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New aspects of sex change among reef fishes: recent studies in Japan

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Synopsis

New aspects of sex change in reef fishes are reviewed with special emphasis on recent studies in Japan. For protogyny, studies on both monandric and diandric species have been conducted, but the distinction of primary males from prematurational secondary males seems to need further examination. For protandry, detailed field studies on anemonefishes have revealed alternative life-history styles associated with movements between hosts before or after maturation. The most interesting new aspect has been the discovery of 2-way sex change within a species. Conditions for evolution of 2-way sex change are examined in relation to the size-advantage model and social control mechanisms. A fish may change sex when it becomes dominant in a mating group, but a dominant fish may also change sex in the reverse direction when its social status changes to subordinate through inter-group movement. Two-way sex change has hitherto been reported only from basically protogynous fishes (e.g., Gobiidae, Pomacanthidae, Cirrhitidae, Epinephelinae). Possibilities of the reverse sex change in the protandrous anemonefishes are discussed with data from some unpublished studies.

Introduction

Sex change from female to male or vice versa is well known among teleost fishes. The evolution of sex change, as a life-history style alternative to gonochorism, has been explained by the size-advantage model (Gishelin 1969, Warner 1975, 1988a, Charnov 1982). If the product of the probability of survival to a particular age and expected fecundity at that age increases with age or size faster for one sex than the other, then an individual that changes sex will have a higher lifetime reproductive success than one that does not. This model predicts that the direction of sex change, protogyny or protandry, will be determined by the mating system of each species, as has been confirmed in many reef fishes (Warner 1984, 1988b).

Sex change has also been one of the main interests of Japanese ichthyologists. Theoretical and empirical studies on sex change among fishes were reviewed by Nakazono & Kuwamura (1987). The book was one of the products of the research project 'Optimal strategy and social structure of vertebrates' (1983–1986, supported by the Japan Ministry of Education, Science and Culture), which was headed by Hiroya Kawanabe. An English translation of the book was prepared by K. Asoh, T. Yoshikawa and D. Shapiro, but unfortunately it has not yet been published.

The purpose of this essay is to review recent studies on sex change of fishes conducted in Japan and to evaluate new aspects in this field. First, we give a brief summary of each chapter of the above-mentioned book (Nakazono & Kuwamura op. cit.). Then we review the recent studies in Japan, focusing on ecological and evolutionary aspects of sex

change. The most interesting new aspect in this field seems to be the finding of sex change in either direction within a species, which has been confirmed in several species of fishes by Japanese researchers (e.g., Kuwamura et al. 1994). Therefore, we put special emphasis on this aspect and discuss requisites and possibilities of the reverse-directional sex change among other hermaphroditic fishes including protandrous anemonefishes.

Recent studies on sex change of fishes in Japan

Until 1987

First, we briefly introduce each chapter of Nakazono & Kuwamura (1987). Chapter 1 'Hermaphroditism and the evolutionary aspects of its occurrences in fishes' (by Y. Yogo) is a phylogenetic review of hermaphroditic fishes with lists of species. By that time, functional hermaphroditism had been reported from at least 350 species of 34 families in eight orders of teleost fishes. Chapter 2 'Histology and physiology of sex change in fishes' (by M. Nakamura) reviews histological and hormonal changes in sex-changing fishes, e.g., a protogynous wrasse *Thalassoma duperrey*. Chapter 3 'Theories for sex change' (by Y. Yanagisawa) reviews the evolutionary models of Ghiselin (1969), Warner (1975), Charnov (1982), etc.

