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Small and poor females change sex: A theoretical and empirical study on protogynous sex change in a triggerfish under varying resource abundance

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HIGHLIGHTS

- As opposed to the classical theory, smaller female triggerfish change sex.
- Variation in female fecundity probably causes sex change by less-fertile females.
- Our model and field survey predict that less-fertile females change sex earlier.

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ABSTRACT

Sex change is known from various fish species. In many polygynous species, the largest female usually changes sex to male when the dominant male disappeared, as predicted by the classical size-advantage model. However, in some fishes, the disappearance of male often induces sex change by a smaller female, instead of the largest one. The halfmoon triggerfish *Sufflamen chrysopterum* is one of such species. We conducted both field investigation and theoretical analysis to test the hypothesis that variation in female fecundity causes the sex change by less-fertile females, even if they are not the largest. We estimated the effect of body length and residual body width (an indicator of nutrition status) on clutch size based on field data. Sex-specific growth rates were also estimated from our investigation and a previous study. We incorporated these estimated value into an evolutionarily stable strategy model for status-dependent size at sex change. As a result, we predict that rich females change sex at a larger size than poor ones, since a rich fish can achieve high reproductive success as a female. In some situations, richer females no longer change sex (i.e. lifelong females), and poorer fish changes sex just after maturation (i.e. primary males). We also analyzed the effect of size-specific growth and mortality.

1. Introduction

Sex change (sequential hermaphroditism) has been reported from various fish species (Kuwamura and Nakashima, 1998; Munday et al., 2006; Sadovy and Liu, 2008). The traditional size-advantage model had been successful to explain the evolution of sex change (Ghiselin, 1969; Warner, 1975; Charnov, 1982), and had predicted that protogyny should evolve when large males monopolize matings (Warner, 1984, 1988). In haremic species, the largest female typically changes sex when the territorial male disappeared: e.g. a cleaner wrasse *Labroides dimidiatus* (Robertson, 1972; Kuwamura, 1984). Or in case of early sex change (i.e., protogynous sex change without the disappearance of territorial males), it is also the largest female who changes sex (Moyer and Zaiser, 1984; Aldenhoven, 1986; Sakai, 1997).

However, the traditional size-advantage model cannot explain the phenomenon that not the largest female but smaller one changes sex in some protogynous fish species (Muñoz and Warner, 2003a, 2003b, 2004; Takamoto et al., 2003; Manabe et al., 2008). Muñoz and Warner (2003a) constructed a mathematical model called "a new version of size-advantage model" or the expected reproductive success threshold model (the ERST model), and explained the pattern of sex change in the bucktooth parrotfish *Sparisoma radians* (Muñoz and Warner, 2003b, 2004). They considered sperm competition and size–fecundity skew to

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explain why sex change is not adaptive for the largest females. Manabe et al. (2008) reported that the largest female usually does not change sex, but the smaller one do so when two or three females of *Trimma kudoi* were kept together, and suggested that the ERST model may be applicable to this species.

We introduce the halfmoon triggerfish *Sufflamen chrysopterum* as another example of such non-traditional sex change. Takamoto et al. (2003) found protogynous sex change of *S. chrysopterum* (Balistidae; Tetraodontiformes) in Sesoko Island, Okinawa, Japan. After the removal of several males, not the largest females, but smaller ones changed sex.

S. chrysopterum is a monogamous or polygynous fish with maternal egg care (Kawase and Nakazono, 1993; Ishihara and Kuwamura, 1996; Seki et al., 2009) and exhibits female-defense polygyny in Sesoko Island (Seki et al., 2009). In this species, a female guards a small territory for foraging. A large male (a harem male) defends a large territory which include one to three female territories. Sometimes, smaller males whose territories include no females are observed. We call them "bachelors". Since no alternative mating behavior, such as sneaking or streaking, is observed in this species (Ishihara and Kuwamura, 1996), these males are not sneakers or streakers, and perhaps do not reproduce at all. The size of the smallest harem male is about 138 mm in standard length (SL) (Takamoto et al., 2003). The sizes of all observed sex changers are smaller than 138 mm, thus individuals become bachelors just after sex change (Takamoto et al., 2003). These sex changers leaved their former territories, and their new territories included no females. Therefore, this is an example of bachelor sex change (Sakai, 1997).

