puniceus*	Protogyny	Histology	Unknown	Temperate Sea	Garratt 1986	
Sparidae	*Dentex gibbosus*	Protogyny	Histology	Unknown	Temperate Sea	Pajuelo & Lorenzo 1995	
Sparidae	*Dentex tumifrons*	Protogyny	Histology	Unknown	Temperate Sea	Aoyama 1955	*Taius*
Sparidae	*Diplodus annularis*	Protandry (1), gonochorism (2)	Histology (1, 2, 3)	Unknown	Temperate Sea	(1) Lissia-Frau et al. 1976, (2) Pajuelo & Lorenzo 2001, (3) Chaouch et al. 2013	
Sparidae	*Diplodus argenteus*	Protandry	Histology	Unknown	Coastal upwelling of tropical sea	David et al. 2005	
Sparidae	*Diplodus cadenati*	Protandry	Macroscopic	Unknown	Temperate Sea	Pajuelo & Lorenzo 2004	*D. sargus cadenati*
Sparidae	*Diplodus capensis*	Protandry (2, 3), juvenile hermaphroditism (1, 4)	Histology (1, 2, 3, 4)	Group spawning? (2)	Temperate Sea	(1) Joubert 1981, (2) Coetzee 1986, (3) Mann & Buxton 1998, (4) Richardson et al. 2011	*D. sargus capensis*
Sparidae	*Diplodus kotschyi*	Protandry	Microscopic	Unknown	Temperate Sea	Abou-Seedo et al. 1990	*D. sargus kotschyi*

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Sparidae	*Diplodus puntazzo*	Protandry	Histology (1, 2)	Unknown	Temperate Sea	(1) Lissia-Frau et al. 1976, (2) Pajuelo et al. 2008	*Puntazzo* (1)
Sparidae	*Diplodus sargus*	Protandry	Histology (1, 2, 3)	Unknown	Temperate Sea	(1) Lissia-Frau et al. 1976, (2) Micale & Perdichizzi 1994, (3) Mouine et al. 2007	
Sparidae	*Diplodus vulgaris*	Protandry	Histology (1, 2)	Unknown	Temperate Sea	(1) Gonçalves & Erzini 2000, (2) Pajuelo et al. 2006a	
Sparidae	*Lithognathus mormyrus*	Protandry (1, 2, 3), juvenile hermaphroditism (2)	Histology (1, 2, 3)	Unknown	Temperate Sea	(1) Lissia-Frau & Casu 1968, (2) Besseau & Bruslé-Sicard 1995, (3) Lorenzo et al. 2002	
Sparidae	*Pachymetopon aeneum*	Protogyny	Macroscopic, microscopic	Unknown	Temperate Sea	Buxton & Clarke 1985	
Sparidae	*Pagellus acarne*	Protandry	Histology (1, 2)	Unknown	Temperate Sea	(1) Reinboth 1962, (2) Lamrini 1986	
Sparidae	*Pagellus bellottii*	Protogyny (1), gonochore (2)	Histology (1), macroscopic (2)	Unknown	Temperate Sea	(1) Ndiaye 2014, (2) Kouame et al. 2018	
Sparidae	*Pagellus bogaraveo*	Protandry	Histology (1, 2, 3)	Unknown	Temperate Sea	(1) Krug 1990, (2) Krug 1998, (3) Micale et al. 2002	
Sparidae	*Pagellus erythrinus*	Protogyny	Histology (1, 2)	Unknown	Temperate Sea	(1) Zei 1950, (2) Pajuelo & Lorenzo 1998	
Sparidae	*Pagrus auriga*	Protogyny	Histology (1, 2, 3)	Unknown	Temperate Sea	(1) Alekseev 1982, (2) Alekseev 1983, (3) Pajuelo et al. 2006b	

Sparidae	*Pagrus caeruleostictus*	Protogyny	Histology	Unknown	Temperate Sea	Ismail et al. 2018	
Sparidae	*Pagrus ehrenbergii*	Protogyny, prematurational sex change	Histology (1, 2)	Unknown	Temperate Sea	(1) Alekseev 1982, (2) Alekseev 1983	
Sparidae	*Pagrus major*	Protogyny (1), juvenile hermaphroditism (2)	Histology (1, 2)	Unknown	Temperate Sea	(1) Huang et al. 1974, (2) Matsuyama et al. 1988	*Chrysophrys* (1)
Sparidae	*Pagrus pagrus*	Protogyny	Histology (1, 2, 3)	Unknown	Temperate Sea	(1) Alekseev 1982, (2) Alekseev 1983, (3) Kokokiris et al. 1999	
Sparidae	*Rhabdosargus sarba*	Protandry (1, 2), gonochorism (3), juvenile hermaphroditism (3)	Histology (1, 2, 3), aquarium (2)	Pair spawning (aquarium: 4)	Temperate Sea	(1) Kinoshita 1939, (2) Yeung & Chan 1987, (3) Hesp & Potter 2003, (4) Leu 1994	*Sparus aries* (1)
Sparidae	*Sarpa salpa*	Protandry (1, 3), juvenile hermaphroditism (2, 3)	Histology (1, 2, 3), aquarium (3)	Spawning aggregation (3)	Temperate Sea	(1) Lissia-Frau et al. 1976, (2) Joubert 1981, (3) van der Walt & Mann 1998	*Boops*
Sparidae	*Sparidentex hasta*	Protandry	Histology (1, 2)	Unknown	Tropical Sea	(1) Abu-Hakima 1984, (2) Lone & Al-Marzouk 2000	*Acanthopagrus cuvieri* (1)
Sparidae	*Sparus aurata*	Protandry	Histology and aquarium (1, 2)	Pair and group spawning (aquarium: 3)	Temperate Sea	(1) Zohar et al. 1978, (2) Brusléa-Sicard & Fourcault 1997, (3) Ibarra-Zatarain & Duncan 2015	
Sparidae	*Spicara chryselis*	Protogyny	Histology	Unknown	Temperate Sea	Zei 1950	*Maena*
Sparidae	*Spicara smaris*	Protogyny	Histology (1), microscopic (2)	Unknown	Temperate Sea	(1) Zei 1950, (2) Dulčić et al. 2003	*Maena* (1)

(continued)

Order-family	Species	Type of hermaphroditism	Evidence	Mating system	Habitat	References	Remarks
Sparidae	*Spicara maena*	Protogyny	Histology (1), microscopic (2, 3)	Unknown	Temperate Sea	(1) Sellami & Bruslé 1979, (2) Zamboni & Relini 1986, (3) Dulčić et al. 2000	*Maena* (1)
Sparidae	*Spondyliosoma cantharus*	Protogyny	Microscopic (1, 2)	Male territory, nest guard (3)	Temperate Sea	(1) Pajuelo & Lorenzo 1999, (2) Mouine et al. 2011, (3) Wilson 1958	
Sparidae	*Spondyliosoma emarginatum*	Protogyny	Macroscopic (1, 2)	Male territory, nest guard (1)	Temperate Sea	(1) Tunley et al. 2009, (2) Attwood & Ensair 2020	
Tetraodontiformes							
Balistidae	*Sufflamen chrysopterus*	Protogyny	Histology, field (1)	Harem (1,2,3)	Coral reef	(1) Takamoto et al. 2003, (2) Ishihara & Kuwamura 1996, (3) Seki et al. 2009	

For the mating system, “MTV polygamy” means “male-territory-visiting polygamy (Kuwamura 1997), and any reproductive behavior related to mating system is described
The asterisks (*) are explained in “Remarks,” and (1), (2), (3), etc. are the reference numbers in “References”

References

Abdel-Aziz ESH, Bawazeer FA, El-Sayed Ali T, Al-Otaibi M (2012) Sexual patterns and protogynous sex reversal in the rusty parrotfish, *Scarus ferrugineus* (Scaridae): histological and physiological studies. Fish Physiol Biochem 38:1211–1224

Abou-Seedo F, Wright JM, Clayton DA (1990) Aspects of the biology of *Diplodus sargus kotschyi* (Sparidae) from Kuwait Bay. Cybium 14:217–223

Abu-Hakima R (1984) Some aspects of the reproductive biology of *Acanthopagrus* spp. (family: Sparidae). J Fish Biol 25:515–526

Adams S (2003) Morphological ontogeny of the gonad of three plectropomid species through sex differentiation and transition. J Fish Biol 63:22–36

Adams S, Williams AJ (2001) A preliminary test of the transitional growth spurt hypothesis using the protogynous coral trout *Plectropomus maculatus*. J Fish Biol 59:183–185

Adreani MS, Allen LG (2008) Mating system and reproductive biology of a temperate wrasse, *Halichoeres semicinctus*. Copeia 2008:467–475

Adreani MS, Erisman BE, Warner RR (2004) Courtship and spawning behavior in the California sheephead, *Semicossyphus pulcher* (Pisces: Labridae). Environ Biol Fish 71:13–19

Akazaki M (1962) Studies on the spariform fishes: anatomy, phylogeny, ecology and taxonomy. Misaki Mar Biol Inst Kyoto Univ Spec Rep 1:1–368

Akazaki M, Tokito A, Takamatsu S, Nakajima H, Kawahara H (1989) Spawning behavior, embryonic development and metamorphosis of larvae of the lethrinid fish, *Lethrinus nebulosus*. Bull Fac Agr, Miyazaki Univ 36:165–173

Akita Y, Tachihara K (2014) Age, growth, maturity, and sex changes of monogrammed monocle bream *Scolopsis monogramma* in the waters around Okinawa-jima Island, Japan. Fish Sci 80:679–685

Aldenhoven JM (1984) Social organization and sex change in an angelfish, *Centropyge bicolor* on the Great Barrier Reef. Doctoral dissertation, Macquarie University, North Ryde, NSW

Aldenhoven JM (1986) Different reproductive strategies in a sex-changing coral reef fish *Centropyge bicolor* (Pomacanthidae). Aust J Mar Freshwat Res 37:353–360

Alekseev FE (1982) Hermaphroditism in sparid fishes (Perciformes, Sparidae). I. Protogyny in porgies, *Pagrus pagrus*, *P. orphus*, *P. ehrenbergi* and *P. auriga*, from West Africa. J Ichthyol 22:85–94

Alekseev FE (1983) Hermaphroditism in porgies (Perciformes, Sparidae). II. Sexual structure of the populations, mechanism of its formation and evolution in scups, *Pagrus pagrus*, *P. orphus*, *P. ehrenbergi* and *P. auriga*. J Ichthyol 23:61–67

Allsop DJ, West SA (2004) Sex allocation in the sex-changing marine goby *Coryphopterus personatus* on atoll fringing reefs. Evol Ecol Res 6:843–855

Amira S, Alioua Z, Harchouche K (2019) Gonadal development and fecundity of bogue *Boops boops* (Linnaeus, 1958) (Sparidae) on the central Algerian coast. Turk J Zool 43:12–29

Anam RO, Munga CN, Gonda JR (2019) The biology of Goldsilk Sea Bream (family: Sparidae) from the inshore waters of north coast Kenya. WIO J Mar Sci 18:77–86

Anderson WD, Baldwin CC (2000) A new species of *Anthias* (Teleostei: Serranidae: Anthiinae) from the Galápagos Islands, with keys to *Anthias* and eastern Pacific Anthiinae. Proc Biol Soc Wash 113:369–385

Andrew TG, Buxton CD, Hecht T (1996) Aspects of the reproductive biology of the concha wrasse, *Nelabrichthys ornatus*, at Tristan da Cunha. Environ Biol Fish 46:139–149

Aoyama T (1955) On the hermaphroditism in the yellow sea bream, *Taius tumifrons*. Jpn J Ichthyol 4:119–129

Aoyama T, Kitajima T, Mizue K (1963) Study of the sex reversal of inegochi, *Cociella crocodila* (Tilesius). Bull Seikai Region Fish Res Lab 29:11–33

Arellano-Martínez M (1997) Biología reproductiva del ángel rey *Holacanthus passer* Valenciennes, 1864 y del ángel de cortés *Pomacanthus zonipectus* (Gill, 1863) (Teleostei:

Pomacanthidae), en la coasta sur-occidental del Golfo de California, México, Master thesis. Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, La Paz

Arellano-Martínez M, Ceballos-Vázquez BP, García-Domínguez F, Galván-Magaña F (1999) Reproductive biology of the king angelfish *Holacanthus passer* Valenciennes 1846 in the Gulf of California, Mexico. Bull Mar Sci 65:677–685

Aronov A, Goren M (2008) Ecology of the mottled grouper (*Mycteroperca rubra*) in the eastern Meditterranean. Elec J Ichthyol 2:43–55

Asoh K (2003) Gonadal development and infrequent sex change in a population of the humbug damselfish, *Dascyllus aruanus*, in continuous coral-cover habitat. Mar Biol 142:1207–1218

Asoh K (2004) Gonadal development in the coral reef damselfish *Dascyllus flavicaudus* from Moorea, French Polynesia. Mar Biol 146:167–179

Asoh K (2005a) Frequency of functional sex change in two populations of *Dascyllus melanurus* conforms to a prediction from sex allocation theory. Copeia 2005:732–744

Asoh K (2005b) Gonadal development and diandric protogyny in two populations of *Dascyllus reticulatus* from Madang, Papua New Guinea. J Fish Biol 66:1127–1148

Asoh K, Yoshikawa T (2003) Gonadal development and an indication of functional protogyny in the Indian damselfish (*Dascyllus carneus*). J Zool Lond 260:23–39

Attwood CG, Ensair HAM (2020) Life-history trade-offs among four sympatric seabreams. Afr J Mar Sci 42:323–337

Badcock J (1986) Aspects of the reproductive biology of *Gonostoma bathyphilum* (Gonostomatidae). J Fish Biol 29:589–603

Badcock J, Merrett NR (1976) Midwater fishes in the eastern North Atlantic I. vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. Prog Oceanogr 7:3–58

Baird TA (1988) Female and male territoriality and mating system of the sand tilefish, *Malacanthus plumieri*. Environ Biol Fish 22:101–116

Baldwin CC, Weigt LA, Smith DG, Mounts JH (2009) Reconciling genetic lineages with species in western Atlantic *Coryphopterus* (Teleostei: Gobiidae). Smithsonian Contr Mar Sci 38:111–138

Barazona CA, Demayo CG, Torres MAJ, Gorospe JG (2015) Landmark-based geometric morphometric analysis on bodyshape variation of *Mesopristes cancellatus* (Cuvier, 1829). Adv Environ Biol 9(19 S4):32–37

Barlow GW (1975) On the sociobiology of some hermaphroditic serranid fishes, the hamlets, in Puerto Rico. Mar Biol 33:195–300

Barrett NS (1995) Aspects of the biology and ecology of six temperate reef fishes (families: Labridae and Monacanthidae). Doctoral dissertation, University of Tasmania

Bean K, Mapstone BD, Davies CR, Murchie CD, Williams AJ (2003) Gonad development and evidence of protogyny in the red-throat emperor on the Great Barrier Reef. J Fish Biol 62:299–310

Beentjes MP, Carbines GD (2005) Population structure and relative abundance of blue cod (*Parapercis colias*) off Banks Peninsula and in Dusky Sound, New Zealand. N Z J Mar Freshw Res 39:77–90

Bell LJ (1983) Aspects of the reproductive biology of the wrasse, *Cirrhilabrus temminckii*, at Miyake-jima, Japan. Jpn J Ichthyol 30:158–167

Bentivegna F, Rasotto MB (1987) Protogynous hermaphroditism in *Xyrichthys novacula* (L. 1758). Cybium 3:75–78