Chapter 4 'Social control of sex change in harems of *Labroides dimidiatus*' (by T. Kuwamura) reviews the well-known example of the protogynous cleaner wrasse, mainly referring to Robertson (1974) and Kuwamura (1984). Chapter 5 'Social organization and protogynous hermaphroditism in marine angelfishes (Pomacanthidae)' (by J.T. Moyer) is a review with special emphasis on the occurrence of early sex change (Moyer & Zaiser 1984, also see Moyer 1990). Chapter 6 'Group structure and mechanism of sex change in *Anthias squamipinnis*' (by Y. Yogo) reviews its mating system (Yogo 1985) and the sex-ratio threshold model (e.g., Shapiro & Lubbock 1980). Chapter 7 'Diandry in Japanese labrid fishes and alternative strategies of primary males' (by A. Nakazono) compares three Japanese wrasses (Nakazono 1979) and the bluehead wrasse *Thalassoma bifasciatum* (e.g., Warner & Hoffman 1980).

Chapter 8 'Sexual patterns in damselfishes (Pomacentridae) with special reference to protandry in anemonefishes' (by H. Ochi) compares social systems of protogynous *Dascyllus* (e.g., Coates 1982) and protandrous *Amphiprion* (e.g., Fricke & Fricke 1977, also see Ochi 1989a, b). Chapter 9 'Partial protandry in the alpheid shrimp *Athanas kominatoensis*: a case of sex change in Crustacea' (by Y. Nakashima; also see Nakashima 1987) was included, though it is not a fish, because examples of protandrous fishes whose social systems were well known were very limited. Thus, the book is composed of these nine chapters with more than 400 references cited.

Since 1987

Since Nakazono & Kuwamura (1987), the study of sex change has been attracting many Japanese ichthyologists. Hermaphroditism in fishes was reviewed by Nakazono (1991) in various aspects, and by Suzuki (1989) from the viewpoint of comparative gonad histology. Physiological aspects of sex change, such as on function of sex hormones, have also been studied (e.g., Nakamura et al. 1994). For theoretical aspects Iwasa (1991) developed a model of sex-change evolution by dynamic programming, and proposed that the evolutionary stable sexual style may include an extended nonreproductive period that intervenes between male and female phases, if costs of reproduction are concerned. This may correspond to early sex change. Iwasa (op. cit.) also showed that the difference between sexes either in mortality (mortality advantage) or in growth rate (growth-rate advantage) favors the evolution of sex change even if the size advantage (size-fecundity advantage) is the same between the sexes. For ecological and histological aspects of hermaphroditic fishes living in Japanese waters, more than 30 papers have been published since 1987, summarized as follows.

Protogynous fishes

Among protogynous fishes, labrids have been most

intensively studied. Three sexual pathways in individual life histories are known (Figure 1). Males derived without sex change are called primary males and those through sex change secondary males; species containing both primary and secondary males are called diandric and those containing only secondary males monandric (e.g., Warner & Robertson 1978). Dichromatism (i.e. two color phases) related to body size is often referred to as initial phase (IP) and terminal phase (TP).

Jack Moyer, who conducted much of the pioneer work on reproductive behavior of hermaphroditic fishes in Japan, reported spawning behavior and mating systems of nine protogynous labrids from Miyake-jima Island, Izu Islands (Moyer 1991). Fukui et al. (1991) studied a temperate wrasse *Halichoeres poecilopterus* in Seto Inland Sea, western Japan. The population showed higher density, higher percentage of primary males (about 40% in both IP and TP fish) and smaller size at sex change (or change from IP to TP) than the conspecific population of northern Kyushu studied by Nakazono (1979). Fukui et al. (1991) observed only group spawning by a female and IP and TP males, suggesting that TP males could not monopolize females in such a high-density population. They also suggested that the fishing pressure on large individuals may have reduced the size at sex change to a smaller size in fishes in their study area.