Why do smaller individuals change sex, whereas the largest ones do not? Muñoz and Warner (2003a) argued that intensity of sperm competition and size–fecundity skew increases the reproductive value of female for larger fish, relative to the value of male. The former factor is, however, not applicable to *S. chrysopterum* which exhibits haremic mating system and no alternative reproductive tactics of males. Currently no data is available for size–fecundity relationship of this fish. Although female fecundity is often assumed to be determined by body length, it may also depend on the amount of resources available, that is, the nutrition status. In a theoretical model on environmental sex determination, individuals are predicted to be a sex with greater advantage of resources (Charnov and Bull, 1977). If female fecundity is strongly affected by the nutrition status, individuals should be females under resource-rich conditions. This prediction may be important for sex change, though it is not fully explored. In addition, sexual difference in growth rate may affect the relative expected reproductive success of males and females and hence the direction and timing of sex change (Iwasa, 1991). Growth rate is also a possible explanation of bachelor sex change, if bachelors show faster growth (Iwasa, 1991).

We construct a mathematical model to explain this pattern of sex change. In addition, we also conducted a field investigation to estimate the growth rate of females and the size–fecundity relationship among females. The female fecundity (the number of eggs) may correlate with not only the body length, but also the nutrition status of the female. Therefore, we included the effect of individual variation in nutrition status among females on the size of sex change in our model. We used the actual data on the growth rate of bachelor males from Takamoto et al. (2003).

2. Model: Evolutionarily stable strategy of the size at sex change

Females in this species guard foraging territories in the triggerfish *S. chrysopterum*. We assume that the body width of each female is determined by the quality of her territory, and that the quality is constant through lifetime of each female. We define the quality of territory for a female as the nutrition status. The purpose of this paper is to investigate how that the evolutionarily stable size of sex change depends on the nutrition status.

The assumptions of the model are:

(1) Females grow with a constant speed.
(2) The female fecundity (the number of eggs) at age t, f, depends on the body width and the body length of a female.
(3) Most of individuals in a population change their sex from females to males. The age of sex change (τ) depends on the nutrition status (x).
(4) After sex change, non-reproductive bachelor males grow with very large speed, because they do not pay the cost of reproduction (Iwasa, 1991).
(5) Non-reproductive small bachelor males have high mortality rate, because they do not have stable territories. On the other hand, as bachelor males grow, their mortality rates decreases.
(6) A male can reproduce as a harem male only by reaching the critical body length (L_m), because small males in this species are bachelors (Seki et al., 2009).

Assumptions 1, 2 and 4 are based on our field investigations (see Result 3-1 and 3-2).

When L_0 is the length of a female at maturation and a is the growth rate of a female, the length at age t, $L(t)$, is written by

$$L(t) = L_0 + at \tag{1}$$

Let $W(t)$ and $L(t)$ be the body width and the body length of the focal individual at age t, respectively. By Assumption 2, the female fecundity, f, is represented by $f(W(t),L(t))$. The reproductive success as a female with the nutrition status x, $\phi_f(x)$, is calculated by integrating the female fecundity $f(W(t),L(t))$, weighted by the survivorship until the age of sex change $\tau(x)$:

$$\phi_f(x,\tau) = \int_0^{\tau(x)} e^{-\mu t} f(W(t),L(t))dt, \tag{2}$$

where μ is the mortality rate of females. Recall that the timing of sex change, $\tau(x)$, depends on the nutrition status x of the female. See the female fecundity, $f(W(t),L(t))$, estimated by multiple regressions in Appendix A and Section 3.1.

As for non-reproductive bachelor males, we assume that smaller ones have higher mortality rate. We assume that the mortality rate of a bachelor male is inversely proportional to his body length. The probability of surviving from sex change until he attains the length L_m is

$$\exp\left(\int_{\tau(x)}^{\tau(x)+h(x)} \frac{b}{L(t)}\, dt\right),$$

where $h(x)$ is the time to attaining L_m from the sex change who was a female with the nutrition status x, and b is a proportionality constant for the mortality of a bachelor male.

From Assumption 4, non-reproductive bachelor males grow with very faster speed comparing to the growth speed of females. We use the symbol a' as the growth rate of a bachelor male after sex change. We assume that the length of a bachelor male after sex change is written as

$$L(t) = L(\tau(x)) + a'(t-\tau(x)). \tag{3}$$

We assume that a male attaining the length L_m is a harem male (Assumption 6). The average reproductive success of a harem male, ϕ_m, is calculated as total fecundity of all females divided by the number of harem males, because the summation of reproductive success of all males must be identical to that of all