Berbel-Filho WM, Espírito-Santo H, Lima SM (2016) First record of a male of *Kryptolebias hermaphroditus* Costa, 2011 (Cyprinodontiformes: Cynolebiidae). Neotrop Ichthyol 14(3): e160024

Berbel-Filho WM, Tatarenkov A, Espírito-Santo HMV, Lira MG, Garcia de Leaniz C, Lima SMQ, Consuegra S (2020) More than meets the eye: syntopic and morphologically similar mangrove killifish species show different mating systems and patterns of genetic structure along the Brazilian coast. Heredity 125:340–352

Bertelsen E, Krefft G, Marshall NB (1976) The fishes of the family Notosudidae. Dana Reports 86: 1–114

Besseau L, Bruslé-Sicard S (1995) Plasticity of gonad development in hermaphroditic sparids : ovotestis ontogeny in a protandric species, *Lithognathus mormyrus*. Environ Biol Fish 43:255–267

Bhandari RK, Komuro H, Nakamura S, Higa M, Nakamura M (2003) Gonadal restructuring and correlative steroid hormone profiles during natural sex change in protogynous honeycomb grouper (*Epinephelus merra*). Zool Sci 20:1399–1404

Blaber SJM, Brewer DT, Milton DA, Merta GS, Efizon D, Fry G, Van der Velde T (1999) The life history of the protandrous tropical shad *Tenualosa macrura* (Alosinae: Clupeidae): fishery implications. Estuar Coast Shelf Sci 49:689–701

Blaber SJM, Fry G, Milton DA, Van der Velde T, Boon-Teck O, Pang J, Wong P (2005) The life history of *Tenualosa macrura* in Sarawak, further notes on protandry in the genus and management strategies. Fish Manag Ecol 12:201–210

Blaber SJM, Milton DA, Pang J, Wong P, Boon-Teck O, Lolin N, Lubin D (1996) The life history of the tropical shad *Tenualosa toli* from Sarawak: first evidence of protandry in the Clupeiformes? Environ Biol Fish 46:225–242

Black MP, Balthazart J, Baillien M, Grober MS (2005a) Socially induced and rapid increases in aggression are inversely related to brain aromatase activity in a sex-changing fish, *Lythrypnus dalli*. Proc R Soc B 272:2435–2440

Black MP, Moore B, Canario AVM, Ford D, Reavis RH, Grober MS (2005b) Reproduction in context: field testing a laboratory model of socially controlled sex change in *Lythrypnus dalli* (Gilbert). J Exp Mar Biol Ecol 318:127–143

Black MP, Reavis RH, Grober MS (2004) Socially induced sex change regulates forebrain isotocin in *Lythrypnus dalli*. Neuroreport 15:185–189

Blackwell RG (1998) Abundance, size and age composition, and yield-per-recruit of blue cod in the Marlborough Sounds, September 1996. NIWA Technical Report 30:1–47

Boddington DK, Wakefield CB, Fisher EA, Fairclough DV, Harvey ES, Newman SJ (2021) Age, growth and reproductive life-history characteristics infer a high population productivity for the sustainably fished protogynous hermaphroditic yellowspotted rockcod (*Epinephelus areolatus*) in north-western Australia. J Fish Biol 99:1869–1886

Bortone SA (1971) Studies on the biology of the sand perch, *Diplectrum formosum* (Perciformes: Serranidae). Tech Ser Florida Dept Nat Res 65:1–27

Bortone SA (1974) *Diplectrum rostrum*, a hermaphroditic new species (Pisces: Serranidae) from the eastern Pacific coast. Copeia 1974:61–64

Bortone SA (1977a) Revision of the seabasses of the genus *Diplectrum* (Pisces: Serranidae). US Dept Com, NOAA Tech Rep, NMFS Circ 404:1–49

Bortone SA (1977b) Gonad morphology of the hermaphroditic fish *Diplectrum pacificum* (Serranidae). Copeia 1977:448–453

Brickle P, Laptikhovsky V, Arkhipkin A (2005) Reproductive strategy of a primitive temperate notothenioid *Eleginops maclovinus*. J Fish Biol 66:1044–1059

Bruce RW (1980) Protogynous hermaphroditism in two marine angelfishes. Copeia 1980:353–355

Brulé T, Colás-Marrufo T, Tuz-Sulub A, Déniel C (2000) Evidence for protogynous hermaphroditism in the serranid fish *Epinephelus drummondhayi* (Perciformes: Serranidae) from the Campeche Bank in the southern Gulf of Mexico. Bull Mar Sci 66:513–521

Brulé T, Renán X, Colás-Marrufo T, Hauyon Y, Tuz-Sulub A (2003) Reproduction in the protogynous black grouper (*Mycteroperca bonaci* (Poey)) from the southern Gulf of Mexico. Fish Bull 101:463–475

Bruslé S (1983) Contribution to the sexuality of a hermaphroditic teleost, *Serranus hepatus* L. J Fish Biol 2:283–292

Bruslé J, Bruslé S (1975) Ovarian and testicular intersexuality in two protogynous Mediterranean groupers, *Epinephelus aeneus* and *Epinephelus guaza*. In: Reinboth R (ed) Intersexuality in the animal kingdom. Springer, Berlin, pp 222–227

Bruslé S (1987) Sex-inversion of the hermaphroditic, protogynous teleost *Coris julis* L. (Labridae). J Fish Biol 30:605–616

Bruslé-Sicard S, Fourcault B (1997) Recognition of sex-inverting protandric *Sparus aurata*: ultrastructural aspects. J Fish Biol 50:1094–1103

Bullock LH, Murphy MD (1994) Aspects of the life history of the yellowmouth grouper, *Mycteroperca interstitialis*, in the eastern Gulf of Mexico. Bull Mar Sci 55:30–45

Bullock LH, Godcharles MF, Crabtree RE (1996) Reproduction of yellowedge grouper, *Epinephelus flavolimbatus*, from the eastern Gulf of Mexico. Bull Mar Sci 59:216–224

Bullock LH, Smith GB (1991) Seabasses (Pisces : Serranidae). Mem Hourglass Cruis 8:1–206

Burgos JM, Sedberry GR, Wyanski DM, Harris PJ (2007) Life history of red grouper (*Epinephelus morio*) off the coasts of North Carolina and South Carolina. Bull Mar Sci 80:45–65

Butler EC, Childs AR, Milner MV, Farthing MW, Duncan MI, Winkler AC, Potts WM (2021) Do contemporary age-growth models overlook life-history complexities in protandrous fishes? A case study on the large protandrous polynemid, the giant African threadfin *Polydactylus quadrifilis*. Fish Res 233:105770

Buxton CD (1989) Protogynous hermaphroditism in *Chrysoblephus laticeps* (Cuvier) and *C. cristiceps* (Cuvier) (Teleostei: Sparidae). S Afr J Zool 24:212–216

Buxton CD (1990) The reproductive biology of *Chrysoblephus laticep*s and *C. cristicep*s (Teleostei: Sparidae). J Zool Lon 220:497–511

Buxton CD, Clarke JR (1985) Age, growth and feeding of the blue hottentot *Pachymetopon aeneum* (Pisces: Sparidae) with notes on reproductive biology. S-Afr Tydskr Dierk 21:33–38

Cabiddu S, Follesa MC, Porcu C, Cau A (2010) Gonad development and reproduction in the monoecious species *Chlorophthalmus agassizi* (Actinopterygii: Aulopiformes: Chlorophthalmidae) from the Sardinian waters (Central-Western Mediterranean). Acta Ichthyol Piscat 40:167–177

Calvo J, Morriconi E, Rae GA, SanRoman A (1992) Evidence of protandry in a subantarctic notothenid, *Eleginops maclovinus* (Cuv. & Val., 1830) from the Beagle Channel, Argentina. J Fish Biol 40:157–164

Candi G, Castriota L, Andaloro F, Finoia MG, Marino G (2004) Reproductive cycle and sex inversion in razor fish, a protogynous labrid in the southern Mediterranean Sea. J Fish Biol 64: 1498–1513

Carbines G (2004) Age, growth, movement and reproductive biology of blue cod (*Parapercis colias* – Pinguipedidae): implications for fisheries management in the South Island of New Zealand. Doctoral dissertation, University of Otago

Carlson BA (1982) The masked angelfish *Genicanthus personatus* Randall 1974. Freshwater Mar Aquar 5:31–32

Carter J, Marrow GJ, Pryor V (1994) Aspects of the ecology and reproduction of Nassau grouper (*Epinephelus striatus*) off the coast of Belize, Central America. Proc Gulf Carib Fish Inst 43:65–111

Casadevall M, Delgado E, Colleye O, Ber Monserrat S, Parmentier E (2009) Histological study of the sex-change in the skunk clownfish *Amphiprion akallopisos*. Open Fish Sci J 2:55–58

Chan STH, Phillips JG (1967) The structure of the gonad during natural sex reversal in *Monopterus albus* (Pisces: Teleostei). J Zool Lond 151:129–141

Chan STH, Ws O, Tang F, Lofts B (1972) Biopsy studies on the natural sex reversal in *Monopterus albus* (Pisces: Teleostei). J Zool Lond 167:415–421

Chang CF, Yueh WS (1990) Annual cycle of gonadal histology and steroid profiles in the juvenile males and adult females of the protandrous black porgy, *Acanthopagrus schlegeli*. Aquaculture 91:179–196

Chaouch H, Hamida-Ben Abdallah O, Ghorbel M, Jarboui O (2013) Reproductive biology of the annular seabream, *Diplodus annularis* (Linnaeus, 1758), in the Gulf of Gabes (Central Mediterranean). J Appl Ichthyol 29:796–800

Chen CP, Hsieh HL, Chang KH (1980) Some aspects of the sex change and reproductive biology of the grouper, *Epinephelus diacanthus* (Cuvier et Valenciennes). Bull Inst Zool Acad Sin 19:11–17

Chen J, Chen H, Peng C, Ye Z, Zhao M, Xiao L, Zhang H, Li S, Lin H, Zhang Y (2020) A highly efficient method of inducing sex change using social control in the protogynous orange-spotted grouper (*Epinephelus coioides*). Aquaculture 517:734787

Chen J, Peng C, Huang J, Shi H, Xiao L, Tang L, Lin H, Li S, Zhang Y (2021) Physical interactions facilitate sex change in the protogynous orange-spotted grouper, *Epinephelus coioides*. J Fish Biol 98:1308–1320

Chen J, Xiao L, Peng C, Ye Z, Wang D, Yang Y, Zhang H, Zhao M, Li S, Lin H, Zhang Y (2019) Socially controlled male-to-female sex reversal in the protogynous orange-spotted grouper, *Epinephelus coioides*. J Fish Biol 94:414–421

Chen KY, Tzeng WN (2009) Reproductive mode of the blue-striped angelfish *Chaetodontoplus septentrionali*s in northeastern Taiwan. Zool Stud 48:468–476

Choat JH (1969) Studies on the biology of labroid fishes (Labridae and Scaridae) at Heron Island, Great Barrier Reef. Doctoral dissertation, University of Queensland

Choat JH, Robertson DR (1975) Protogynous hermaphroditism in fishes of the family Scaridae. In: Reinboth R (ed) Intersexuality in the animal kingdom. Springer, Berlin, pp 263–283

Chung KC (1996) The general biology of the Pomacanthidae. Doctoral dissertation, The Chinese University of Hong Kong

Clark E, Pohle M, Rabin J (1991) Stability and flexibility through community dynamics of the spotted sandperch. Nat Geogr Res Expl 7:138–155

Clarke TA, Wagner PJ (1976) Vertical distribution and other aspects of the ecology of certain mesopelagic fishes taken near Hawaii. Fish Bull 74:635–645

Clavijo IE (1983) Pair spawning and formation of a lek-like mating system in the parrotfish *Scarus vetula*. Copeia 1983:253–256

Clavijo IE, Donaldson PL (1994) Spawning behavior in the labrid, *Halichoeres bivittatus*, on artificial and natural substrates in Onslow Bay, North Carolina, with notes on early life history. Bull Mar Sci 55:383–387

Claydon JAB (2005) The structure and dynamics of spawning aggregations of coral reef fish. Doctoral dissertation, James Cook University

Coates D (1981) Some observations on the sexuality of humbug damselfish, *Dascyllus aruanus* (Pisces, Pomacentridae) in the field. Z Tierpsychol 59:7–18

Coello S, Grimm A (1993) The reproductive biology of *Mycteroperca olfax* (Jenyns) (Pisces: Serranidae): protogyny and breeding season. Rev Cien Mar Limn 3:115–128

Coetzee PS (1986) Diet composition and breeding cycle of blacktail, *Diplodus sargus capensi*s (Pisces: Sparidae), caught off St Croix Island, Algoa Bay, South Africa. S Afr J Zool 21:237–243

Cole KS (1983) Protogynous hermaphroditism in a temperate zone territorial marine goby, *Coryphopterus nicholsi*. Copeia 1983:809–812

Cole KS (1988) Predicting the potential for sex-change on the basis of ovarian structure in gobiid fishes. Copeia 1988:1082–1086

Cole KS (1990) Patterns of gonad structure in hermaphroditic gobies (Teleostei Gobiidae). Environ Biol Fish 28:125–142

Cole KS (2002) Gonad morphology, sexual development, and colony composition in the obligate coral-dwelling damselfish *Dascyllus aruanus*. Mar Biol 140:151–163

Cole KS, Gill AC (2000) Specialization of the urinary bladder in two pseudoplesiopines (Teleostei: Pseudochromidae). Copeia 2000:1083–1089

Cole KS, Hoese DF (2001) Gonad morphology, colony demography and evidence for hermaphroditism in *Gobiodon okinawae* (Teleostei, Gobiidae). Environ Biol Fish 61:161–173

Cole KS, Robertson DR (1988) Protogyny in the Caribbean reef goby, *Coryphopterus personatus*: gonad ontogeny and social influences on sex-change. Bull Mar Sci 42:317–333

Cole KS, Shapiro DY (1990) Gonad structure and hermaphroditism in the gobiid genus *Coryphopterus* (Teleostei: Gobiidae). Copeia 1990:996–1003

Cole KS, Shapiro DY (1992) Gonadal structure and population characteristics of the protogynous goby *Coryphopterus glaucofraenum*. Mar Biol 113:1–9

Cole KS, Shapiro DY (1995) Social faciliation and sensory mediation of adult sex change in a cryptic, benthic marine goby. J Exp Mar Biol Ecol 186:65–75

Coleman FC (1981) Protogynous hermaphroditism in the anthiine serranid fish *Holanthias martinicensis*. Copeia 1981:893–895

Coleman FC (1983) *Hemanthias peruanus*—another hermaphroditic anthiine serranid. Copeia 1983:252–253

Colin PL (1978) Daily and summer-winter variation in mass spawning of the striped parrotfish, *Scarus croicensis*. Fish B-NOAA 76:117–124

Colin PL (2010) Aggregation and spawning of the humphead wrasse *Cheilinus undulatus* (Pisces: Labridae): general aspects of spawning behaviour. J Fish Biol 76:987–1007

Colin PL, Bell LJ (1991) Aspects of the spawning of labrid and scarid fishes (Pisces: Labroidei) at Enewetak atoll, Marshall Islands with notes on other families. Environ Biol Fish 3:229–260

Colin PL, Clavijo IE (1988) Spawning activity of fishes producing pelagic eggs on a shelf edge coral reef, southwestern Puerto Rico. Bull Mar Sci 43:249–279