Halichoeres poecilopterus was also studied by Kobayashi & Suzuki (1994) in Suruga Bay, Central Japan. The percentage of primary males and the size at sex change were similar to those in the Seto Inland Sea. Immature IP fish had either ovaries, intersexual gonads with many oocytes and seminal lobules, or primary testes with markedly developed seminal lobules and a few generating oocytes. This suggests that primary testes may have also experienced ovarian features in their early stages, although primary males have been distinguished from 'prematurational secondary males' whose gonads are derived from immature ovaries through prematurational sex change (Robertson & Warner 1978). Further examination seems to be needed for the distinction of primary males and prematurational secondary males to confirm whether they differ genetically or represent a conditional style.

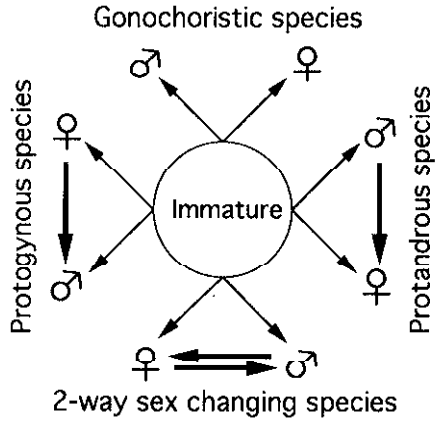

Figure 1. Possible sexual pathways of individual life histories within a species of each category. Arrows indicate sexual maturation (thin line) or functional sex change (thick line).

A congener *H. marginatus* was studied at Kuchierabu-jima Island, south of Kyushu, by Shibuno et al. (1993a). This species is also diandric, but primary males made up only 5% of the population. TP males establish territories in the late afternoon, to which females migrate to spawn either by pair-mating with the TP males (sometimes accompanied by sneaking or streaking IP/TP males) or by group mating with IP and TP males. The spawning sites that a female had used were subsequently used for its mating after it had changed sex (Shibuno et al. 1993b). We (K. Karino, T. Kuwamura, Y. Nakashima, and A. Nema) have also been studying sex change and sexual selection of another diandric labrid *H. melanurus* at Sesoko Island, Okinawa (unpublished).

In *Cirrhilabrus temmincki* from Suruga Bay, no primary (and IP) males were found, all TP fish being secondary males (Kobayashi & Suzuki 1990). The same was found in *Choerodon schoenleinii* from Okinawa Island (Ebisawa et al. 1995). Its congener *C. azurio* in northern Kyushu was also suggested to be monandric (Nakazono & Kusen 1991), as was a temperate parrotfish *Calotomus japonicus* from Makurazaki, southern Kyushu (Kusen & Nakazono 1991). In the latter two species, however, the number of specimens used for the gonad examination was so small (15–17) that it seems difficult to consider them monandric, because the proportion of primary males may sometimes be very small (< 5%; e.g., Shibuno et al. 1993a).

Prematurational sex change may occur even in monandric species (Robertson & Warner 1978, Kuwamura 1981, Tanaka et al. 1990). Alternative mating and life-history style of the monandric wrasse *Labroides dimidiatus* have been studied in Uwa Sea, western Shikoku, by Y. Sakai (1995, p. 77, in 24th International Ethological Conference Abstracts), who has also studied conditions for early sex change in the angelfish *Centropyge ferrugatus* at Sesoko Island, Okinawa (Sakai 1992, 1995).

Studies have also been done for protogynous fishes of other families besides Labridae. The sandiver *Trichonotus filamentosus* in Hakata Bay, northern Kyushu, was found to be protogynous with all males having secondary testes (Kusen et al. 1991). This is the first evidence of protogyny from the family Trichonotidae.

