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[SHORT COMMUNICATION]

Female-female Spawning and Sex Change in a Haremic Coral-reef Fish, *Labroides dimidiatus*

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ABSTRACT—In the polygynous coral-reef fish, *Labroides dimidiatus*, the largest female may complete sex change within a few weeks if the male disappears. We conducted male removal experiments just prior to spawning time. The largest female possessing ovulated eggs spawned in the male role with smaller females, 1–2 hr after the male removal, suggesting that ovulation could not prevent male sexual behavior. During the female-female spawning eggs were actually released, but of course unfertilized. The largest female subsequently spawned in the female role when the male was immediately returned. If the male was never returned, such spawning behavior was repeated almost every day until the largest fish was able to release sperm. Smaller females will participate in such fruitless spawning according to their preference for larger mates. The largest females should perform male sexual behavior to secure future mates, even before completion of gonadal sex change.

INTRODUCTION

Female-female sexual behavior is known from various animals (Bagemihl, 1999), and is supposed to have reproductive or social functions such as cooperative brooding and social appeasement in some birds and mammals (Kovacs and Ryder, 1983; Dagg, 1984; Vasey, 1995). Female-female spawning behavior has also been reported from some gonochoristic fish (Greenberg, 1961), unisexual fish (Schlupp *et al*., 1992), and protogynous fish (Robertson, 1974; Hoffman *et al*., 1985; Warner and Swearer, 1991), but its adaptive function is unknown among them.

Social control of sex change, or sex determination by social status, is well known among various reef fishes (Fishelson, 1970; Fricke and Fricke, 1977; Warner, 1988; Ross, 1990; Nakashima *et al*., 1995; Kuwamura and Nakashima, 1998). In the cleaner wrasse *Labroides dimidiatus*, for example, when males disappear the largest female of their harem will develop functional testes a few weeks later (Robertson, 1972). The largest female may begin male courtship behavior, and even perform an upward 'spawning' rush with a smaller female within a few days after the male loss (Robertson, 1974). Similar female-female spawning behavior has been observed when males are removed in some other protogynous wrasses such as *Bodianus rufus* (Hoffman *et al*., 1985) and *Thalassoma bifasciatum* (Warner and Swearer, 1991; Godwin *et al*., 1996). It has not been explained, however, why the largest female and the smaller female should perform such 'spawning' behavior even before the former completes gonadal sex change.

Here we report how soon the largest female would begin to perform complete male spawning behavior after the male loss, and how often such 'spawning' behavior would be repeated until the completion of gonadal sex change in *L. dimidiatus*, and discuss adaptive functions of such 'spawning' behavior.

MATERIALS AND METHODS

Study species

Males of *Labroides dimidiatus* are territorial and always larger than the females of their harem (Robertson, 1972; Kuwamura, 1984). Robertson (1972, 1974) conducted male removal experiment several

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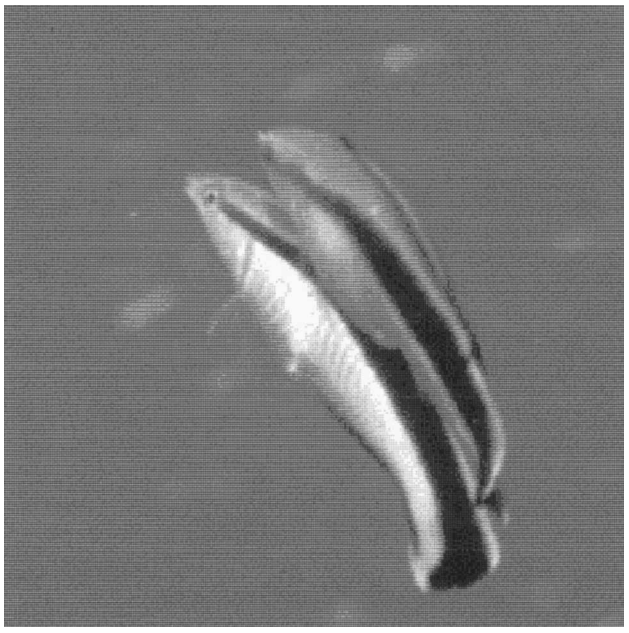

Fig. 1. Female-female spawning behavior of *Labroides dimidiatus* (photographed by TK). The largest female in the male role (above) is riding on the back of the smaller female, while the pair rushes upward 0.5–1.0 m to release gametes. See the swollen abdomen in both females.

times, and found that the largest female may begin to change sexual behavior within a day, and sometimes even conduct an upward 'spawning' rush with the largest female riding on the back of the smaller one (i.e., taking the male position; Fig. 1). The upward rush by two females was called 'pseudospawning' because it was believed that no eggs were released (Robertson 1974; but see Results).

Study location

Underwater experiments and observations were made on the coral reefs of Sesoko Island (26° 39'N; 127° 57'E), Okinawa, southern Japan, in 1998 and 1999. In the study area, the density of *L. dimidiatus* was relatively low, and harems were not adjacent each other.