Cossington S, Hesp SA, Hall NG, Potter IC (2010) Growth and reproductive biology of the foxfish *Bodianus frenchii*, a very long-lived and monandric protogynous hermaphroditic labrid. J Fish Biol 77:600–626

Costa WJ (2011) Identity of *Rivulus ocellatus* and a new name for a hermaphroditic species of *Kryptolebias* from south-eastern Brazil (Cyprinodontiformes: Rivulidae). Ichthyol Explor Freshwaters 22:185–192

Costa WJ, Lima SM, Bartolette R (2010) Androdioecy in *Kryptolebias* killifish and the evolution of self-fertilizing hermaphroditism. Biol J Linn Soc 99:344–349

Costa e Silva GH, Freitas MO, Abilhoa V (2021) Reproductive biology of the fat Snook *Centropomus parallelus* Poey, 1860 (Teleostei, Centropomidae) and implications for its management in the southern Atlantic Ocean. J Fish Biol 99:669–672

Coulson PG, Hesp SA, Hall NG, Potter IC (2009) The western blue groper (*Achoerodus gouldii*), a protogynous hermaphroditic labrid with exceptional longevity, late maturity, slow growth, and both late maturation and sex change. Fish B-NOAA 107:57–75

Cowen RK (1990) Sex change and life history patterns of the labrid, *Semicossyphus pulcher*, across an environmental gradient. Copeia 1990:787–795

Crabtree RE, Bullock LH (1998) Age, growth, and reproduction of black grouper, *Mycteroperca bonaci* in Florida waters. Fish Bull 96:735–753

Craig MT (2007) Preliminary observations on the life history of the white-streaked grouper, *Epinephelus ongus*, from Okinawa, Japan. Ichthyol Res 54:81–84

Craig PC (1998) Temporal spawning patterns of several surgeonfishes and wrasses in American Samoa. Pac Sci 52:35–39

D'Ancona U (1949) Il differenziamento della gonade e I'inversione sessuale degli sparidi. Arch Oceanogr Limnol 6:97–164

David GS, Coutinho R, Quagio-Grassiotto I, Verani JR (2005) The reproductive biology of *Diplodus argenteus* (Sparidae) in the coastal upwelling system of Cabo Frio, Rio de Janeiro, Brazil. Afr J Mar Sci 27:439–447

De Girolamo M, Scaggiante M, Rasotto MB (1999) Social organization and sexual pattern in the Mediterranean parrotfish *Sparisoma cretense* (Teleostei: Scaridae). Mar Biol 135:353–360

DeMartini EE, Everson AR, Nichols RS (2011) Estimates of body sizes at maturation and at sex change, and the spawning seasonality and sex ratio of the endemic Hawaiian grouper (*Hyporthodus quernus*, F. Epinephelidae). Fish Bull 109:123–134

Devine B, Guelpen LV (2021) Loss of gill rakers and teeth in adult specimens of barracudina *Arctozenus risso* (Aulopiformes: Paralepididae) from the western North Atlantic. Fish Biol 98: 329–332

Devlin RH, Nagahama Y (2002) Sex determination and sex differentiation in fish: an overview of genetic, physiological, and environmental influences. Aquaculture 208:191–364

Diener DR (1977) Protogynous hermaphroditism in the labrid *Decodon melasma*. Copeia 1977: 589–591

Dipper FA, Pullin RSV (1979) Gonochorism and sex-inversion in British Labridae (Pisces). J Zool 187:97–112

Donaldson TJ (1987) Social organization and reproductive behavior of the hawkfish *Cirrhitichthys falco* (Cirrhitidae). Bull Mar Sci 41:531–540

Donaldson TJ (1989) Facultative monogamy in obligate coral-dwelling hawkfishes (Cirrhitidae). Environ Biol Fish 26:295–302

Donaldson TJ (1990) Reproductive behavior and social organization of some Pacific hawkfishes (Cirrhitidae). Jpn J Ichthyol 36:439–458

Donaldson TJ (1995a) Courtship and spawning behavior of the pygmy grouper, *Cephalopholis spiloparaea* (Serranidae: Epinephelinae), with notes of *C. argus* and *C. urodeta*. Environ Biol Fish 43:363–370

Donaldson TJ (1995b) Courtship and spawning of nine species of wrasses (Labridae) from the Western Pacific. Jpn J Ichthyol 42:311–319

Dorairaj K (1973) Hermaphroditism in the threadfin fish, *Polynemus microstoma* Bleeker. Indian J Fish 20:256–259

Dulčić J, Kraljević M, Grbec B, Cetinić P (2000) Age, growth and mortality of blotched picarel *Spicara maena* L. (Pisces: Centracanthidae) in the eastern central Adriatic. Fish Res 48:69–78

Dulčić J, Pallaoro A, Cetinić P, Kraljević M, Soldo A, Jardas I (2003) Age, growth and mortality of picarel, *Spicara smaris* L. (Pisces: Centracanthidae), from the eastern Adriatic (Croatian coast). J Appl Ichthyol 19:10–14

Ebisawa A (1990) Reproductive biology of *Lethrinus nebulosus* (Pisces: Lethrinidae) around the Okinawan waters. Nippon Suisan Gakkaishi 56:1941–1954

Ebisawa A (1997) Some aspects of reproduction and sexuality in the spotcheek emperor, *Lethrinus rubrioperculatus*, in waters off the Ryukyu Islands. Ichthyol Res 44:201–212

Ebisawa A (1999) Reproductive and sexual characteristics in the Pacific yellowtail emperor, *Lethrinus atkinsoni*, in waters off the Ryukyu Islands. Ichthyol Res 46:341–358

Ebisawa A (2006) Reproductive and sexual characteristics in five *Lethrinus* species in waters off the Ryukyu Islands. Ichthyol Res 53:269–280

Ebisawa A, Kanashiro K, Kyan T, Motonaga F (1995) Aspects of reproduction and sexuality in the black-spot tuskfish, *Choerodon schoenleinii*. Jpn J Ichthyol 42:121–130

El-Sayed AFM, Abdel-Bary K (1993) Population biology of sparid fishes in Qatari waters. 1: Reproductive cycle and fecundity of longspine seabream, *Argyrops spinifer* (Forskal). Qutar Univ Sci J 13:177–181

El-Sayed AT, Osman AM, Abdel-Aziz SH, Bawazeer FA (2011) Growth and longevity of the protogynous parrotfish, *Hipposcarus harid*, *Scarus ferrugineus* and *Chlorurus sordidus* (Teleostei, Scaridae), off the eastern coast of the Red Sea. J Appl Ichthyol 27:840–846

Erisman BE (2008) Reproductive biology and evolution of epinephelid and serranid fishes (Perciformes, Epinephelidae, Serranidae). Doctoral dissertation, University of California, San Diego

Erisman BE, Craig MT, Hastings PA (2010) Reproductive biology of the Panama graysby *Cephalopholis panamensis* (Teleostei: Epinephelidae). J Fish Biol 76:1312–1328

Etessami S (1983) Hermaphroditism in one Sparidae of the Persian Gulf: *Acanthopagrus bifasciatus* (Forssk.). Cybium 7:87–91

Fairclough D (2005) The biology of four tuskfish species (Choerodon: Labridae) in Western Australia. Doctoral dissertation, Murdoch University

Fennessy ST, Sadovy Y (2002) Reproductive biology of a diandric protogynous hermaphrodite, the serranid *Epinephelus andersoni*. Mar Freshw Res 53:147–158

Ferreira BP (1995) Reproduction of the common coral trout *Plectropomus leopardus* (Serranidae: Epinephelinae) from the central and northern Great Barrier Reef, Australia. Bull Mar Sci 56:653–669

Ferrell DJ (1987) The population and reproductive biology of *Pseudochromis queenslandica* at One Tree Island, Great Barrier Reef. Master thesis, The University of Sydney

Filous A, Daxboeck C, Beguet T, Cook C (2022) The life history of longnose emperors (*Lethrinus olivaceus*) and a data limited assessment of their stock to support fisheries management at Rangiroa Atoll, French Polynesia. J Fish Biol 100:632–644

Fischer EA (1980) The relationship between mating system and simultaneous hermaphroditism in the coral reef fish, *Hypoplectrus nigricans* (Serranidae). Anim Behav 28:620–633

Fischer EA (1981) Sexual allocation in a simultaneously hermaphroditic coral reef fish. Am Nat 117:64–82

Fischer EA (1984) Egg trading in the chalk bass, *Serranus tortugarum*, a simultaneous hermaphrodite. Z Tierpsychol 66:143–151

Fischer EA, Hardison PD (1987) The timing of spawning and egg production as constraints on male mating success in a simultaneous hermaphroditic fish. Environ Biol Fish 20:301–310

Fischer EA, Petersen CW (1986) Social behavior of male and simultaneous hermaphrodites in the lantern bass. Ethology 73:235–246

Fishelson L (1970) Protogynous sex reversal in the fish *Anthias squamipinnis* (Teleostei, Anthiidae) regulated by the presence or absence of a male fish. Nature 227:90–91

Fishelson L (1989) Bisexuality and pedogenesis in gobies (Gobiidae: Teleostei) and other fish, or, why so many little fish in tropical seas? Senckenberg Marit 20:147–169

Fishelson L (1990) *Rhinomuraena* spp. (Pisces: Muraenidae): the first vertebrate genus with post-anally situated urogenital organs. Mar Biol 105:253–257

Fishelson L (1992) Comparative gonad morphology and sexuality of the Muraenidae (Pisces, Teleostei). Copeia 1992:197–209

Fishelson L, Galil BS (2001) Gonad structure and reproductive cycle in the deep-sea hermaphrodite tripodfish, *Bathypterois mediterraneus* (Chlorophthalmidae, Teleostei). Copeia 2001:556–560

Fisher RA (1983) Protandric sex reversal in *Gonostoma elongatum* (Pisces: Gonostomatidae) from the eastern Gulf of Mexico. Copeia 1983:554–557

Forrester G, Harmon L, Helyer J, Holden W, Karis R (2011) Experimental evidence for density-dependent reproductive output in a coral reef fish. Popul Ecol 53:155–163

Fricke HW (1979) Mating system, resource defence and sex change in the anemonefish *Amphiprion akallopisos*. Z Tierpsychol 50:313–326

Fricke HW (1980) Control of different mating systems in a coral reef fish by one environmental factor. Anim Behav 28:561–569

Fricke HW (1983) Social control of sex: field experiments with the anemonefish *Amphiprion bicinctus*. Z Tierpsychol 61:71–77

Fricke H, Fricke S (1977) Monogamy and sex change by aggressive dominance in coral reef fish. Nature 266:830–832

Fricke HW, Holzberg S (1974) Social units and hermaphroditism in a pomacentrid fish. Naturwissenschaften 61:367–368

Fujii T (1970) Hermaphroditism and sex reversal in the fishes of the Platycephalidae I. Sex reversal of *Onigocia macrolepis* (Bleeker). Jpn J Ichthyol 17:14–21

Fujii T (1971) Hermaphroditism and sex reversal in the fishes of the Platycephalida II. *Kumococius detrusus* and *Inegocia japonica*. Jpn J Ichthyol 18:109–117

Fukuda K, Sunobe T (2020) Group structure and putative mating system of three hermaphrodite gobiid fish, *Priolepis akihitoi*, *Trimma emeryi*, and *Trimma hayashii* (Actinopterygii: Gobiiformes). Ichthyol Res 67:552–555

Fukuda K, Tanazawa T, Sunobe T (2017) Polygynous mating system and field evidence for bidirectional sex change in the gobiid fish *Trimma grammistes*. Int J Pure Appl Zool 5:92–99

Fukui Y, Gushima K, Kakuda S, Hashimoto H (1991) Growth-related changes in color and sex in *Halichoeres poecilopterus*. Jpn J Ichthyol 37:395–401

Furness AI, Tatarenkov A, Avise JC (2015) A genetic test for whether pairs of hermaphrodites can cross-fertilize in a selfing killifish. J Hered 106:749–752

García-Cagide A, García T (1996) Reproducción de *Mycteroperca bonaci* y *Mycteroperca venenosa* (Pisces: Serranidae) en la plataforma cubana. Rev Biol Trop 44:771–780

García-Díaz MM, Lorente MJ, González JA, Tuset VM (2002) Morphology of the ovotestis of *Serranus atricauda* (Teleostei, Serranidae). Aqua Sci 64:87–96

García-Díaz MM, Tuset VM, González JA, Socorro J (1997) Sex and reproductive aspects in *Serranus cabrilla* (Osteichthyes: Serranidae): macroscopic and histological approaches. Mar Biol 127:379–386

Garratt PA (1986) Protogynous hermaphroditism in the slinger, *Chrysoblephus puniceus* (Gilchrist & Thompson, 1908) (Teleostei: Sparidae). J Fish Biol 28:297–306

Garratt PA (1993) Spawning of riverbream, *Acanthopagrus berda*, in Kosi estuary. Afr Zool 28:26–31

Gibbs RH (1960) *Alepisaurus brevirostris*, a new species of lancetfish from the western North Atlantic. Breviora 123:1–14

Gillanders BM (1995) Reproductive biology of the protogynous hermaphrodite *Achoerodus viridis* (Labridae) from south-eastern Australia. Mar Freshw Res 46:999–1008

Gilmore RG, Jones RS (1992) Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode & Bean) and *M. phenax* (Jordan & Swain). Bull Mar Sci 51: 83–103

Godwin J (1994a) Histological aspects of protandrous sex change in the anemonefish *Amphiprion melanopus* (Pomacentridae, Teleostei). J Zool Lond 232:199–213

Godwin J (1994b) Behavioural aspects of protandrous sex change in the anemonefish, *Amphiprion melanopus*, and endocrine correlates. Anim Behav 48:551–567

Godwin J (1995) Phylogenetic and habitat influences on mating system structure in the humbug damselfishes (*Dascyllus*, Pomacentridae). Bull Mar Sci 57:637–652

Gonçalves JMS, Erzini K (2000) The reproductive biology of the two-banded sea bream (*Diplodus vulgaris*) from the southwest coast of Portugal. J Appl Ichthyol 16:110–116

Grandcourt EM (2002) Demographic characteristics of a selection of exploited reef fish from the Seychelles: preliminary study. Mar Freshw Res 53:123–130

Guiguen Y, Cauty C, Fostier A, Fuchs J, Jalabert B (1994) Reproductive cycle and sex inversion of the seabass, *Lates calcarifer*, reared in sea cages in French Polynesia: histological and morphometric description. Environ Biol Fish 39:231–247

Gust N (2004) Variation in the population biology of protogynous coral reef fishes over tens of kilometres. Can J Fish Aquat Sci 61:205–218

Hamzeh S, Keivany Y, Mahboobi Soofiani N, Aein Jamshid K (2017) Reproductive biology of kingsoldier bream (*Argyrops spinifer*) in the Persian Gulf. Iran Sci Fish J 26(3):91–105

Hara N, Sunobe T (2021) Mating system and protandrous sex change in “Magochi” *Platycephalus* sp. 2 (Platycephalidae). Ichthyol Res 68:541–547

Harrington RW (1961) Oviparous hermaphroditic fish with internal self-fertilization. Science 134: 1749–1750

Harrington RW (1967) Environmentally controlled induction of primary male gonochorists from eggs of the self-fertilizing hermaphroditic fish, *Rivulus marmoratus* Poey. Biol Bull 132:174–199

Harrington RW (1971) How ecological and genetic factors interact to determine when self-fertilizing hermaphrodites of *Rivulus marmoratus* change into functional secondary males, with a reappraisal of the modes of intersexuality among fishes. Copeia 1971:389–432