The sandperch *Parapercis snyderi* (Parapercidae) has been intensively studied in recent years. In Suruga Bay it is monandric and, different from the labrid secondary males, the ovarian cavity clearly remains only in the early stage and later disappears in the secondary testis (Kobayashi et al. 1993a). The secondary males maintained territories including a harem of 3–10 females, and not only pair-spawning but also streaking by other males were observed. When females were kept together in a tank, not only the largest fish changed sex to male but also the remaining came to have intersexual gonads. However, when females were kept singly no gonadal change occurred (Kobayashi et al. 1993b). Mating system and sex change of *P. snyderi* have been studied also in other localities: Uwa Sea, western Shikoku [N. Onishi & Y. Yanagisawa 1992, p. 47 in Advance Abstracts for 25th Annual Meeting of the Ichthyological Society of Japan (in Japanese; hereafter abbreviated to AMIJ); N. Onishi 1995, p. 53 in 28th AMIJ], and two localities in Kagoshima, southern Kyushu (M. Kobayakawa, K. Baba and A. Shinomiya 1992, p. 23 in 25th AMIJ; K. Baba, M. Kobayakawa and A. Shinomiya 1995, p. 52 in 28th AMIJ). Among these localities, differences have been found in longevity and size at sex change.

Protandrous fishes

Detailed studies on protandry are still limited to those on the anemonefishes. Females are larger than males in monogamous pairs, and it was believed that a male would always change sex after death of his mate (e.g., Fricke & Fricke 1977). However, alternative life-history styles have been revealed by intensive field work both in temperate waters (Uwa Sea, western Shikoku) and on the subtropical coral reefs of southern Japan (Sesoko Island, Okinawa).

In *Amphiprion clarkii* living in the temperate water where host sea anemones occur in high density, Ochi (1989a) found that after mate loss, males often moved between hosts to acquire new mates, usually without sex change. He suggested that sex change is a style rather like the BBS (best of a bad situation) in this habitat, because it may take a longer time to change sex than to acquire a new heterosexual mate by movement. This was confirmed by the experimental removal of females from breeding pairs (Hattori & Yanagisawa 1991a).

In this high host-density habitat (Uwa Sea), breeding pairs establish almost contiguous territories, and nonbreeders shelter in relatively small hosts in the fringes of the pairs' territories. The nonbreeders may mature into either sex according to their social status, or body size relative to their new mates (Ochi 1989b, Hattori & Yanagisawa 1991b). The examination of gonad histology in relation to body color change revealed three sexual pathways in life histories of the anemonefish: (1) from immature male to functional male, (2) and then to functional female by sex change, or (3) from immature male to immature female and then to functional female (prematurational sex change or femininity differentiation in nonbreeder state; Hattori & Yanagisawa 1991b; see Figure 1).

Even in coral reefs where the host sea anemones occur in much lower densities (Sesoko Island), *A. clarkii*, especially nonbreeders, often move between hosts to acquire new mates and breeding sites, and the same three life-history pathways were detected (Hattori 1994). Hattori & Yamamura (1995) developed an ESS model for the co-existence of immature males and females under frequency-dependent selection, suggesting that the alternative life-history pathways in *A. clarkii* have evolved as style of breeding site acquisition.

Amphiprion frenatus living in the same coral

reefs with lower host-densities sometimes moves between hosts (Hattori 1991, Hirose 1995). By contrast, *A. perideraion*, a smaller species inhabiting the same host species as *A. clarkii*, seldom moves (Hattori 1995, Hirose 1995). Since dominant females strongly suppress growth of their mates in *A. frenatus*, the size difference between the sexes in pairs of *A. frenatus* is much larger than in *A. clarkii*, although females sizes are similar between the two species (Hattori 1991, 1994). It is suggested that the difference in mobility among the three species of anemonefishes may affect the patterns of mate acquisition and the size composition of breeding groups (Hirose 1995).

These studies on monogamous anemonefishes indicate that if movement between hosts is strictly limited, protandrous life-history may be optimal as predicted by the size-advantage model, but the ability of movement may determine the frequencies of sex change and other life-history styles. In addition, social systems and gonad histology of *A. ocellaris*, which is believed to be most strictly host-attached, have been studied at Iriomote Island, Okinawa (Y. Inagaki 1992, p. 3 in 25th AMIJ; A. Yamashita, K. Koike and A. Hattori 1993, p. 35 in 26th AMIJ).

