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Time required for sex change in teleost fishes: Hormonal dynamics shaped by selection

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HIGHLIGHTS

- Size advantage hypothesis cannot explain the time required for sex change.
- I consider hormone–enzyme dynamics to reveal temporal difference in two directions.
- Haremic species promote a faster degradation of aromatase when changing to male.
- A female-to-male transition takes shorter than the opposite one in haremic species.
- Monogamous species have approximately equal durations in either sex transition.

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ABSTRACT

Bidirectional sex change is observed in many teleost fish. When social conditions change, the sex transition may take place over a period of several days to a few months. To understand temporal differences for sex change in either direction, I propose a simple mathematical model for the hormone–enzyme dynamics. Aromatase (P450arom) catalyses the synthesis of estradiol from testosterone. I assume that a change in social conditions for individuals affects the rates of production and degradation of P450arom. I then consider the evolution of parameters in the dynamics. Optimal parameter values are those that minimize total fitness cost, defined as the sum of fitness losses due to delay in being a functional male or female, and the cost of accelerated degradation of P450arom in changing from female to male sex. The model predicts that, in haremic species, sex change promotes a faster degradation of P450arom, resulting in a faster female-to-male transition than male-to-female transition. In contrast, in monogamous species, or with a small number of females, there is no benefit in a faster degradation of P450arom when changing to male, resulting in approximately equal timespans for sex change in either direction.

1. Introduction

Many species of teleost fish show a transition from one sex to the other within their lifetime (e.g. Warner, 1978; Kuwamura and Nakashima, 1998; Munday et al., 2006; Sadovy de Mitcheson and Liu, 2008). In protogynous sex change, individuals first mature as females and then change to the male sex, while in protandrous sex change they first mature as males and change into females. Bidirectional sex change has been reported since the 1990s in some fish in which individuals change sex in either direction when a same-sex pair are reared together in an aquarium (e.g. the grouper *Epinephelus akaara*, Tanaka et al., 1990; the hawkfish *Cirrhittchthys aureus*, Kobayashi and Suzuki, 1992; the goby *Trimma okinawae*, Sunobe and Nakazono, 1993). Bidirectional sex change in natural populations has been observed in the coral goby *Paragobiodon echinocephalus* (Kuwamura et al., 1994), several species of *Gobiodon* (Nakashima et al., 1996; Munday et al., 1998), the cleaner wrasse *Labroides dimidiatus* (Kuwamura et al., 2002), the magenta dottyback *Pictichromis porphyrea* (Kuwamura et al., 2015), the hawkfish *Cirrhitichthys falco* (Kadota et al., 2012), the rusty angelfish *Centropyge ferrugata* (Kuwamura et al., 2011) and the damselfish *Dascyllus aruanus* (Kuwamura et al., 2016). It is hypothesized to be an adaptation to low population density (Kuwamura et al., 2002, 2011, 2014, 2015, 2016; Kadota et al., 2012) and/or limited capacity of mate-search (Munday et al., 1998; Munday, 2002).

The direction of sex change and its timing have been explained successfully by a game-theoretical model called the 'size-advantage hypothesis', in which each individual chooses the more profitable sex given its body size (Ghiselin, 1969; Warner, 1975;

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Charnov, 1982). Reproductive success of a female increases with her body size, as it is almost proportional to the number of eggs she produces. In contrast, a male's reproductive success is determined by the number of eggs fertilized by his own sperm, and it strongly depends on mating systems. With random mating (Sunobe et al., 2016) or monogamous systems (e.g. anemonefish, genus *Amphiprion*, Fricke and Fricke, 1977), reproductive success of males does not depend on their size; the smaller individuals become males and the larger ones become females, with the direction of sex change being from male to female (protandrous). In contrast, when the mating system is haremic or polygynous (e.g. the cleaner wrasse *Labroides dimidiatus*, Robertson, 1972; Kuwamura, 1984), a large dominant male monopolizes the fertilization of eggs produced by many females in the mating group and achieves a much higher mating success than a small subordinate male. As a result, small fish become females and large fish become males (protogynous). When a dominant male disappears for some reason, the largest female in the group undergoes a sex change to male and finally becomes a new dominant. Social environment and status have a strong influence on the timing and direction of sex change (Shapiro, 1984; Warner, 1988; Ross, 1990).