Harris PJ, Wyanski DM, White DB, Moore JL (2002) Age, growth, and reproduction of scamp, *Mycteroperca phenax*, in the southwestern North Atlantic, 1979–1997. Bull Mar Sci 70:113–132

Hart MK, Kratter AW, Crowley PH (2016) Partner fidelity and reciprocal investments in the mating system of a simultaneous hermaphrodite. Behav Ecol 27:1471–1479

Hastings PA (1981) Gonad morphology and sex succession in the protogynous hermaphrodite *Hemanthias vivanus* (Jordan and swain). J Fish Biol 18:443–454

Hastings PA (1989) Protogynous hermaphroditism in *Paralabrax maculatofasciatus* (Pisces: Serranidae). Copeia 1989:184–188

Hastings PA, Bortone SA (1980) Observations on the life history of the belted sandfish, *Serranus subligarrius* (Serranidae). Environ Biol Fish 5:365–374

Hastings PA, Petersen CW (1986) A novel sexual pattern in serranid fishes: imultaneous hermaphrodites and secondary males in *Serranus fasciatus*. Environ Biol Fish 15:59–68

Hastings RW (1973) Biology of the pygmy sea bass, *Serraniculus pumilio* (Pisces: Serranidae). Fish Bull 1:235–242

Hattori A (1991) Socially controlled growth and size-dependent sex change in the anemonefish *Amphiprion frenatus* in Okinawa, Japan. Jpn J Ichthyol 38:165–177

Hattori A (2000) Social and mating systems of the protandrous anemonefish *Amphiprion perideraion* under the influence of a larger congener. Austral Ecol 25:187–192

Hattori A, Yanagisawa Y (1991a) Life-history pathways in relation to gonadal sex differentiation in the anemonefish, *Amphiprion clarkii*, in temperate waters of Japan. Environ Biol Fish 31:139–155

Hattori A, Yanagisawa Y (1991b) Sex change of the anemonefish *Amphiprion clarkii* in a habitat of high host density: a removal study. Jpn J Ecol 41:1–8

Hayasaka O, Matsui H, Matsuoka M, Yamada M, Kotani T (2019) Sex change in protogynous fish red-belted anthias *Pseudanthias rubrizonatus* (Serranidae) in Kagoshima Bay, Japan. J Ichthyol 59:366–371

Heemstra PC (1973) *Anthias conspicuus* sp. nova (Perciformes: Serranidae) from the Indian Ocean, with comments on related species. Copeia 1973:200–210

Hesp SA, Potter IC (2003) Reproductive biology of *Rhabdosargus sarba* (Sparidae) in Western Australian waters, in which it is a rudimentary hermaphrodite. J Mar Biol Ass UK 83:1333–1346

Hesp SA, Potter IC, Hall NG (2004) Reproductive biology and protandrous hermaphroditism in *Acanthopagrus latus*. Environ Biol Fish 70:257–272

Hioki S (2002) Sexuality in angelfishes of the genus *Centropyge* (Teleostei, Pomacanthidae) with special reference to gonadal structure and subgeneric relationship. Sci Rep Mus Tokai Univ 4: 37–43

Hioki S, Suzuki K (1995) Spawning behavior, eggs, larvae, and hermaphroditism of the angelfish, *Apolemichthys trimaculatus*, in captivity. Bull Inst Oceanic Res & Develop, Tokai Univ 16:13–22

Hioki S, Suzuki K (1996) Sex changing from male to female on the way of protogynous process in three *Centropyge* angelfishes (Pomacanthidae: Teleostei). Bull Inst Oceanic Res & Develop, Tokai Univ 17:27–34

Hioki S, Oyama T, Yoshinaka A (2001) Reproductive behavior, eggs, larvae, and sexuality in the anthiine fish, *Pseudoanthias pleurotaenia* (Serranidae; Teleostei), in the aquarium. Sci Rep Mus, Tokai Univ 3:19–27

Hioki S, Suzuki K, Tanaka Y (1982) Spawning behavior, egg and larval development, and sex succession of the hermaphroditic pomacanthine, *Genicanthus melanospilos*, in the aquarium. J Fac Mar Sci Tech, Tokai Univ 15:359–366

Hioki S, Tanaka Y, Suzuki K (1995) Reproductive behavior, eggs, larvae, and sexuality of two angelfishes, *Genicanthus watanabei* and *G. bellus*, in an aquarium. J Fac Mar Sci Tech, Tokai Univ 40:151–171

Hoffman SG (1980) Sex-related social, mating, and foraging behavior in some sequentially hermaphroditic reef fishes. Doctoral dissertation, University of California, Santa Barbara

Hoffman SG (1985) Effects of size and sex on the social organization of reef-associated hogfishes, *Bodianus* spp. Environ Biol Fish 14:185–197

Hoffman SG, Schildhauer MP, Warner RR (1985) The costs of changing sex and the ontogeny of males under contest competition for mates. Evolution 39:915–927

Hourigan TF (1986) A comparison of haremic social systems in two reef fishes. In: Dickamer LC (ed) Behavioral ecology and population biology, readings from the 19th International Ethological Conference, Toulouse, pp 23–28

Hourigan TF, Kelley CD (1985) Histology of the gonads and observations on the social behavior of the Caribbean angelfish *Holacanthus tricolor*. Mar Biol 88:311–322

Howe JC (1996) Sexual dimorphism in the bicolor bass, *Anthias bicolor* (Pisces: Serranidae), with comments on stomach contents. J Aquaricul Aqua Sci 8:16–18

Huang CC, Lo CF, Chang KH (1974) Sex reversal in one sparid fish, *Chrysophrys major* (Perciformes, Sparidae). Bull Inst Zool Acad Sin 13:55–60

Hubble M (2003) The ecological significance of body size in tropical wrasses (Pisces: Labridae). Doctoral dissertation, James Cook University

Ibarra-Zatarain Z, Duncan N (2015) Mating behaviour and gamete release in gilthead seabream (*Sparus aurata*, Linnaeus 1758) held in captivity. Span J Agric Res 13:e04-001

Ishihara M, Kuwamura T (1996) Bigamy or monogamy with maternal egg care in the triggerfish, *Sufflamen chrysopterus*. Ichthyol Res 43:307–313

Ismail RF, Mourad MM, Farrag MM (2018) Gonadal development and hermaphroditism of bluespotted seabream, *Pagrus caeruleostictus* (Valenciennes, 1830) from the Mediterranean Sea, Egypt. Egypt J Aquat Res 44:163–171

Johnson RK, Bertelsen E (1991) The fishes of the family Giganturidae: systematics, development, distribution and aspects of biology. Dana Report 91:1–45

Jones GP (1980a) Growth and reproduction in the protogynous hermaphrodite *Pseudolabrus celidotus* (Pisces: Labridae) in New Zealand. Copeia 1980:660–675

Jones GP (1980b) Contribution to the biology of the redbanded perch, *Ellerkeldia huntii* (Hector) with a discussion on hermaphroditism. J Fish Biol 17:197–207

Jones GP (1981) Spawning-site choice by female *Pseudolabrus celidotus* (Pisces: Labridae) and its influence on the mating system. Behav Ecol Sociobiol 8:129–114

Joubert CSW (1981) Aspects of the biology of five species of inshore reef fishes on the Natal coast, South Africa. Invest Rep Oceanogr Res Ins 51:1–16

Junnan LAN, Youjun OU, Jiufu WEN, Junwei LI, Yingyue NIU, Jia'er LI (2020) A preliminary study on process of sex reversal in *Eleutheronema tetradactylum*. South China Fish Sci 16:67–74

Kadota T, Osato J, Hashimoto H, Sakai Y (2011) Harem structure and female territoriality in the dwarf hawkfish *Cirrhitichthys falco* (Cirrhitidae). Environ Biol Fish 92:79–88

Kadota T, Osato J, Nagata K, Sakai Y (2012) Reversed sex change in the haremic protogynous hawkfish *Cirrhitichthys falco* in natural conditions. Ethology 118:226–234

Kagwade PV (1967) Hermaphroditism in a teleost, *Polynemus heptadactylus* Cuv. And Val. Indian J Fish 14:187–197

Katayama M (1978) The anthiine fish, *Pseudanthias taeniatus*, from Hachijo Island and the coast of Izu, Japan. Jpn J Ichthyol 25:216–218

Kawaguchi K, Marumo R (1967) Biology of *Gonostoma gracile* (Gonostomatidae). I. Morphology, life history, and sex reversal. Information Bulletin on Planktology in Japan, Commemoration Number of Dr. Y Matsue's Sixtieth Birthday, pp 53–69

Kinoshita Y (1936) On the conversion of sex in *Sparus longispinis* (Temminck & Schlegel), (Teleostei). J Sci Hiroshima Univ Ser B Div 1 4:69–79

Kinoshita Y (1939) Studies on the sexuality of genus *Sparus* (Teleostei). J Sci Hiroshima Univ Ser B Div 1 7:25–38

Kline RJ, Khan IA, Holt GJ (2011) Behavior, color change and time for sexual inversion in the protogynous grouper (*Epinephelus adscensionis*). PLoS One 6:e19576

Kobayashi K, Suzuki K (1990) Gonadogenesis and sex succession in the protogynous wrasse *Cirrhilabrus temmincki* in Suruga Bay, Central Japan. Jpn J Ichthyol 37:256–264

Kobayashi K, Suzuki K (1992) Hermaphroditism and sexual function in *Cirrhitichthys aureus* and the other Japanese hawkfishes (Cirrhitidae: Teleostei). Jpn J Ichthyol 38:397–410

Kobayashi K, Suzuki K (1994) Intersexuality and reproduction in *Halichoeres poecilopterus* in Suruga Bay, Central Japan. J School Mar Sci Technol, Tokai Univ 38:233–256

Kobayashi K, Suzuki K, Shiobara Y (1993) Studies on the gonadal sex succession in *Parapercis snyderi* cross examined in captivity. Bull Inst Oceanic Res Develop, Tokai Univ 14:83–91

Kohda M, Sasaki K, Sakai Y, Ohnishi N, Matsumoto K (2005) Preliminary study on female choice of mates versus sites in a wrasse, *Cirrhilabrus temminckii*. Ichthyol Res 52:406–409

Kokokiris L, Bruslé S, Kentouri M, Fostier A (1999) Sexual maturity and hermaphroditism of the red porgy *Pagrus pagrus* (Teleostei: Sparidae). Mar Biol 134:621–629

Kouame AC, Sylla S, Arra S, Kouakou KF, Yao SS (2018) Parameters of reproductive biology of red pandra *Pagellus bellottii* (Steindachner, 1882) in the Ivoirian coast (Cote d'Ivoire). J Biodivers Environ Sci 12:185–193

Kramer A, Van Tassell JL, Patzner RA (2009) Aspects of spawning behaviour in five gobiids of the genus *Coryphopterus* (Pisces: Gobiidae) in the Caribbean Sea. Open Fish Sci J 2:50–54

Kroon FJ, Munday PL, Pankhurst NW (2003) Steroid hormone levels and bi-directional sex change in *Gobiodon histrio*. J Fish Biol 62:153–167

Krug HM (1990) The Azorean blackspot seabream, *Pagellus bogaraveo* (Brünnich, 1768) (Teleostei, Sparidae). Reproductive cycle, hermaphroditism, maturity and fecundity. Cybium 14:151–159

Krug HM (1998) Variation in the reproductive cycle of the blackspot seabream, *Pagellus bogaraveo* (Brünnich, 1768) in the Azores. Arquipélago Life Marine Sci 16:37–47

Kume G, Kubo Y, Yoshimura T, Kiriyama T, Yamaguchi A (2010) Life history characteristics of the protogynous parrotfish *Calotomus japonicas* from northwest Kyushu, Japan. Ichthyol Res 57:113–120

Kupchik MJ, Benfield MC, Sutton TT (2018) The first in situ encounter of *Gigantura chuni* (Giganturidae: Giganturoidei: Aulopiformes: Cyclosquamata: Teleostei), with a preliminary investigation of pair-bonding. Copeia 106:641–645

Kusen JD, Nakazono A (1991) Protogynous hermaphroditism in the parrotfish, *Calotomus japonicus*. Jpn J Ichthyol 38:41–45

Kusen JD, Nakagawa K, Yogo Y, Nakazono A (1991) Protogynous hermaphroditism in the sand diver, *Trichonotus filamentosus*. Nippon Suisan Gakkaishi 57:35–40

Kuwamura T (1997) The evolution of parental care and mating systems among Tanganyikan cichlids. In: Kawanabe H, Hori M, Nagoshi M (eds) Fish communities in Lake Tanganyika. Kyoto University Press, Kyoto, pp 57–86

Kuwamura T, Kadota T, Suzuki S (2014) Testing the low-density hypothesis for reversed sex change in polygynous fish: experiments in *Labroides dimidiatus*. Sci Rep 4:4369

Kuwamura T, Kadota T, Suzuki S (2015) Bidirectional sex change in the magenta dottyback *Pictichromis porphyrea*: first evidence from the field in Pseudochromidae. Environ Biol Fish 98:201–207

Kuwamura T, Karino K, Nakashima Y (2000) Male morphological characteristics and mating success in a protogynous coral reef fish, *Halichoeres melanurus*. J Ethol 18:17–23

Kuwamura T, Nakashima Y, Yogo Y (1994) Sex change in either direction by growth-rate advantage in the monogamous coral goby, *Paragobiodon echinocephalus*. Behav Ecol 5:434–438

Kuwamura T, Sagawa T, Suzuki S (2009) Interspecific variation in spawning time and male mating tactics of the parrotfishes on a fringing coral reef at Iriomote Island, Okinawa. Ichthyol Res 56: 354–362

Kuwamura T, Sunobe T, Sakai Y, Kadota T, Sawada K (2020) Hermaphroditism in fishes: an annotated list of species, phylogeny, and mating system. Ichthyol Res 67:341–336

Kuwamura T, Suzuki S, Kadota T (2011) Reversed sex change by widowed males in polygynous and protogynous fishes: female removal experiments in the field. Naturwissenschaften 98:1041–1048

Kuwamura T, Suzuki S, Kadota T (2016a) Male-to-female sex change in widowed males of the protogynous damselfish *Dascyllus aruanus*. J Ethol 34:85–88

Kuwamura T, Suzuki S, Kadota T (2016b) Interspecific variation in the spawning time of labrid fish on a fringing reef at Iriomote Island, Okinawa. Ichthyol Res 63:460–469

Kuwamura T, Suzuki S, Tanaka N, Ouchi E, Karino K, Nakashima Y (2007) Sex change of primary males in a diandric labrid *Halichoeres trimaculatus*: coexistence of protandry and protogyny within a species. J Fish Biol 70:1898–1906

Kuwamura T, Tanaka N, Nakashima Y, Karino K, Sakai Y (2002) Reversed sex-change in the protogynous reef fish *Labroides dimidiatus*. Ethology 108:443–450

Kuwamura T, Yogo Y, Nakashima Y (1993) Size-assortative monogamy and paternal egg care in a coral goby *Paragobiodon echinocephalus*. Ethology 95:65–75

Lamrini A (1986) Sexualite de *Pagellus acarne*, (Risso 1826) (Teleosteen Sparidae) de la cote Atlantique Meridionale du Maroc (21°–26° N). Cybium 10:3–14

Langston RC (2004) Gonad morphology and sex change in sandburrowers (Teleostei: Creediidae). Doctoral dissertation, University of Hawaii