Two-way sex change

The occurrence of reverse-directional sex change was first, but only briefly, reported from a protogynous grouper *Epinephelus akaara*. Males larger than 30 cm TL were observed to change sex in captivity (Tanaka et al. 1990). After about 30 males were kept together in a tank for nine months, a few of them, larger than the average size, were found to have mature oocytes in their gonads (K. Nogami & H. Tanaka personal communication).

Similarly, although protogyny is common in polygynous angelfishes (Pomacanthidae; Moyer 1990), the reverse sex change was suggested in *Apolemichthys trimaculatus*. When two functional males were kept in an aquarium, the smaller came to have an intermediate gonad at the end of the experiment (Hioki & Suzuki 1995). Later, spawning after male-to-female sex change was observed in 2-male experiments of *Centropyge flavissimus*, *C. fisheri*, and *C. acanthops* (Hioki & Suzuki 1996).

In the hawkfish *Cirrhitichthys aureus* (Cirrhitidae), spawning was observed after female-to-male sex change in a 2-female experiment, and also after male-to-female sex change in a 2-male experiment in a tank (Kobayashi & Suzuki 1992). Specimens collected from Suruga Bay had either immature ovaries, secondary testes, or in most cases ambisexual gonads. The smaller ambisexual fish showed active oogenetic processes in the major ovarian zones, while the larger ambisexual ones had slender androgenic gonads with active spermatogenesis in various testicular zones. Similar ambisexual gonads were also found in other hawkfishes, *Cyprinocirrhites polyactis* from Suruga Bay and *Cirrhitichthys aprinus*, *C. falco* and *Cirrhitopus hubbardi* from Hachijo-jima Island, Izu Islands. Kobayashi & Suzuki (1992) regarded these bisexual gonadal aspects as an intermediate between sequential (protogynous) and simultaneous hermaphroditism. However, simultaneously functional hermaphrodites have not been reported from the hawkfishes, and it is uncertain whether the gonad structure represents an evolutionarily intermediate interval. The ambisexual gonads may be maintained because of the advantage in changing sex in either direction.

Two way sex change has been also confirmed by aquarium experiments in a small goby *Trimma okinawae*, whose males have ovarian tissue within a functional testis (Sunobe & Nakazono 1993). In Kagoshima, southern Kyushu, its mating system was resource defense polygyny, with paternal egg care. The largest female of a social unit changed sex following the removal of the dominant male, indicating socially controlled protogyny (Sunobe & Nakazono 1990). In aquarium experiments, however, when males were kept together, the smaller changed back to female and spawned within 4–12 days (Sunobe & Nakazono 1993). Also, in a congener *T. grammistes*, the larger changed sex in a 2-female experiment and the smaller in a 2-male experiment (Y. Shiobara, G. Nishi, N. Okutomi, M. Takahashi and H. Takeoka 1992, p. 24 in 25th AMIJ).

Evidence for 2-way sex change in natural populations was obtained for the first time in the coral goby *Paragobiodon echinocephalus* at Sesoko Island, Okinawa (Kuwamura et al. 1994). In this monogamous fish inhabiting *Stylophora* corals, sex change occurs according to the relative size of new part-

ners; usually the larger becomes male and the smaller female. This was confirmed by monitoring marked individuals in the field (Kuwamura et al. 1994), and by a mate removal experiment in the field as well as an aquarium experiment with 2 consexuals (Nakashima et al. 1995). Both sexes of gobies showed equal ability to change sex both ways in the experiments (within 3–4 weeks at the shortest). In the natural population, however, maturation as female and subsequent female-to-male sex change occurred much more frequently than the other way. In any event, the sexual life-history pathways of the gobies were more flexible than protandrous or protogynous species (Figure 1).