However, sex change does not occur instantly, and it commonly takes from several days to a few months (Munday et al., 2010; Sakai et al., 2003, therein references; see Table 1). Interestingly, the length of time required for sex change in each direction differs between species. In some species in the family Gobiidae, sex change in both directions takes a similar period of time; for example, in the coral goby *Gobiodon histrio*, it is around one month (Munday et al., 1998). In contrast, in Labridae and Pomacanthidae, e.g., the cleaner wrasse *Labroides dimidiatus*, a male-to-female sex change takes much longer (53–77 days) than a female-to-male sex change (14–18 days) (Kuwamura et al., 2002). The list of reports in Table 1 show that monogamous species such as coral-dwelling gobies need a similar length of time for sex change in either direction, but haremic species in Labridae and Pomacanthidae often require a clearly longer time for a male-to-female sex change than for a sex change in the opposite direction.

To understand the time difference required for sex change in the two different directions, I here consider the hormonal dynamics. Gonadal steroid hormones, such as testosterone (androgen) and estradiol (estrogen), play important roles in the regulation of sexual phenotype (Fostier et al., 1983; Liley and Stacey,

Table 1
Mating system and duration required for sex change in each direction.

		Mating system	Female-to-male Duration (days)	Male-to-female Duration (days)	Exp.	References
Gobiidae	*Gobiodon histrio*	Monogamy	(< 28)	(< 28)	F	Munday et al. (1998)
	G. micropus	Monogamy	(< 49)	(< 49)	A	Nakashima et al. (1996)
	G. oculolineatus	Monogamy	(< 49)	(< 49)	A	Nakashima et al. (1996)
	G. okinawae	Unknown	(< 21*)	(< 21*)	A	Cole and Hoese (2001)
	G. quinquestrigatus	Monogamy	(30–49)	(23–49)	A, F	Nakashima et al. (1996)
	G. rivulatus rivulatus	Monogamy	(< 49)	(< 90)	A, F	Nakashima et al. (1996)
	Paragobidon echinocephalus	Monogamy	27	24	A	Nakashima et al. (1995)
	Lythrypnus dalli	Polygyny	5–11	14–53	A	Reavis and Grober (1999); Black et al. (2005)
	Trimma okinawae	Polygyny	6–14	4–11	A	Sunobe and Nakazono (1993)
	T. kudoi	Polygyny	16–34	10–20	A	Manabe et al. (2008)
	T. yanagitai	Unknown	6–47	15–44	A	Sakurai et al. (2009)
	Priolepis cincta	Monogamy	10	No data	A, F	Sunobe and Nakazono (1999); Manabe et al. (2013)
	P. akihitoi	Unknown	25	21, 35	A	Manabe et al. (2013)
	P. latifascima	Unknown	35	48	A	Manabe et al. (2013)
	P. semidoliata	Unknown	21	No data	A	Manabe et al. (2013)
Pseudochromidae	*Pseudochromis flavivertex*	Unknown	28	52	A	Wittenrich and Munday (2005)
	P. aldabraensis	Unknown	18–43	64–92	A	Wittenrich and Munday (2005)
	P. cyanotaenia	Unknown	23–56	67–93	A	Wittenrich and Munday (2005)
	Pictichromis porphyria	Unknown	28–107	37–72	F	Kuwamura et al. (2015)
Pomacanthidae	*Centropyge acanthops*	Harem	8	91*	A	Hioki and Suzuki (1996)
	C. ferrugata	Harem	15–22	47, 89*	A	Sakai (1997); Sakai et al. (2003); Sakai (unpublished)
	C. fisheri	Harem	6	35*	A	Hioki and Suzuki (1996)
	C. flavissimus	Harem	No data	81	A	Hioki and Suzuki (1996)
	Apolemichthys trimaculatus	Unknown	25	123*	A	Hioki and Suzuki (1995)
Pomancentridae	*Dascyllus aruanus*	Polygyny	(< 30)	(< 60)	F	Kuwamura et al. (2016)
Cirrhitidae	*Cirrhitichthys aureus*	Unknown	230	207	A	Kobayashi and Suzuki (1992)
Labridae	*Labroides dimidiatus*	Harem	14–18	53–77	A	Robertson (1972); Nakashima et al. (2000); Kuwamura et al. (2002)
	Labroides dimidiatus	Harem	No data	40-61	F	Kuwamura et al. (2011)

Note: Duration of sex change is the number of days from the start of mate-removal or same-sex cohabitation experiments to the confirmation of functional sex change. Ideally functional sex change should be judged by the observation of spawning (sperm release in female-to-male sex change and egg release in male-to-female sex change) or fertilized egg clutch. However, in some cases (indicated by asterisk) it was judged by the morphological change of urogenital papillae (for Gobiidae and Pomancentridae) or gonad (for Pomacanthidae). Data from studies that were not designed to precisely measure the duration are shown in the parentheses. For the column of experiment (shown by Exp.), 'A' and 'F' indicate that data were reported by aquarium experiment and by field experiment, respectively. This table is made from data in Sakai et al. (2003) and Munday et al. (2010) and includes additional data.