Lassig BR (1976) Field observations on the reproductive behaviour of *Paragobiodon* spp. (Osteichthyes: Gobiidae) at Heron Island Great Barrier Reef. Mar Behav Physiol 3:283–293

Lassig BR (1977) Socioecological strategies adopted by obligate coral-dwelling fishes. In: Proc 3rd Int Coral Reef Symp, pp 565–570

Law CSW, Sadovy de Mitcheson Y (2017) Reproductive biology of black seabream *Acanthopagrus schlegelii*, threadfin porgy *Evynnis cardinalis* and red pargo *Pagrus major* in the northern South China Sea with consideration of fishery status and management needs. J Fish Biol 91:101–125

Lawson EO, Olagundoye AU (2011) Growth patterns, diet composition and sex ratios in giant African threadfin, *Polydactylus quadrifilis* from Ologe Lagoon, Lagos, Nigeria. Int J Agr Bio 13:559–564

Lee KA, Huveneers C, Macdonald T, Harcourt RG (2014) Size isn't everything: movements, home range, and habitat preferences of eastern blue gropers (*Achoerodus viridis*) demonstrate the efficacy of a small marine reserve. Aquat Conserv 25:174–186

Lee YH, Du JL, Yueh WS, Lin BY, Huang JD, Lee CY, Lee MF, Lau EL, Lee FY, Morrey C, Nagahama Y, Chang CF (2001) Sex change in the protandrous black porgy, *Acanthopagrus schlegeli*: a review in gonadal development, estradiol, estrogen receptor, aromatase activity and gonadotropin. J Exp Zool 290:715–726

Leem JB, Sakamoto K, Tsuruta K, Nakazono A (1998) Sexual pattern of the labrid fishes collected from Kuchinoerabu-jima, Kagoshima, Japan. J Fac Agric Kyushu Univ 42:409–419

Lejeune P (1987) The effect of local stock density on social behavior and sex change in the Mediterranean labrid *Coris julis*. Environ Biol Fish 18:135–141

Lek E (2011) Comparisons between the biological characteristics of three co-occuring and reef-dwelling labrid species at two different latitudes. Doctoral dissertation, Murdoch University

Leu MY (1994) Natural spawning and larval rearing of silver bream, *Rhabdosargus sarba* (Forsskål), in captivity. Aquaculture 120:115–122

Leu MY, Meng PJ, Huang CS, Tew KS, Kuo J, Liou CH (2010) Spawning behaviour, early development and first feeding of the bluestriped angelfish [*Chaetodontoplus septentrionalis* (Temminck & Schlegel, 1844)] in captivity. Aqua Res 41:e39–e52

Licandeo RR, Barrientos CA, Gonzalez MT (2006) Age, growth rates, sex change and feeding habits of notothenioid fish *Eleginops maclovinus* from the central-southern Chilean coast. Environ Biol Fish 77:51–61

Liem KF (1963) Sex reversal as a natural process in the synbranchiform fish *Monopterus albus*. Copeia 1963:303–312

Liem KF (1968) Geographical and taxonomic variation in the pattern of natural sex reversal in the teleost fish order Synbranchiformes. J Zool Lond 156:225–238

Lissia-Frau AM, Casu S (1968) Il differenziamento sessuale di *Lithognathus mormyrus* (L.) e di *Oblada melanura* (L.). Studi Sassar 4:1–19

Lissia-Frau AM, Pala M, Casu S (1976) Observations and considerations on protandrous hermaphroditism in some species of sparid fishes (Teleostei, Perciformes). Studi Sassar 54:147–167

Liu M, Sadovy Y (2004a) Early gonadal development and primary males in the protogynous epinepheline, *Cephalopholis boenak*. J Fish Biol 65:987–1002

Liu M, Sadovy Y (2004b) The influence of social factors on adult sex change and juvenile sexual differentiation in a diandric, protogynous epinepheline, *Cephalopholis boenak* (Pisces, Serranidae). J Zool Lond 264:239–248

Liu M, Sadovy Y (2005) Habitat association and social structure of the chocolate hind, *Cephalopholis boenak* (Pisces, Serranidae: Epinephelinae), at Ping Chau Island, northeastern Hong Kong waters. Environ Biol Fish 74:9–18

Liu M, Sadovy de Mitcheson Y (2011) The influence of social factors on juvenile sexual differentiation in a diandric, protogynous grouper *Epinephelus coioides*. Ichthyol Res 58:84–89

Lobel PS (1978) Diel, lunar, and seasonal periodicity in the reproductive behavior of the pomacanthud fish, *Centropyge potteri*, and some other reef fishes in Hawaii. Pac Sci 32:193–207

Lodi E (1967) Sex reversal of *Cobitis taenia* L. (Osteichthyes, fam. Cobitidae). Experientia 23:446–447

Lodi E (1979) Instances of sex inversion in the domesticated swordtail, *Xiphophorus helleri* Heckel (Pisces, Osteichthyes). Experientia 35:1440–1441

Lodi E (1980a) Hermaphroditic and gonochoric populations of *Cobitis taenia bilineata* Canestrini (Cobitidae Osteichthyes). Monit Zool Ital 14:235–243

Lodi E (1980b) Sex inversion in domesticated strains of the swordtail *Xiphophorus helleri* Heckel (Pisces, Osteichthyes). Bulletin Zool 47:1–8

Lone KP, Al-Marzouk A (2000) First-observations on natural sex reversal in a protandrous bream (*Sparidentex hasta*: Sparidae) from Kuwait. Pakistan J Zool 32:229–243

Longhurst AR (1965) The biology of West African polynemid fishes. J Conseil 30:58–74

Lo Nostro FL, Guerrero GA (1996) Presence of primary and secondary males in a population of the protogynous *Synbranchus marmoratus*. J Fish Biol 49:788–800

Lorenzi V, Earley R, Grober M (2006) Preventing behavioural interactions with a male facilitates sex change in female bluebanded gobies, *Lythrypnus dalli*. Behav Ecol Sociobiol 59:715–722

Lorenzo JM, Pajuelo JG, Méndez-Villamil M, Coca J, Ramos AG (2002) Age, growth, reproduction and mortality of the striped seabream, *Lithognathus mormyrus* (Pisces, Sparidae), off the Canary Islands (Central-east Atlantic). J Appl Ichthyol 18:204–209

Lou DC (1992) Age specific patterns of growth and reproduction in tropical herbivorous fishes. Doctoral dissertation, James Cook University

Lowe JR, Russ GR, Bucol AA, Abesamis RA, Choat JH (2021) Geographic variability in the gonadal development and sexual ontogeny of *Hemigymnus*, *Cheilinus* and *Oxycheilinus* wrasses among Indo-Pacific coral reefs. J Fish Biol 99:1348–1363

Lutnesky MMF (1994) Density-dependent protogynous sex change in territorial-haremic fishes: models and evidence. Behav Ecol 5:375–383

Lutnesky MMF (1996) Size-dependent rate of protogynous sex change in the pomacanthid angelfish, *Centropyge potteri*. Copeia 1996:209–212

Mackie MC (2003) Socially controlled sex-change in the half-moon grouper, *Epinephelus rivulatus*, at Ningaloo Reef, Western Australia. Coral Reefs 22:133–142

Mackie MC (2007) Reproductive behavior of the halfmoon grouper, *Epinephelus rivulatus*, at Ningaloo Reef, Western Australia. Ichthyol Res 54:213–220

Madhu K, Madhu R (2006) Protandrous hermaphroditism in the clown fish *Amphiprion percula* from Andaman and Nicobar islands. Indian J Fish 53:373–382

Madhu R, Madhu K, Venugopalan KM (2010) Sex change of hatchery produced *Amphiprion ocellaris*: influence of mating system removal on gonad maturation and nesting success. J Mar Biol Ass India 52:62–69

Manabe H, Ishimura M, Shinomiya A, Sunobe T (2007a) Inter-group movement of females of the polygynous gobiid fish *Trimma okinawae* in relation to timing of protogynous sex change. J Ethol 25:133–137

Manabe H, Ishimura M, Shinomiya A, Sunobe T (2007b) Field evidence for bi-directional sex change in the polygynous gobiid fish *Trimma okinawae*. J Fish Biol 70:600–609

Manabe H, Matsuoka M, Goto K, Dewa S, Shinomiya A, Sakurai M, Sunobe T (2008) Bi-directional sex change in the gobiid fish *Trimma* sp.: does size-advantage exist? Behaviour 145:99–113

Manabe H, Toyoda K, Nagamoto K, Dewa S, Sakurai M, Hagiwara K, Shinomiya A, Sunobe T (2013) Bidirectional sex change in seven species of *Priolepis* (Actinopterygii: Gobiidae). Bull Mar Sci 89:635–642

Mann BQ, Buxton CD (1998) The reproductive biology of *Diplodus sargus capensis* and *D. cervinus hottentotus* (Sparidae) off the south-east Cape coast, South Africa. Cybium 22:31–47

Marconato A, Tessari V, Marin G (1995) The mating system of *Xyrichthys novacula*: sperm economy and fertilization success. J Fish Biol 47:292–301

Marriott RJ, Jarvis NDC, Adams DJ, Gallash AE, Norriss J, Newman SJ (2010) Maturation and sexual ontogeny in the spangled emperor *Lethrinus nebulosus*. J Fish Biol 76:1396–1414

Mathew G (2010) Spontaneous spawning of *Epinephelus tauvina* (Forskal) in captivity. J Mar Biol Ass India 52:14–18

Mathew G, Mathew K (2010) Anatomical changes during early gonad development in the protogynous greasy grouper *Epinephelus tauvina* (Forsskal). Indian J Fish 57:21–24

Matos E, Santos MNS, Azevedo C (2002) Biflagellate spermatozoon structure of the hermaphrodite fish *Satanoperca jurupari* (Heckel, 1840) (Teleostei, Cichlidae) from the Amazon River. Braz J Biol 62(4B):847–852

Matsumoto S, Takeyama T, Ohnishi N, Kohda M (2011) Mating system and size advantage of male mating in the protogynous swamp eel *Monopterus albus* with paternal care. Zool Sci 28:360–367

Matsuyama M, Lara RT, Matsuura S (1988) Juvenile bisexuality in the red sea bream, *Pagrus majo*r. Environ Biol Fish 21:27–36

Maxfield JM, Cole KS (2019a) Patterns of structural change in gonads of the divine dwarfgoby *Eviota epiphanes* as they sexually transition. J Fish Biol 94:142–153

Maxfield JM, Cole KS (2019b) Structural changes in the ovotestis of the bidirectional hermaphrodite, the blue-banded goby (*Lythrypnus dalli*), during transition from ova production to sperm production. Environ Biol Fish 102:1393–1404

McBride RS, Johnson MR (2007) Sexual development and reproductive seasonality of hogfish (Labridae: *Lachnolaimus maximus*), an hermaphroditic reef fish. J Fish Biol 71:1270–1292

McBride RS, Sulak KJ, Thurman PE, Richardson AK (2009) Age, growth, mortality, and reproduction of roughtongue bass, *Pronotogrammus martinicensis* (Serranidae), in the northeastern Gulf of Mexico. Gulf Mex Sci 27:30–38

McErlean AJ, Smith CL (1964) The age of sexual succession in the protogynous hermaphrodite *Mycteroperca microlepis*. Trans Am Fish Soc 93:301–302

McPherson GR (1977) Sex change in the wrasse *Pseudolabrus gymnogenis* (Labridae). Aust Zool 19:185–200

Mead GW (1960) Hermaphroditism in archibenthic and pelagic fishes of the order Iniomi. Deep-Sea Res 6:234–235

Merrett NR (1980) *Bathytyphlops sewelli* (Pisces: Chlorophthalmidae) a senior synonym of *B. azorensis*, from the eastern North Atlantic with notes on its biology. Zool J Linnean Soc 68:99–109

Merrett NR, Badcock J, Herring PJ (1973) The status of *Benthalbella infans* (Pisces: Myctophoidei), its development, bioluminescence, general biology and distribution in the eastern North Atlantic. J Zool 170:1–48

Meyer KA (1977) Reproductive behavior and patterns of sexuality in the Japanese labrid fish *Thalassoma cupido*. Jpn J Ichthyol 24:101–112

Micale V, Maricchiolo G, Genovese L (2002) The reproductive biology of blackspot sea bream *Pagellus bogaraveo* in captivity. I. Gonadal development, maturation and hermaphroditism. J Appl Ichthyol 18:172–176

Micale V, Perdichizzi F (1994) Further studies on the sexuality of the hermaphroditic teleost *Diplodus sargus*, with particular reference to protandrous sex inversion. J Fish Biol 45:661–670

Militelli MI, Rodrigues KA (2011) Morphology of the ovotestis of a hermaphroditic teleost, *Serranus auriga* (Osteichthyes: Serranidae). Pan-Am J Aqua Sci 6:320–324

Miya M, Nemoto T (1985) Protandrous sex reversal in *Cyclothone atraria* (family Gonostomatidae). Jpn J Ichthyol 31:438–440

Miya M, Nemoto T (1987) Reproduction, growth and vertical distribution of the meso-and bathypelagic fish *Cyclothone atraria* (Pisces: Gonostomatidae) in Sagami Bay, Central Japan. Deep-Sea Res 34:1565–1577

Miyake Y, Nishigakiuchi J, Sakai Y, Kuniyoshi H (2012) Ovarian degeneration during the female-to-male sex change in the protogynous hermaphroditic fish, *Halichoeres poecilopterus*. Ichthyol Res 59:276–281

Moiseeva EB, Sachs O, Zak T, Funkenstein B (2001) Protandrous hermaphroditism in Australian silver perch, *Bidyanus bidyanus* (Mitchell, 1836). Isr J Aquac–Bamidgeh 53:57–68

Monteiro P, Bentes L, Coelho R, Correia C, Gonçalves JMS, Lino PG, Ribeiro J, Erzini K (2006) Age and growth, mortality, reproduction and relative yield per recruit of the bogue, *Boops boops* Linné, 1758 (Sparidae), from the Algarve (south of Portugal) longline fishery. J Appl Ichthyol 22:345–352

Moore BR (2022) Age-based life history of Pacific longnose parrotfish *Hipposcarus longiceps* from New Caledonia. J Fish Biol 100:997–1008

Moore BR, Stapley JM, Williams AJ, Welch DJ (2017) Overexploitation causes profound demographic changes to the protandrous hermaphrodite king threadfin (*Polydactylus macrochir*) in Queensland's Gulf of Carpentaria, Australia. Fish Res 187:199–208

Morton JK, Gladstone W, Hughes JM, Stewart J (2008) Comparison of the life histories of three co-occurring wrasses (Teleostei: Labridae) in coastal waters of south-eastern Australia. Mar Freshw Res 59:560–574

Moser M, Whipple J, Sakanari J, Reilly C (1983) Protandrous hermaphroditism in striped bass from Coos Bay, Oregon. T Am Fish Soc 112:567–569

Mosse JW, Adams S, Welch DJ (2002) Bommie cod, (*Cephalopholis cyanostigma*): a big surprise from a little fish. CRC reef Research Centre Technical Report 48:94–104

Mouine N, Francour P, Ktari MH, Chakroun-Marzouk N (2007) The reproductive biology of *Diplodus sargus sargus* in the Gulf of Tunis (Central Mediterranean). Sci Mar 71:461–469

Mouine N, Ktari MH, Chakroun-Marzouk N (2011) Reproductive characteristics of *Spondyliosoma cantharus* (Linnaeus, 1758) in the Gulf of Tunis. J Appl Ichthyol 27:827–831