Two-way sex change has been confirmed also in other monogamous gobies (*Gobiodon micropus, G. oculolineatus, G. quinquestrigatus* and *G. rivulatus rivulatus*), inhabiting *Acropora* corals, by the field and aquarium experiments at Sesoko Island (Nakashima et al. 1996).

Thus during the last few years, sex change in either direction, or in the reverse direction to the former sex, has been revealed by Japanese researchers among several groups of reef fishes. However, in most cases at present it has been confirmed only in captive conditions.

Social control of 2-way sex change

Social control of sex change is well known among reef fishes. The dominant fish becomes male in polygynous mating groups, while the dominant becomes female in monogamous anemonefishes (Robertson 1972, Fricke & Fricke 1977, Warner 1984, Nakazono & Kuwamura 1987, Ross 1990). The size-advantage model predicts that the dominant should do so to increase its fitness. It is also evident that the 2-way sex change is socially controlled at least in the gobies *Trimma, Paragobiodon,* and *Gobiodon* (Sunobe & Nakazono 1993, Kuwamura et al. 1994, Nakashima et al. 1995, 1996). In these species, the dominant fish becomes male, although the evolutionary factors differ between *Trimma* and the others.

Trimma has polygynous mating systems, and so the dominant fish takes advantages of becoming male as in many other protogynous fishes. By contrast, mating occurs monogamously in *Paragobiodon* and *Gobiodon*, so the dominant should be a female, if the size-fecundity advantage exists as in the anemonefishes. However, no size-fecundity advantage was detected in *Paragobiodon* (Kuwamura et al. 1993, 1994). Breeding pairs are formed by a male and a female of similar size, and reproductive success is positively correlated with body size of the male and female almost equally. In other words, females' fecundity and males' ability of egg care may change with body size in similar fashion. In such size-assortative mating, which was also the case in *Gobiodon* (Nakashima et al. 1996), gonochorism should be favored if other factors than the size-fecundity advantage are not acting (Warner 1984). The major factor was, however, the growth-rate advantage in *Paragobiodon* and at least two species of *Gobiodon* (Kuwamura et al. 1994, Nakashima et al. 1996). That is, because females grow faster than their mates after new pair formation until the start of breeding, and because the smaller sex limits the pair's reproductive success, the smaller individual should become female. Thus, the larger, dominant fish in new pairs should be male in these monogamous gobies.

If the dominant fish becomes a male, protogyny will be favored, as observed in the natural population of *Trimma* (Sunobe & Nakazono 1990) and *Paragobiodon* (Kuwamura et al. 1994). This is because when small, a fish may usually reproduce as female with a larger mate, and when it becomes large and dominant, it had better change sex to male to mate with smaller fish. Sex change in the reverse direction, i.e., male to female, will occur only when the social status of the dominant fish (male) changes by inter-group movement of itself or its new mate (Figure 2). This was confirmed by field observations and experiments in *Paragobiodon* (Kuwamura et al. 1994, Nakashima et al. 1995) and *Gobiodon* (Nakashima et al. 1996). Inter-coral movement often occurred to acquire new mates in these gobies, and unmated fish preferred pairing with nearby consexuals over searching for heterosexuals from farther distances.

Change of social status of the dominant fish has not been observed in the field in *Trimma*. Sunobe & Nakazono (1993) suggested that if the largest fe-

male, whose size was sometimes similar to the dominant male, grows faster than the male, change of their status within a social group would occur. In *Paragobiodon*, however, even if social status changed within a pair due to the faster growth in females, simultaneous sex change in both mates was never observed, probably because the cost of sex change may exceed the growth-rate advantage (Kuwamura et al. 1994).

