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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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 Size assortative monogamy	Harem	MTV polygamy	Group spawning	Spawning aggregation	References
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					References
			Size assortative monogamy	Harem	MTV polygamy	Group spawning	Spawning aggregation	
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: Size assortative monogamy	Harem	MTV polygamy	Group spawning	Spawning aggregation	References
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).

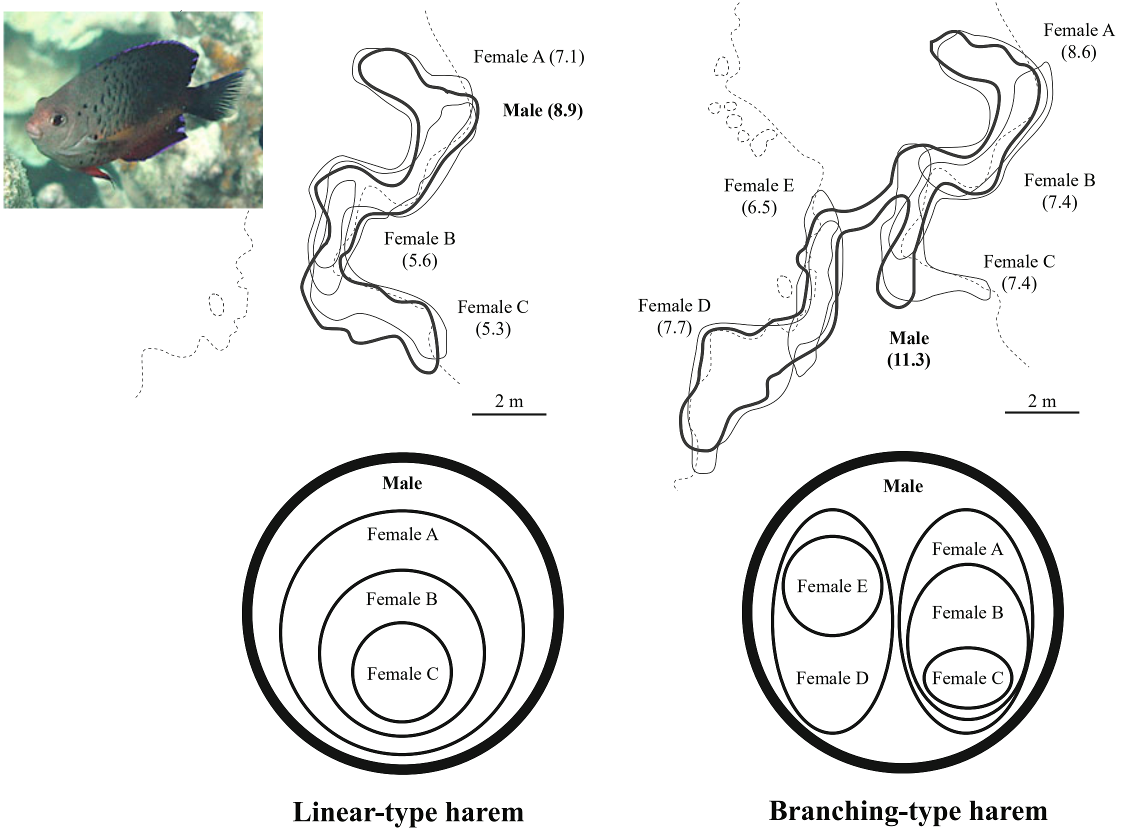

Fig. 4.1 Typical example of the spatial relationship of the cohabiting female-type harem. Male territories (*thick lines*) and female home ranges (*thin lines*) of two adjacent harems of the angelfish *Centropyge ferrugata* on reefs of Sesoko Island, Okinawa, are shown (redrawn from Sakai and Kohda 1997). 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