Moussac G (1986) Mise en evidence de l'hermaphrodisme protogyne d'*Epinephelus chlorostigma* (Valenciennes, 1828) aux Seychelles (Pisces, Serranidae). Cybium 10:249–262

Moyer JT (1984) Reproductive behavior and social organization of the pomacanthid fish *Genicanthus lamarck* at Mactan Island, Philippines. Copeia 1984:194–200

Moyer JT (1987) Social organization and protogynous hermaphroditism in marine angelfishes (Pomacanthidae). In: Nakazono A, Kuwamura T (eds) Sex change in fishes. Tokai University Press, Tokyo, pp 120–147

Moyer JT (1990) Social and reproductive behavior of *Chaetodontoplus mesoleucus* (Pomacanthidae) at Bantayan Island, Philippines, with notes on pomacanthid relationships. Jpn J Ichthyol 36:459–467

Moyer JT (1991) Comparative mating strategies of labrid fishes. Watanabe Ichthyol Inst Monogr 1:1–90

Moyer JT, Nakazono A (1978a) Population structure, reproductive behavior and protogynous hermaphroditism in the angelfish *Centropyge interruptus* at Miyake-jima, Japan. Jpn J Ichthyol 25:25–39

Moyer JT, Nakazono A (1978b) Protandrous hermaphroditism in six species of the anemonefish genus *Amphiprion* in Japan. Jpn J Ichthyol 25:101–106

Moyer JT, Yogo Y (1982) The Lek-like mating system of *Halichoeres melanochir* (Pisces: Labridae) at Miyake-jima, Japan. Z Tierpsychol 60:209–226

Moyer JT, Zaiser MJ (1984) Early sex change: a possible mating strategy of *Centropyge* angelfishes (Pisces: Pomacanthidae). J Ethol 2:63–67

Moyer JT, Thresher RE, Colin PL (1983) Courtship, spawning and inferred social organization of American angelfishes (genera *Pomacanthus*, *Holacanthus* and *Centropyge*; Pomacanthidae). Environ Biol Fish 9:25–39

Muncaster S, Norberg B, Andersson E (2013) Natural sex change in the temperate protogynous Ballan wrasse *Labrus bergylta*. J Fish Biol 82:1858–1870

Munday PL (2002) Bi-directional sex change: testing the growth-rate advantage model. Behav Ecol Sociobiol 52:247–254

Munday PL, Molony B (2002) The energetic cost of protogynous versus protandrous sex change in the bi-directional sex-changing fish *Gobiodon histrio*. Mar Biol 141:1011–1017

Munday PL, Caley MJ, Jones GP (1998) Bi-directional sex change in a coral-dwelling goby. Behav Ecol Sociobiol 43:371–377

Munday PL, Pierce SJ, Jones GP, Larson HK (2002) Habitat use, social organization and reproductive biology of the seawhip goby, *Bryaninops yongei*. Mar Freshw Res 53:769–775

Munday PL, Ryen CA, McCormick MI, Walker SPW (2009) Growth acceleration, behavior and otolith check marks associated with sex change in the wrasse *Halichoeres miniatus*. Coral Reefs 28:623–634

Muñoz RC, Warner RR (2003) Alternative contexts of sex change with social control in the bucktooth parrotfish, *Sparisoma radians*. Environ Biol Fish 68:307–319

Muñoz RC, Warner RR (2004) Testing a new version of the size-advantage hypothesis for sex change: sperm competition and size-skew effects in the bucktooth parrotfish, *Sparisoma radians*. Behav Ecol 15:129–136

Muñoz-Arroyo S, Rodríguez-Jaramillo C, Balart EF (2019) The goby L*ythrypnus pulchellus* is a bi-directional sex changer. Environ Biol Fish 102:1377–1391

Nagelkerken WP (1979) Biology of the graysby, *Epinephelus cruentatus*, of the coral reef of Curaçao. Studies on the fauna of Curaçao and other Caribbean Islands 60:1–118

Nakabo T, Kai Y (2013) Platycephalidae. In: Nakabo T (ed) Fishes of Japan with pictorial keys to the species, 3rd edn. Tokai University Press, Tokyo, Japan, pp 734–740, 1953–1955

Nakai T, Sano M (2002) Evidence of protogynous hermaphroditism in the darkfin hind *Cephalopholis urodeta* (Serranidae) at Iriomote Island, southern Japan. Fish Sci 68:697–699

Nakamura M, Hourigan TF, Yamauchi K, Nagahama Y, Grau EG (1989) Histological and ultrastructural evidence for the role of gonadal steroid hormones in sex change in the protogynous wrasse *Thalassoma duperrey*. Environ Biol Fish 24:117–136

Nakashima Y, Kuwamura T, Yogo Y (1995) Why be a both-ways sex changer? Ethology 101:301–307

Nakashima Y, Kuwamura T, Yogo Y (1996) Both-ways sex change in monogamous coral gobies, *Gobiodon* spp. Environ Biol Fish 46:281–288

Nakazono A (1979) Studies on the sexual reversal and spawning behavior of five species of Japanese labrid fishes. Rep Fish Res Lab, Kyushu Univ 4:1–64

Nakazono A, Kusen JD (1991) Protogynous hermaphroditism in the wrasse *Choerodon azurio*. Nippon Suisan Gakkaishi 57:417–420

Nakazono A, Kuwamura T (eds) (1987) Sex change in fishes. Tokai University Press, Tokyo

Nakazono A, Nakatani H, Tsukahara H (1985) Reproductive ecology of the Japanese reef fish, *Parapercis snyderi*. Proc 5th Int Coral Reef Congr Tahiti 5:355–360

Nanami A, Sato T, Ohta I, Akita Y, Suzuki N (2013) Preliminary observations of spawning behavior of white-streaked grouper (*Epinephelus ongus*) in an Okinawan coral reef. Ichthyol Res 60:380–385

Nayak PD (1959) Occurrence of hermaphroditism in *Polynemus heptadactylus* Cuv. & Val. J Mar Biol Ass India 1:257–258

Nelson JS, Grande TC, Wilson MVH (2016) Fishes of the world, 5th edn. John Wiley & Sons, New Jersey

Nemeth RS, Blondeau J, Herzlieb S, Kadison E (2007) Spatial and temporal patterns of movement and migration at spawning aggregations of red hind, *Epinephelus guttatus*, in the U.S. Virgin Islands. Environ Biol Fish 78:365–381

Nemtzov SC (1985) Social control of sex change in the Red Sea razorfish *Xyrichtys pentadactylus* (Teleostei, Labridae). Environ Biol Fish 14:199–211

Ndiaye AM (2014) Etude du cycle sexuel et I'inversion sexuelle de *Pagellus bellottii* (Téléostéen: Sparidae) dans les eaux sénégalaises. Afr Sci 10:257–266

Nielsen JG (1966) Synopsis of the Ipnopidae (Pisces, Iniomi) with description of two new abyssal species. Galathea Report 8:49–75

Noichi T, Kanbara T, Senta T (1991) Depth distribution of the percophid *Matsubaraea fusiforme* in Fukiagehama beach, Kyushu. Jpn J Ichthyol 38:245–248

Ochi H (1989) Mating behavior and sex change of the anemonefish, *Amphiprion clarkii*, in the temperate waters of southern Japan. Environ Biol Fish 26:257–275

Ochi Y, Fukui Y, Sakai Y, Hashimoto H (2017) Age, growth and reproduction of the Asian sheephead wrasse *Semicossyphus reticulatus* in the western Seto Inland Sea, Japan. Ichthyol Res 64:415–422

Oda DL, Lavenberg RJ, Rounds JM (1993) Reproductive biology of three California species of *Paralabrax* (Pisces: Serranidae). Calif Coop Ocean Fish Invest Rep 34:122–132

Oh SR, Kang HC, Lee CH, Hur SW, Lee YD (2013) Sex reversal and masculinization according to growth in longtooth grouper *Epinephelus burunneus*. Dev Reprod 17:79–85

Ohnishi N (1998) Studies on the life history and the reproductive ecology of the polygynous sandperch *Parapercis snyderi*. Doctoral dissertation, Osaka City University, Osaka

Ohnishi N, Yanagisawa Y, Kohda M (1997) Sneaking by harem masters of the sandperch, *Parapercis snyderi*. Environ Biol Fish 50:217–223

Ohshima Y (1942) An ecological note on the fish, *Sparus swinhonis* Günther. Nippon Suisan Gakkaishi 10:249–255

Ohta I, Ebisawa A (2015) Reproductive biology and spawning aggregation fishing of the white-streaked grouper, *Epinephelus ongus*, associated with seasonal and lunar cycles. Environ Biol Fish 98:1555–1570

Ohta K (1987) Study on life history and sex change in a haremic protogynous sandperch, *Parapercis snyderi*. Bull Biol Soc, Hiroshima Univ 53:11–19

Ohta K, Sundaray JK, Okida T, Sakai M, Kitano T, Yamaguchi A, Takeda T, Matsuyama M (2003) Bi-directional sex change and its steroidogenesis in the wrasse, *Pseudolabrus sieboldi*. Fish Physiol Biochem 28:173–174

Okada YK (1962) Sex reversal in the Japanese wrasse, *Halichoeres poecilopterus*. Proc Japan Acad 38:508–513

Okada YK (1965a) Sex reversal in the serranid fish, *Sacura margaritacea* I. Proc Jpn Acad 41:737–740

Okada YK (1965b) Sex reversal in the serranid fish, *Sacura margaritacea* II. Proc Jpn Acad 41:741–745

Okada YK (1966a) Sex reversal in *Inegocia meerdevoorti*, with special reference to repetition of hermaphroditic state. Proc Japan Acad 42:374–378

Okada YK (1966b) Observations on the sex reversal in the symbranchoid eel, *Fluta alba* (Zuiew). Proc Japan Acad 42:491–496

Okumura S (2001) Evidence of sex reversal towards both directions in reared red spotted grouper *Epinephelus akaara*. Fish Sci 67:535–537

Okumura S, Okamoto K, Oomori R, Nakazono A (2002) Spawning behavior and artificial fertilization in captive reared red spotted grouper, *Epinephelus akaara*. Aquaculture 206:165–173

Oliver AS (1997) Size and density dependent mating tactics in the simultaneously hermaphroditic seabass *Serranus subligarius* (Cope, 1870). Behaviour 134:563–594

Osman HM, El Ganainy AA, Shaaban AM, Saber MA (2021) Reproductive biology of the two commercially important grouper species *Epinephelus summana* and *E. polyphekadion* in the Egyptian coast of the Red Sea. Egypt J Aquat Biol Fish 2:665–679

Oyama T, Tomatsu S, Manabe H, Sakurai M, Matsuoka M, Shinomiya A, Dewa S, Sunobe T (2022) Monogamous mating system and protandrous-like sexuality in the goby *Trimma taylori*. Ichthyol Res 70. https://doi.org/10.1007/s10228-022-00876-z

Pajuelo JG, Lorenzo JM (1995) Biological parameters reflecting the current state of the exploited pink dentex *Dentex gibbosus* (Pisces: Sparidae) population off the Canary Islands. South African J Mar Sci 16:311–319

Pajuelo JG, Lorenzo JM (1998) Population biology of the common pandora *Pagellus erythrinus* (Pisces: Sparidae) off the Canary Islands. Fish Res 36:75–86

Pajuelo JG, Lorenzo JM (1999) Life history of black seabream, *Spondyliosoma cantharus,* off the Canary Islands, Central-east Atlantic. Environ Biol Fish 54:325–336

Pajuelo JG, Lorenzo JM (2001) Biology of the annular seabream, *Diplodus annularis* (Sparidae), in coastal waters of the Canary Islands. J Appl Ichthyol 17:121–112

Pajuelo JG, Lorenzo JM (2004) Basic characteristics of the population dynamic and state of exploitation of Moroccan white seabream *Diplodus sargus cadenati* (Sparidae) in the Canarian archipelago. J Appl Ichthyol 20:15–21

Pajuelo JG, Lorenzo JM, Domínguez-Seoane R (2008) Gonadal development and spawning cycle in the digynic hermaphrodite sharpsnout seabream *Diplodus puntazzo* (Sparidae) off the Canary Islands, northwest of Africa. J Appl Ichthyol 24:68–76

Pajuelo JG, Lorenzo JM, Bilbao A, Ayza O, Ramos AG (2006a) Reproductive characteristics of the benthic coastal fish *Diplodus vulgaris* (Teleostei: Sparidae) in the Canarian archipelago, northwest Africa. J Appl Ichthyol 22:414–418

Pajuelo JG, Socorro J, González JA, Lorenzo JM, Pérez-Peñalvo JA, Martînez I, Hernández-Cruz CM (2006b) Life history of the red-banded seabream *Pagrus auriga* (Sparidae) from the coasts of the Canarian archipelago. J Appl Ichthyol 22:430–436

Pears R, Choat JH, Mapstone BD, Beggs GA (2007) Reproductive biology of a large, aggregation-spawning serranid, *Epinephelus fuscoguttatus* (Forskål): management implications. J Fish Biol 71:795–817

Penrith MJ (1972) Sex reversal in the sparid fish *Chrysoblephus laticeps*. Koedoe 15:135–139

Petersen CW (1987) Reproductive behaviour and gender allocation in *Serranus fasciatus*, a hermaphrodite reef fish. Anim Behav 35:1601–1614

Petersen CW (1990a) The relationship among population density, individual size, mating tactics, and reproductive success in a hermaphroditic fish, *Serranus fasciatus*. Behaviour 113:57–80

Petersen CW (1990b) Variation in reproductive success and gonadal allocation in the simultaneous hermaphrodie, *Serranus fasciatus*. Oecologia 83:62–67

Petersen CW (1991) Sex allocation in hermaphroditic sea basses. Am Nat 138:650–667

Petersen CW (1995) Reproductive behavior, egg trading, and correlates of male mating success in the simultaneous hermaphrodite, *Serranus tabacarius*. Environ Biol Fish 43:351–361

Petersen CW, Fischer EA (1986) Mating system of the hermaphroditic coral-reef fish, *Serranus baldwini*. Behav Ecol Sociobiol 19:171–178

Platten JR, Tibbetts IR, Sheaves MJ (2002) The influence of increased line-fishing mortality on the sex ratio and age of sex reversal of the venus tusk fish. J Fish Biol 60:301–318

Pollock BR (1985) The reproductive cycle of yellowfin bream, *Acanthopagrus australis* (Günther), with particular reference to protandrous sex inversion. J Fish Biol 26:301–311

Porcu C, Follesa MC, Grazioli E, Deiana AM, Cau A (2010) Reproductive biology of a bathyal hermaphrodite fish, *Bathypterois mediterraneus* (Osteichthyes: Ipnopidae) from the south-eastern Sardinian Sea (central-western Mediterranean). J Mar Biol Assoc UK 90:719–728

Pressley PH (1981) Pair formation and joint territoriality in a simultaneous hermaphrodite: the coral reef fish *Serranus tigrinus*. Z Tierpsychol 56:33–46

Pyle RL (1990) Rare and unusual marines: the masked angelfish, *Genicanthus personatus* Randall. Freshw Mar Aquar 13:112–118

Quinitio GF, Caberoy NB, Reyes DM (1997) Induction of sex change in female *Epinephelus coioides* by social control. Isr J Aquacult-Bami 49:77–83

Randall JE, Bruce RW (1983) The parrotfishes of the subfamily Scarinae of the western Indian Ocean with descriptions of three new species. Ichthyol Bull, JLB Smith Inst Ichthyol 47:1–49