It is noteworthy here that the subordinate fish changes sex in the 'returning' sex change: in 2 male pairs the smaller changes sex in the gobies (Figure 2). The dominant fish will increase its reproductive success by forcing the subordinate to change sex. This is quite different from the suppression theory of social control (i.e., the dominant fish changes sex and socially suppresses sex change of the subordinate) in the former one-way sex change theory (e.g., Ross 1990). Sex change of subordinate males as BBS was reported in a shrimp *Anthanas kominatoensis*, in which secondary sex change (female-to-male) when becoming dominant was also suggested but not confirmed (Nakashima 1987). In case of the polygynous *Trimma*, the subordinate male may change sex as BBS when it has lost mates or has been taken over by the larger male; the same may occur in the angelfishes. By contrast, in the monogamous *Paragobiodon* and *Gobiodon*, the subordinate male would increase its reproductive success by pairing with a larger male and changing sex to grow faster as a female.

The case of the hawkfish *Cirrhitichthys aureus* appears to be contradictory. The larger fish (90.0 mm vs. 74.5 mm SL) became male in a 2-female experiment, while the larger (93.6 mm vs. 89.2 mm) became female in a 2-male experiment (Kobayashi & Suzuki 1992). However, it seems to be the rule that the larger becomes male, because the larger ambisexual specimens had male-biased functions (Kobayashi & Suzuki 1992) and also because males were larger in monogamous pairs in the field (Yogo 1987). Further field observations are needed to confirm whether this species is strictly monogamous or polygynous with facultative monogamy. It is also unknown at present why the relatively large males of the protogynous grouper *Epinephelus akaara* developed oocytes in multi-male

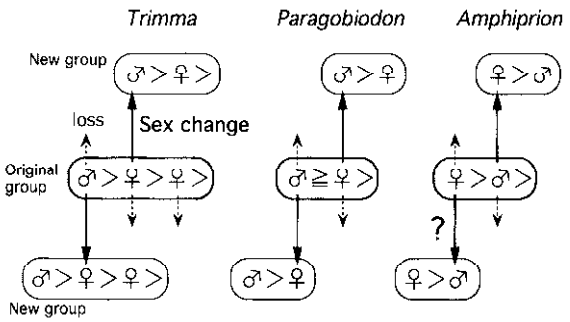

Figure 2. Social dominance and control of 2-way sex change in polygynous (*Trimma*) and monogamous (*Paragobiodon* and *Amphiprion*) groups. Sex change in different directions may occur after loss (shown by dashed arrows) of the dominant mate (top) or after loss of the subordinate mate(s) (bottom). In newly formed pairs of *Paragobiodon* males are initially larger than their mates, but later become the same size due to the growth-rate advantage of females.

experiments (Tanaka et al. 1990, K. Nogami & H. Tanaka personal communication). It would be the smaller subordinate males that should change sex, if there is a social control of functional sex.

In addition to the fishes of the Japanese waters, another two gobies, *Lythrypnus dalli* and *L. zebra*, inhabiting the rocky shore of southern California and Mexico, have been reported to exhibit 2-way sex change in laboratory experiments (St. Mary 1993, 1994, 1996). These gobies have only vitellogenic eggs, only tailed sperm, or both active gametes of various proportions in the gonad. The behavioral (functional) sex can be altered within a few weeks by reallocation of the gonad. Although St. Mary called these species as simultaneous hermaphrodites based on gonadal sex (also see Fishelson 1989), it sounds confusing to call such sex-changing (i.e., sequential) hermaphrodites as 'simultaneous' even if they often have bisexual gonads. The gonad structure of *Lythrypnus*, separated into ovarian and testicular parts, is similar to *Trimma*, but different from *Paragobiodon* and *Gobiodon* (Fishelson 1989, Cole 1990, St. Mary 1993, Sonobe & Nakazono 1993). As in *Trimma*, the mating systems of *Lythrypnus* are polygynous with paternal egg care (St. Mary 1994, 1996). Egg-guarding males tend to be larger than females, but with a large overlap within a stock. When consexuals were kept together, larger fish tended to become males, although no

such tendency was found in female-group experiment of *L. zebra* (St. Mary 1994, 1996). Because they occur in high densities, social units of *Lythrypnus* may not be so fixed as they are in *Trimma*. Further investigations are needed in the field to know whether, or how, social conditions such as change of social status induce sex change in individuals of *Lythrypnus*.