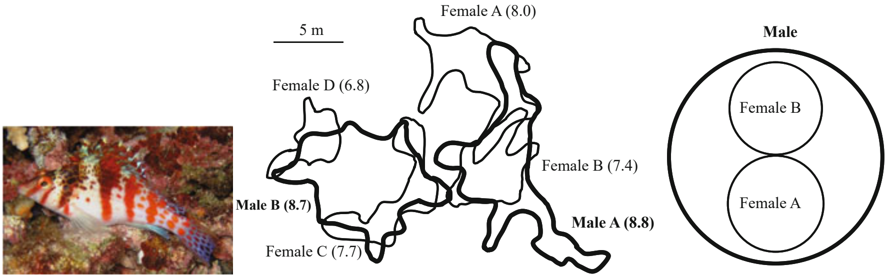

Fig. 4.2 Typical example of the spatial relationship of the territorial female-type harem. Male territories (*thick lines*) and female territories (*thin lines*) of two harems of the hawkfish *Cirrhitichthys falco* on the reefs of Kuchierabu-jima Island, southern Japan (*left*; redrawn from Kadota et 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

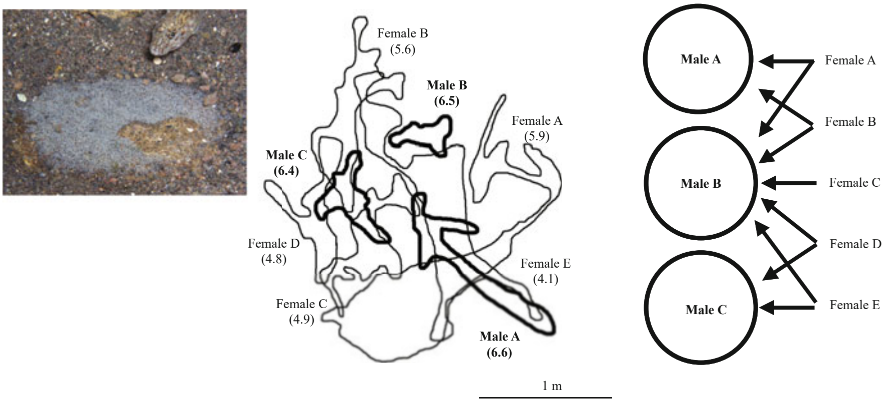

Fig. 4.4 Typical example of the spatial relationship of the male territory-visiting (MTV) polygamy. Home ranges of females (*thin lines*) and territories of nest-holding males (*thick lines*) of *Fusigobius neophytus* on the reefs of Kuchierabu-jima Island, southern Japan (*left*; redrawn from Tsuboi 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

Family/species	Mating system	Takeover sex change	Sex change in the male presence			References
			Bachelor sex change	Harem-fission sex change	Remarks	
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		Gonadal sex change	Body coloration change	References
	Courtship (male role)	Spawning (male role)			
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

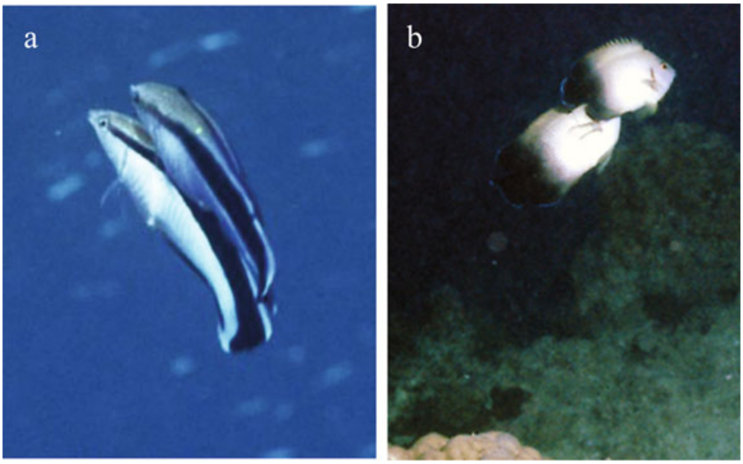

Fig. 4.5 Spawning behaviors by a pair consisting of a sex-changing female and a smaller female in haremic fishes. The largest females of *Labroides dimidiatus* (**a**; above of ascending pair) and *Centropyge vrolikii* (**b**; below of ascending pair) started male sexual behaviors and spawned with subordinate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

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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