Rasotto MB (1992) Gonadal differentiation and the mode of sexuality in *Cobitis taenia* (Teleostei; Cobitidae). Copeia 1992:223–228

Rattanayuvakorn S, Mungkornkarn P, Thongpan A, Chatchavalvanich K (2006) Gonadal development and sex inversion in saddleback anemonefish *Amphiprion polymnus* Linnaeus (1758). Kasetsart J (Nat Sci) 40:196–203

Reavis RH, Grober MS (1999) An integrative approach to sex change: social, behavioural and neurochemical changes in *Lythrypnus dalli* (Pisces). Acta Ethol 2:51–60

Reid MJ, Atz JW (1958) Oral incubation in the cichlid fish *Geophagus jurupari* Heckel. Zoologica 43:77–88

Reinboth R (1962) Morphologische und funktionelle Zweigeschlechtigkeit bei marinen Teleostiern (Serranidae, Sparidae, Centracanthidae, Labridae). Zool Jahrb, Abt allg Zool Physiol Tiere 69:405–480

Reinboth R (1963) Naturlicher Geschlechtswechsel bei *Sacura margaritacea* (Hilgendorf) (Serranidae). Japan Annot Zool 36:173–178

Reinboth R (1964) Inversion du sexe chez *Anthias anthias* (L.) (Serranidae). Vie Milieu (Suppl) 17: 499–503

Reinboth R (1967) Protogynie bei *Chelidoperca hirudinacea* (Cuv. Et Val.) (Serranidae). Japan Annot Zool 40:181–186

Reinboth R (1968) Protogyny in parrotfishes (Scaridae). Z Naturforsch 23b:852–855

Reinboth R (1973) Dualistic reproductive behavior in the protogynous wrasse *Thalassoma bifasciatum* and some observations on its day-night changeover. Helgoländer wiss Meeresunters 24:174–191

Reinboth R (1975) Spontaneous and hormone-induced sex-inversion in wrasses (Labridae). Pubbl Stn Zool Napoli 39(Suppl):550–573

Reñones O, Grau A, Mas X, Riera F, Saborido-Rey F (2010) Reproductive pattern of an exploited dusky grouper *Epinephelus marginatus* (Lowe 1834) (Pisces: Serranidae) population in the western Mediterranean. Sci Mar 74:523–537

Richardson TJ, Potts WM, Sauer WHH (2011) The reproductive style of *Diplodus capensis* (Sparidae) in southern Angola: rudimentary hermaphroditism or partial protandry? African J Mar Sci 33:321–326

Roberts BH, Morrongiello JR, Morgan DL, King AJ, Saunders TM, Crook DA (2021) Faster juvenile growth promotes earlier sex change in a protandrous hermaphrodite (barramundi *Lates calcarifer*). Sci Rep 11(1):1–10

Robertson DR (1972) Social control of sex reversal in a coral-reef fish. Science 177:1007–1009

Robertson DR (1981) The social and mating systems of two labrid fishes, *Halichoeres maculipinna* and *H. garnoti*, off the Caribbean coast of Panama. Mar Biol 64:327–340

Robertson DR, Choat JH (1974) Protogynous hermaphroditism and social systems in labrid fish. Proc 2nd Int Coral Reef Symp 1:217–224

Robertson DR, Hoffman SG (1977) The roles of female mate choice and predation in the mating systems of some tropical labroid fishes. Z Tierpsychol 45:298–320

Robertson DR, Justines G (1982) Protogynous hermaphroditism and gonochorism in four Caribbean reef gobies. Environ Biol Fish 7:137–142

Robertson DR, Warner RR (1978) Sexual patterns in the labroid fishes of the Western Caribbean, II: the parrotfishes (Scaridae). Smithsonian Contr Zool 255:1–26

Robertson DR, Reinboth R, Bruce RW (1982) Gonochorism, protogynous sex-change and spawning in three sparisomatinine parrotfishes from the western Indian Ocean. Bull Mar Sci 32:868–879

Robinson GA (1976) Sex reversal in the dageraad *Chrysoblephus cristiceps* (Pisces, Sparidae). Koedoe 19:43–48

Rodgers EW, Drane S, Grober S (2005) Sex reversal in pairs of *Lythrypnus dalli*: behavioral and morphological changes. Biol Bull 208:120–126

Rodgers EW, Earley RL, Grober MS (2007) Social status determines sexual phenotype in the bi-directional sex changing bluebanded goby *Lythrypnus dalli*. J Fish Biol 70:1660–1668

Roede MJ (1972) Color as related to size, sex and behavior in seven Caribbean labrid fish species, (genera *Thalassoma, Halichoeres* and *Hemipteronotus*). Studies on the Fauna of Curaçao and Other Caribbean Islands 138:1–266

Ross RM (1978) Reproductive behavior of the anemonefish *Amphiprion melanopus* on Guam. Copeia 1978:103–107

Ross RM (1981) Experimental evidence for stimulation and inhibition of sex change in the Hawaiian reef fish *Thalassoma duperrey*. Proc 4th Int Coral Reef Symp 2:575–580

Ross RM (1982) Sex change in the endemic Hawaiian labrid *Thalassoma duperrey* (Quoy and Gaimard): a behavioral and ecological analysis. Doctoral dissertation, The University of Hawaii

Ross RM, Losey GS, Diamond M (1983) Sex change in a coral-reef fish: dependence of stimulation and inhibition on relative size. Science 217:574–576

Sadovy Y, Domeier ML (2005) Perplexing problems of sexual patterns in the fish genus *Paralabrax* (Serranidae, Serraninae). J Zool Lond 267:121–133

Sadovy Y, Donaldson TJ (1995) Sexual pattern of *Neocirrhites armatus* (Cirrhitidae) with notes on other hawkfish species. Environ Biol Fish 42:143–150

Sadovy Y, Eklund AM (1999) Synopsis of biological data on the Nassau grouper, *Epinephelus striatus* (Bloch, 1792), and the jewfish, *E. itajara* (Lichtenstein, 1822). NOAA Tech Rep NMFS 146:1–65

Sadovy Y, Rosario A, Román A (1994) Reproduction in an aggregating grouper, the red hind, *Epinephelus guttatus*. Environ Biol Fish 41:269–286

Sadovy Y, Shapiro DY (1987) Criteria for the diagnosis of hermaphroditism in fishes. Copeia 1987: 136–156

Sadovy de Mitcheson Y, Liu M (2008) Functional hermaphroditism in teleosts. Fish Fish (Oxf) 9:1–43

Sadovy de Mitcheson Y, Liu M, Suharti S (2010) Gonadal development in a giant threatened reef fish, the humphead wrasse *Cheilinus undulatus*, and its relationship to international trade. J Fish Biol 77:706–718

Sakai Y (1997) Alternative spawning tactics of female angelfish according to two different contexts of sex change. Behav Ecol 8:372–377

Sakai Y, Kohda M (1997) Harem structure of the protogynous angelfish, *Centropyge ferrugatus* (Pomacanthidae). Environ Biol Fish 49:333–339

Sakai Y, Karino K, Nakashima Y, Kuwamura T (2002) Status-dependent behavioural sex change in a polygynous coral-reef fish, *Halichoeres melanurus*. J Ethol 20:101–105

Sakai Y, Karino K, Kuwamura T, Nakashima Y, Maruo Y (2003a) Sexually dichromatic protogynous angelfish *Centropyge ferrugata* (Pomacanthidae) males can change back to females. Zool Sci 20:627–633

Sakai Y, Tsujimura C, Nakata Y, Tanabe H, Maejima G (2003b) Rapid transition in sexual behaviors during protogynous sex change in the haremic angelfish *Centropyge vroliki* (Pomacanthidae). Ichthyol Res 50:30–35

Sakakura Y, Noakes DLG (2000) Age, growth, and sexual development in the self-fertilizing hermaphroditic fish *Rivulus marmoratus*. Environ Biol Fish 59:309–317

Sakakura Y, Soyano K, Noakes DLG, Hagiwara A (2006) Gonadal morphology in the self-fertilizing mangrove killifish, *Kryptolebias marmoratus*. Ichthyol Res 53:427–430

Sakanoue R, Sakai Y (2022) Cryptic bachelor sex change in haremic colonial groups of the coral-dwelling damselfish *Dascyllus reticulatus* depending on body size and sheltering coral structures. J Ethol 40:181–192

Sakurai M, Nakakoji S, Manabe H, Dewa S, Shinomiya A, Sunobe T (2009) Bi-directional sex change and gonad structure in the gobiid fish *Trimma yanagitai*. Ichthyol Res 56:82–86

Salinas-de-León P, Rastoin E, Acuña-Marrero D (2015) First record of a spawning aggregation for the tropical eastern Pacific endemic grouper *Mycteroperca olfax* in the Galapagos Marine Reserve. J Fish Biol 87:179–186

Samoilys MA, Squire LC (1994) Preliminary observations on the spawning behavior of coral trout *Plectropomus leopardus* (Pisces: Serranidae), on the Great Barrier Reef. Bull Mar Sci 54:332–342

Sancho G, Solow AR, Lobel P (2000) Environmental influences on the diel timing of spawning in coral reef fishes. Mar Ecol Prog Ser 206:193–212

Sato T, Kobayashi M, Kurihara T, Takebe T, Hirai N et al (2018) Impact of fishing losses of males on the reproductive outut of the large protogynous fish, *Choerodon schoenleinii*. Mar Ecol Prog Ser 602:225–235

Schärer MT, Nemeth MI, Mann D, Locascio J, Appeldoorn RS, Rowell TJ (2012) Sound production and reproductive behavior of yellowfin grouper, *Mycteroperca venenosa* (Serranidae) at a spawning aggregation. Copeia 2012:135–144

Schwarz AL, Smith LC (1990) Sex change in the damselfish *Dascyllus reticulatus* (Richardson) (Perciformes: Pomacentridae). Bull Mar Sci 46:790–779

Seki S, Kohda M, Takamoto G, Karino K, Nakashima Y, Kuwamura T (2009) Female defense polygyny in the territorial triggerfish *Sufflamen chrysopterum*. J Ethol 27:215–220

Sellami A, Buslé J (1979) Contribution a l'etude de la peche, de la sexualité et de la reproduction de la mendole *Maena maena* (Linnaeus, 1758), Teleosteen Maenidé des cotes Tunisiennes. Mem Biol Mar Ocean 9:91–109

Shapiro DY (1992) Plasticity of gonadal development and protandry in fishes. J Exp Zool 261:194–203

Shapiro DY, Rasotto MB (1993) Sex differentiation and gonadal development in the diandric, protogynous wrasse, *Thalassoma bifasciatum* (Pisces, Labridae). J Zool 230:231–245

Shapiro DY, Sadovy Y, McGehee MA (1993) Periodicity of sex change and reproduction in the red hind, *Epinephelus guttatus*, a protogynous grouper. Bull Mar Sci 53:1151–1162

Sheaves M (1995) Large lutjanid and serranid fishes in tropical estuaries: are they adults or juveniles? Mar Ecol Prog Ser 129:31–41

Shen SC, Liu CH (1976) Ecological and morphological study of the fish-fauna from the waters around Taiwan and its adjacent islands. 17. A study of sex reversal in a pomacanthid fish, *Genicanthus semifasciatus* (Kamohara). Acta Oceanogr Taiwan 6:140–150

Shen SC, Lin RP, Liu FCC (1979) Redescription of a protandrous hermaphroditic moray eel (*Rhinomuaena quaesita* Garman). Bull Inst Zool, Acad Sin 18:79–87

Shibuno T, Chiba I, Gushima K, Kakuda S, Hashimoto H (1993a) Reproductive behavior of the wrasse, *Halichoeres marginatus*, at Kuchierabu-jima. Jpn J Ichthyol 40:351–359

Shibuno T, Chiba I, Hashimoto H, Gushima K (1994a) Reproductive behavior of the wrasse, *Thalassoma lutescens*, at Kuchierabu-jima. J Fac Appl Biol Sci, Hiroshima Univ 33:43–50

Shibuno T, Gushima K, Kakuda S (1993b) Female spawning migrations of the protogynous wrasse, *Halichoeres marginatus*. Jpn J Ichthyol 39:357–362

Shibuno T, Ogata S, Hashimoto H, Gushima K (1994b) Reproductive behavior of the parrotfish, *Calotomus japonicus*, at Kuchierabu-jima. J Fac Appl Biol Sci, Hiroshima Univ 33:37–41

Shihab I, Gopalakrishnan A, Vineesh N, Muktha M, Akhilesh KV, Vijayagopal P (2017) Histological profiling of gonads depicting protandrous hermaphroditism in *Eleutheronema tetradactylum*. J Fish Biol 90:2402–2411

Shimizu S, Endo S, Kihara S, Sunobe T (2022) Size, age, and social control of protogynous sex change in the labrid fish *Pteragogus aurigarius*. Ichthyol Res 69:75–81

Shimose T (2021) Age, growth, and reproductive traits of two large emperor fishes, *Lethrinus olivaceus* and *L. xanthochilus*, around Yaeyama Islands, Okinawa, southern Japan. Environ Biol Fish 104:181–194

Shinomiya A, Yamada M, Sunobe T (2003) Mating system and protandrous sex change in the lizard flathead, *Inegocia japonica* (Platycephalidae). Ichthyol Res 50:383–386

Shiobara Y (2000) Reproduction and hermaphoroditism of the gobiid fish, *Trimma grammistes*, from Suruga bay, Central Japan. Sci Rep Mus, Tokai Univ 2:19–30

Shitamitsu T, Sunobe T (2017) Notes on protandry in the creediid fishes *Limnichthys fasciatus* and *L. nitidus* (Teleostei: Creediidae). Ichthyol Res 64:365–367

Shitamitsu T, Sunobe T (2018) Protandry of the flathead *Suggrundus meerdervoortii* (Teleostei: Platycephalidae). Ichthyol Res 65:507–509

Shpigel M, Fishelson L (1986) Behavior and physiology of coexistence in two species of *Dascyllus* (Pomacentridae, Teleostei). Environ Biol Fish 17:253–265

Shpigel M, Fishelson L (1991) Territoriality and associated behaviour in three species of the genus *Cephalopholis* (Pisces: Serranidae) in the Gulf of Aqaba, Red Sea. J Fish Biol 38:887–896

Siau Y (1994) Population structure, reproduction and sex-change in a tropical East Atlantic grouper. J Fish Biol 44:205–211

Smith CL (1959) Hermaphroditism in some serranid fishes from Bermuda. Pap Michigan Acad Sci, Arts, Let 44:111–119

Smith CL (1965) The patterns of sexuality and the classification of serranid fishes. Amer Mus Novitates 2207:1–20

Smith CL, Atz JW (1969) The sexual mechanism of the reefbass *Pseudogramma bermudensis* and its implications in the classification of the Pseudogrammidae (Pisces: Perciformes). Z Morphol Tiere 65:315–326

Smith CL, Atz EH (1973) Hermaphroditism in the mesopelagic fishes *Omosudis lowei* and *Alepisaurus ferox*. Copeia 1973:41–44

Smith CL, Erdman DS (1973) Reproductive anatomy and color pattern of *Bullisichthys caribbaeus* (Pisces: Serranidae). Copeia 1973:149–151

Sordi M (1962) Ermafroditismo proteroginico in *Labrus turdus* L. e in *L. merula* L. Monit Zool Ital 69:69–89

Sordi M (1964) Ermafroditismo proteroginico in *Labrus bimaculatus* L. Monit Zool Ital 72:21–30

