Chapter 2
Simultaneous Hermaphroditism in Fishes

Kota Sawada

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

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

2.1 What Is Simultaneous Hermaphroditism?

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

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K. Sawada (✉)
Oceanic Resources Group, Highly Migratory Resources Division, Fisheries Resources Institute, Japan Fisheries Research and Education Agency, Yokohama, Kanagawa, Japan
e-mail: sawada_kota27@fra.go.jp

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

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

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

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

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

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

(continued)

Table 2.1 (continued)

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

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

(continued)

Table 2.1 (continued)

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

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

(continued)

Table 2.1 (continued)

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

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

? indicates that it is suggested but not confirmed

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

[a] Male function not confirmed

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

[c] Poor fixation of gonad

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

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

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

2.2 Evolutionary Theory for Simultaneous Hermaphroditism

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

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

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

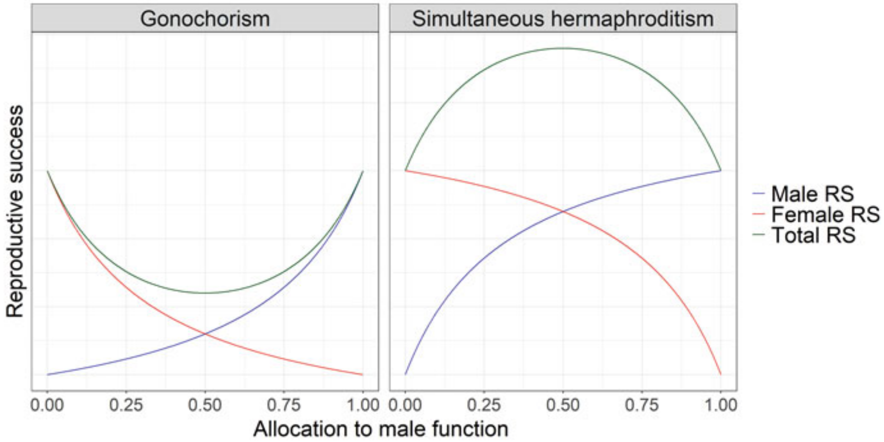

Fig. 2.1 A schematic drawing of evolutionary conditions favoring gonochorism and simultaneous hermaphroditism under diminishing return hypothesis (Charnov et al. 1976; Charnov 1982). The horizontal axis represents the proportion of reproductive resources allocated to male function. The vertical axis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

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

2.3 Deep-Sea Aulopiforms

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

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

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

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

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

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

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

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

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

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

2.4 Self-Fertilization and Androdioecy in Killifishes

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

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

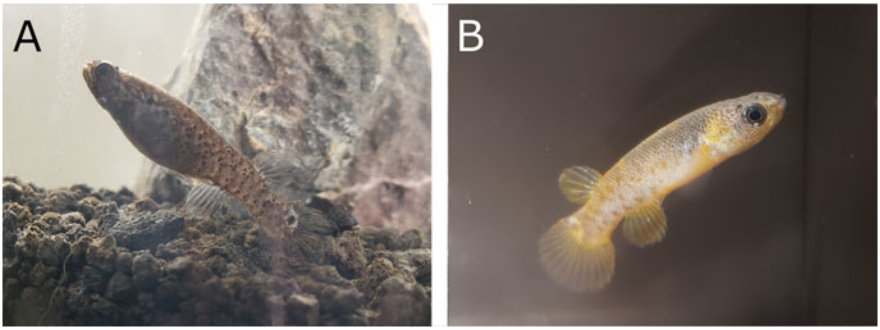

Fig. 2.3 Mangrove rivulus *Kryptolebias marmoratus*, an androdioecious species (Table 2.1) including simultaneous hermaphrodites (**a**) and males (**b**), the latter can be distinguished by orange coloration. (Photos provided by Brooke Fitzwater and Ryan Earley of The University of Alabama)

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

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

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

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

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

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

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

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

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

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

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

2.5 Hermaphroditism and Egg Trading in Serranids

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

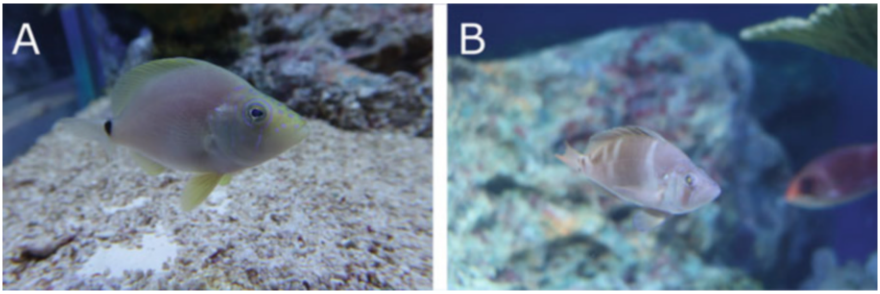

Fig. 2.4 Simultaneously hermaphroditic serranid species, butter hamlet *Hypoplectrus unicolor* (**a**) and barred hamlet *H. puella* (**b**). Both species mate with egg trading (Table 2.1). (Photos taken by the author at Sunshine Aquarium, Tokyo, Japan, and used under the permission from Sunshine Aquarium)

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

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

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

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

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

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

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

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

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

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

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

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

2.6 Other Taxa

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

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

2.7 Future Research Directions

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

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

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

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

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

2.8 Conclusions

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

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

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