Nakashima et al. (1995) suggested that change of social status by inter-group movement may also occur, even if only infrequently, in other hermaphroditic fishes living in social groups, and therefore sex change in the reverse direction, or 2-way sex change, will be detected in many of them. In the case of the protogynous sandperch *Parapercis snyderi*, however, no sex change was observed within 37 days when five males were kept in an aquarium (Kobayashi et al. 1993b). The authors suggested that the gonad structure might constrain the reverse sex change; in the secondary testis the ovarian cavity gradually degenerates and disappears in the sandperch. However, it is also likely that the conditions in the aquarium were not suitable for inducing sex change. Four of five males died after 33–37 days, although no aggressive interactions were observed, and all fish were reduced in size (Kobayashi et al. 1993b).

Reverse sex change has been reported only from basically protogynous fishes (e.g., Gobiidae, Pomacanthidae, Cirrhitidae, Epinephelinae). Is this simply because protogynous species are predominant over protandrous ones among reef fishes (Yogo 1987), or do protandrous species never exhibit the reverse sex change due to some unknown constraints? In the anemonefish *Amphiprion bicinctus*, Fricke & Fricke (1977) reported that forcible pairing of functional females resulted in death or severe injury to the subdominants and that the reversal of sex change from female to male could not be induced.

During our preliminary experiments on *A. clarkii* at Sesoko Island (Kuwamura, Nakashima & Karino unpublished), the smaller of two females kept in a tank changed the shape of its urogenital papilla into one that was intermediate between the sexes within six months. In the field experiment during more than 18 months, however, two unmated females in 15 m distance never moved to form a 2-female pair; they accepted juveniles but never resumed breeding.

In the female-dominance system of the monogamous anemonefishes, the reproductive success of a pair depends on the female body size, which affects fecundity, but not on male size (e.g., Fricke & Fricke 1977, Warner 1984). This is because males of the anemonefishes can take care of a clutch deposited by much larger mates, which is different from *Paragobiodon* males. Therefore, if a female anemone fish could acquire a new mate larger than herself, sex change to male would be more advantageous than remaining a female (Figure 2). For the larger female, however, the size of her mate would not affect her own reproductive success.

In such situations as the anemonefish, a female should accept the smaller female and force it to change sex, but only when the duration needed for the sex change is expected to be shorter than that for maturation of recruited juveniles or their immigration. Although it may take a few years for juveniles to mature, late juveniles can be expected to immigrate and mature within a few months in *A. clarkii* at Sesoko Island (Hattori 1994, Hirose 1995). If sex change from female to male takes more than a few months (cf., about two months in male-to-female change; Hattori 1994), the larger female should wait for immigration of late juveniles. It seems that the two unmated females of *A. clarkii* in our field experiment adopted this style, but unfortunately no immigration of late juveniles occurred for more than a year. Further experiments are needed to study the possibility of reverse sex change in the anemonefishes, although it is suggested that mobility of adults and late juveniles may affect its evolution.

Closing comments

Recent studies on sex change among fishes have revealed various life-history pathways in hermaphroditic species (Figure 1). The discovery of 2-way sex change suggests that the difference between protandrous and protogynous species may be much smaller than has been believed from histological

studies. If there is any social condition that favors evolution of sex change in one direction, the reverse sex change will also be likely to evolve, so far as the social status of the dominant fish can change (Figure 2). This can be explained by the size-advantage model (sensu Warner 1988a, Kuwamura et al. 1994, Nakashima et al. 1995) incorporated with the social-control system. Further studies should focus on finding evolutionary constraints preventing hermaphroditic species from conducting the reverse sex change. The gonad structure, however, should not be regarded as a constraint, but should be treated as an expression of reproductive styles.

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