Soto CG, Leatherland JF, Noakes DLG (1992) Gonadal histology in the self-fertilizing hermaphroditic fish *Rivulus marmoratus* (Pisces, Cyprinodontidae). Can J Zool 70:2338–2347

Soyano K, Masumoto T, Tanaka H, Takushima M, Nakamura M (2003) Lunar-related spawning in honeycomb grouper, *Epinephelus merra*. Fish Physiol Biochem 28:447–448

Sprenger D, Dingemanse NJ, Dochtermann NA, Theobald J, Walker SPW (2012) Aggressive females become aggressive males in a sex-changing reef fish. Ecol Lett 15:986–992

Springer VG, Smith CL, Fraser TH (1977) *Anisochromis straussi*, new species of protogynous hermaphroditic fish, and synonymy of Anisochromidae, Pseudoplesiopidae, and Pseudochromidae. Smithsonian Contr Zool 252:1–15

Stauffer JR Jr, Ruffing RA (2008) Behaviorally induced sex reversal of *Metriaclima* cf. *livingstoni* (Cichlidae) from Lake Malawi. Copeia 2008:618–620

St. Mary CM (1994) Sex allocation in a simultaneous hermaphrodite, the blue-banded goby (*Lythrypnus dalli*): the effects of body size and behavioral gender and the consequences for reproduction. Behav Ecol 5:304–313

St. Mary CM (1996) Sex allocation in a simultaneous hermaphrodite, the zebra goby *Lythrypnus zebra*: insights gained through a comparison with its sympatric congener, *Lythrypnus dalli*. Environ Biol Fish 45:177–190

St. Mary CM (2000) Sex allocation in *Lythrypnus* (Gobiidae): variations on a hermaphroditic theme. Environ Biol Fish 58:321–333

Stroud GJ (1982) The taxonomy and biology of fishes of the genus *Parapercis* (Teleostei: Mugiloididae) in Great Barrier Reef waters. Doctoral dissertation, James Cook University

Sulak KJ, Wenner CA, Sedberry GR, Guelpen LV (1985) The life history and systematics of deep-sea lizard fishes, genus *Bathysaurus* (Synodontidae). Can J Zool 63:623–642

Sumpton W, Brown I (2004) Reproductive biology of the red throat emperor *Lethrinus miniatus* (Pisces: Lethrinidae) from the southern Great Barrier Reef, Australia. Bull Mar Sci 74:423–432

Sunobe T, Nakazono A (1990) Polygynous mating system of *Trimma okinawae* (Pisces: Gobiidae) at Kagoshima, Japan with a note of sex change. Ethology 84:133–143

Sunobe T, Nakazono A (1993) Sex change in both directions by alteration of social dominance in *Trimma okinawae* (Pisces: Gobiidae). Ethology 94:339–345

Sunobe T, Nakazono A (1999) Mating system and hermaphroditism in the gobiid fish, *Priolepis cincta*, at Kagoshima, Japan. Ichthyol Res 46:103–105

Sunobe T, Nakamura M, Kobayashi Y, Kobayashi T, Nagahama Y (2005) Aromatase immunoreactivity and the role of enzymes in steroid pathways for inducing sex change in the hermaphrodite gobiid fish *Trimma okinawae*. Comp Biochem Phys A 141:54–59

Sunobe T, Sado T, Hagiwara K, Manabe H, Suzuki T, Kobayashi Y, Sakurai M, Dewa S, Matsuoka M, Shinomiya A, Fukuda K, Miya M (2017) Evolution of bidirectional sex change and gonochorism in fishes of the gobiid genera *Trimma*, *Priolepis*, and *Trimmatom*. Sci Nat 104: 15

Sunobe T, Sakaida S, Kuwamura T (2016) Random mating and protandrous sex change of the platycephalid fish *Thysanophrys celebica* (Platycephalidae). J Ethol 34:15–21

Suzuki K, Hioki S, Tanaka Y, Iwasa K (1979) Spawning behavior, eggs, larvae, and sex reversal of two pomacanthine fishes, *Genicanthus lamarck*, and *G. semifasciatus*, in the aquarium. J Fac Mar Sci Tech, Tokai Univ 12:149–165

Suzuki K, Kobayashi K, Hioki S, Sakamoto T (1974) Ecological studies of the anthiine fish *Sacura margaritacea* in Suruga Bay, Japan. Jpn J Ichthyol 21:21–33

Suzuki K, Kobayashi K, Hioki S, Sakamoto T (1978) Ecological studies of the anthiine fish, *Franzia squamipinnis*, in Suruga Bay, Japan. Jpn J Ichthyol 25:124–140

Suzuki S, Kuwamura T, Nakashima Y, Karino K, Kohda M (2010) Social factors of group spawning as an alternative mating tactic in the territorial males of the threespot wrasse *Halichoeres trimaculatus*. Environ Biol Fish 89:71–77

Suzuki S, Toguchi K, Makino Y, Kuwamura T, Nakashima Y, Karino K (2008) Group spawning results from the streaking of small males into a sneaking pair: male alternative reproductive tactics in the threespot wrasse *Halichoeres trimaculatus*. J Ethol 26:397–404

Takamoto G, Seki S, Nakashima Y, Karino K, Kuwamura T (2003) Protogynous sex change in the haremic triggerfish *Sufflamen chrysopterus* (Tetraodontiformes). Ichthyol Res 50:281–283

Tanaka H, Hirose K, Nogami K, Hattori K, Ishibashi N (1990) Sexual maturation and sex reversal in red spotted grouper, *Epinephelus akaara*. Bull Natl Res Inst Aquacult 17:1–15

Tanaka Y (1999) Reproductive behavior, eggs and larvae of four *Dascyllus* species in the aquarium. J School Mar Sci Technol, Tokai Univ 47:223–244

Tatarenkov A, Lima SM, Taylor DS, Avise JC (2009) Long-term retention of self-fertilization in a fish clade. Proc Natl Acad Sci U S A 106:14456–14459

Taylor BM (2014) Drivers of protogynous sex change differ across spatial scales. Proc R Soc B 281:1–8

Taylor BM, Choat JH (2014) Comparative demography of commercially important parrotfish species from Micronesia. J Fish Biol 84:383–402

Taylor BM, Cruz E (2017) Age-based and reproductive biology of the Pacific longnose parrotfish *Hipposcarus longiceps* from Guam. PeerJ 5:e4079

Taylor RG, Whittington JA, Grier HJ, Crabtree RE (2000) Age, growth, maturation, and protandric sex reversal in common Snook, *Centropomus undecimalis*, from the east and west coasts of South Florida. Fish Bull 98:612–624

Tyler-Jedlund AJ, Torres JJ (2015) Age, growth, and reproduction of the littlehead porgy, *Calamus proridens*, from the eastern Gulf of Mexico. Bull Mar Sci 91:101–123

Thompson VJ, Munday PL, Jones GP (2007) Habitat patch size and mating system as determinants of social group size in coral-dwelling fishes. Coral Reefs 26:165–174

Thresher RE (1982) Courtship and spawning in the emperor angelfish *Pomacanthus imperator*, with comments on reproduction by other pomacanthid fishes. Mar Biol 70:149–156

Tobin AJ (1998) Protandrous sex change in the tropical sparid *Acanthopagrus berda* and the implications of geographical variability. Doctoral dissertation, James Cook University

Tomatsu S, Ogiso K, Fukuda K, Deki M, Dewa S, Manabe H, Sakurai M, Shinomiya A, Sunobe T (2018) Multi-male group and bidirectional sex change in the gobiid fish, *Trimma caudomaculatum*. Ichthyol Res 65:502–506

Touart LW, Bortone SA (1980) The accessory reproductive structure in the simultaneous hermaphrodite *Diplectrum bivittatum*. J Fish Biol 16:397–403

Tribble GW (1982) Social organization, patterns of sexuality, and behavior of the wrasse *Coris dorsomaculata* at Miyake-jima, Japan. Environ Biol Fish 7:29–38

Trip EDL, Clements KD, Raubenheimer D, Choat JH (2011) Reproductive biology of an odacine labrid, *Odax pullus*. J Fish Biol 78:741–761

Tsuboi M, Sakai Y (2016) Polygamous mating system and protogynous sex change in the gobiid fish *Fusigobius neophytus*. J Ethol 34:263–275

Tunley KL, Attwood CG, Moloney CL, Fairhurst L (2009) Variation in population structure and life-history parameters of steentjies *Spondyliosoma emarginatum*: effects of exploitation and biogeography. Afr J Mar Sci 31:133–143

Tuset VM, García-Díaz MM, González JA, Lorente MJ, Lozano IJ (2005) Reproduction and growth of the painted comber *Serranus scriba* (Serranidae) of the Marine Reserve of Lanzarote Island (central-eastern Atlantic). Estuar Coast Shelf Sci 64:335–346

Tuwo A, Tika IHP, Yunus B, Yasir I, Yanti A, Rahmani PY, Aprinto R, Tresnati J (2020) Sex ratio and maturity of orange-dotted tuskfish *Choerodon anchorago* Bloch, 1791 in Wallace line at Spermonde archipelago. IOP Conf Ser: Earth Environ Sci 564:012004

Vadiya V (1984) Reproductive systems of *Epinephelus aeneus* and *Epinephelus alexandrinus* (Serranidae) from the southeastern Mediterranean. J Ichthyol 24:77–81

van der Walt BA, Mann BQ (1998) Aspects of the reproductive biology of Lone (Pisces: Sparidae) off the east coast of South Africa. South African J Zool 33:241–248

Victor BC (1987) The mating system of the Caribbean rosy razorfish, *Xyrichtys martinicensis*. Bull Mar Sci 40:152–160

Walker SPW, McCormick MI (2004) Otolith-check formation and accelerated growth associated with sex change in an annual protogynous tropical fish. Mar Ecol Prog Ser 266:201–212

Walker SPW, McCormick MI (2009) Sexual selection explains sex-specific growth plasticity and positive allometry for sexual size dimorphism in a reef fish. Proc R Soc B 276:3335–3343

Walker SPW, Ryen CA (2007) Opportunistic hybridization between two congeneric tropical reef fish. Coral Reefs 26:539–539

Walker SPW, Ryen CA, McCormick MI (2007) Rapid larval growth predisposes sex change and sexual size dimorphism in a protogynous hermaphrodite, *Parapercis snyderi* Jordan & Starks 1905. J Fish Biol 71:1347–1357

Waltz CW, Roumillat WA, Wenner CA (1982) Biology of the whitebone porgy, *Calamus leucosteus*, in the South Atlantic Bight. Fish Bull 80:863–874

Warner RR (1975) The reproductive biology of the protogynous hermaphrodite *Pimelometopon pulchrum* (Pisces: Labridae). Fish Bull 73:262–283

Warner RR (1978) Patterns of sex and coloration in the Galapagos wrasses. Noticias de Galapagos 27:16–18

Warner RR (1982) Mating systems, sex change and sexual demography in the rainbow wrasse, *Thalassoma lucasanum*. Copeia 1982:653–661

Warner RR, Lejeune P (1985) Sex change limited by paternal care: a test using four Mediterranean labrid fishes, genus *Symphodus*. Mar Biol 87:89–99

Warner RR, Robertson DR (1978) Sexual patterns in the labroid fishes of the Western Caribbean, I: the wrasses (Labridae). Smithsonian Contr Zool 254:1–27

Warner RR, Swearer SE (1991) Social control of sex change in the bluehead wrasse, *Thalassoma bifasciatum* (Pisces: Labridae). Biol Bull 181:199–204

Webb RO, Kingsford MJ (1992) Protogynous hermaphroditism in the half-banded sea perch, *Hypoplectrodes macullochi* (Serranidae). J Fish Biol 40:951–961

Wenner CA, Roumillat WA, Waltz W (1986) Contributions to the life history of black sea bass, *Centropristis striata*, off the southeastern United States. Fish Bull 84:723–741

Wernerus FM, Tessari V (1991) The influence of population density on the mating system of *Thalassoma pavo*, a protogynous Mediterranean labrid fish. Mar Ecol-Evol Persp 12:361–368

Wilson DP (1958) Notes from the Plymouth Aquarium. III. J Mar Biol Assoc UK 37:299–307

Wittenrich ML, Munday PL (2005) Bi-directional sex change in coral reef fishes from the family Pseudochromidae: an experimental evaluation. Zool Sci 22:797–803

Wong MYL, Munday PL, Jones GP (2005) Habitat patch size, facultative monogamy and sex change in a coral-dwelling fish, *Caracanthus unipinna*. Environ Biol Fish 74:141–150

Wong MYL, Munday PL, Buston PM, Jones GP (2008) Monogamy when there is potential for polygyny: tests of multiple hypotheses in a group-living fish. Behav Ecol 19:353–361

Wong MYL, Fauvelot C, Planes S, Buston PM (2012) Discrete and continuous reproductive tactics in a hermaphroditic society. Anim Behav 84:897–906

Wyanski DM, White DB, Barans A (2000) Growth, population age structure, and aspects of the reproductive biology of snowy grouper, *Epinephelus niveatus*, off North Carolina and South Carolina. Fish Bull 98:199–218

Yeung WSB, Chan STH (1987) The gonadal anatomy and sexual pattern of the protandrous sex-reversing fish, *Rhabdosargus sarba* (Teleostei: Sparidae). J Zool Lond 212:521–532

Yogo Y (1985) Studies on the sexual maturation and reproductive ecology in three protogynous fishes. Rep Fish Res Lab, Kyushu Univ 7:37–83

Yogo Y, Nakazono A, Tsukahara H (1980) Ecological studies on the spawning behavior of the parrotfish, *Scarus sordidus* Forsskål. Sci Bull Fac Agric, Kyushu Univ 34:105–114

Young PC, Martin RB (1982) Evidence for protogynous hermaphroditism in some lethrinid fishes. J Fish Biol 21:475–484

Young PC, Martin RB (1985) Sex ratios and hermaphroditism in nemipterid fish from northern Australia. J Fish Biol 26:273–287

Young JM, Yeiser BG, Whittington JA, Dutka-Gianelli J (2020) Maturation of female common snook *Centropomus undecimalis*: implications for managing protandrous fishes. J Fish Biol 97:1317–1331

Zabala M, García-Rubies A, Louisy P, Sala E (1997a) Spawning behaviour of the Mediterranean dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Pisces: Serranidae) in the Medes Islands Marine Reserve (NW Mediterranean, Spain). Sci Mar 61:65–77

Zabala M, Louisy P, García-Rubies A, Gracia V (1997b) Socio-behavioural context of reproduction in the Mediterranean dusky grouper *Epinephelus marginatus* (Lowe, 1834) (Pisces: Serranidae) in the Medes Islands Marine Reserve (NW Mediterranean, Spain). Sci Mar 61:79–89

Zamboni A, Relini G (1986) Note di biologia di *Spicara flexuosa* (Osteichthyes, Centracanthidae) del Mar Ligure. Bull Mus Inst Biol Univ Genova 52(suppl):251–265

Zei M (1950) Typical sex-reversal in teleosts. Proc Zool Soc Lond 119:917–921

Zohar Y, Abraham M, Gordin H (1978) The gonadal cycle of the captivity-reared hermaphroditic teleost *Sparus aurata* (L.) during the first two years of life. Ann Biol Anim Biochim Biophys 18: 877–888

Zorica B, Sinovčić G, Keč VĈ (2005) Reproductive period and histological analysis of the painted comber, *Serranus scriba* (Linnaeus, 1758). Acta Adriat 46:77–82