Experimental procedures

Male removal-and-return experiments were conducted two times (5–11 days intervals) for each of four isolated harems, which were composed of 2–4 females (the largest: 67–78 mm in total length). The harem male (70–85 mm) was removed about 1 hr prior to the expected spawning time just after high tide or late afternoon (our unpublished data). Female *L. dimidiatus* usually spawn once per day (Robertson, 1974; Kuwamura, 1981). Removed males were kept in a net bag on the sandy bottom, concealed from the females.

We observed the behavior of the largest female, recording (1) the time when it initiated the male courtship display PQ (passing and quivering, Youngbluth, 1968, or flutter-run, Robertson, 1974) toward the smaller female, and (2) the time when the latter began the female courtship display Si (sigmoid posture, Youngbluth, 1968, or body-sigmoid, Robertson, 1974; Robertson and Hoffmann, 1977) toward the largest female, and (3) the time when the two females performed the upward 'spawning' rush.

When female-female (F-F) spawning occurred, we recorded whether a gamete cloud was visible and whether the abdomen of each female had shrunk. At the same time, we swept the water at the apex of the spawning rush, using a hand-held plankton net of 0.4 mm mesh, 47 cm mouth diameter, and a plastic bottle at the end (Sakai, 1996). Eggs of *L. dimidiatus* are pelagic and about 0.7 mm in diameter (Kuwamura, 1981). The water in the bottle was later (2–4 hr) examined under a microscope to see whether eggs were present and fertilized (i.e., developed).

We returned removed males 2–10 min after the F-F spawning, and again observed the behavior of the largest female. When the largest female mated with the male (M-F spawning), we tried to collect eggs by the same methods as above.

To examine whether the largest female would also participate in F-F spawning when she did not possess ovulated eggs, we conducted supplementary male-removal experiments just after the largest female, but not smaller ones, spawned with the male (M-F spawning). The experiments were conducted once each for two of the four harems.

Finally, we removed the male from another harem of two females, and never returned. We observed behavior of the largest female and tried to collect spawned eggs by the same methods as above, every day or every other day, until we could collect fertilized eggs, i.e., until the completion of gonadal sex change of the largest fish.

RESULTS

In every case of the male removal-and-return experiments (n=8; Fig. 2), the largest female of the harem began the male courtship display PQ (passing and quivering) about 1 hr after the male removal (median=59 min, range = 42–85). The smaller females never displayed PQ. They often approached and followed the largest female before the latter began to display PQ (n =7 out of eight experiments). Some small females initiated the female courtship display Si (sigmoid posture) towards the largest female even before the latter began PQ (n = 5 out of 8). F-F spawning occurred in all experiments, 67–144 min (media n=109, n=8) following male removal, with the largest female always in the male position (Fig. 1). In seven cases,

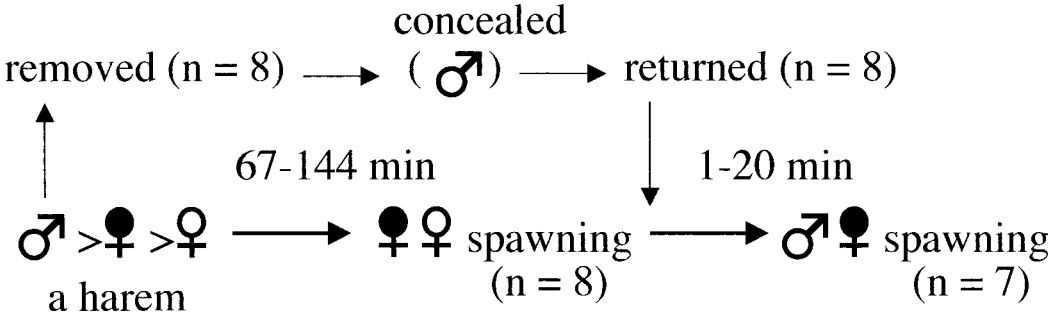

Fig. 2. Schematic for male removal and return experiments. The largest female of a harem is indicated by a solid symbol.

Table 1. Shrinking of abdomen in the largest and smaller females in the male remove-and-return experiments

Harem &	F-F spawning		M-F spawning
expt. #	Smaller	Largest	Largest female
#1–1	+	+	–
#1–2	+	+	+
#2–1	+	+	–
#2–2	+	+	no spawning
#3–1	+	–	+
#3–2	–	+	–
#4–1	+	–	–
#4–2	–	+	–

+ shrunk; – no obvious change

hundreds of unfertilized eggs were collected. In the remaining case a gamete cloud was visible, but we failed to collect eggs due to a strong current. Shrinkage of the abdomen was apparent in both females (n=4 spawnings), or at least in the smaller one (n=2), or at least in the larger one (n=2; Table 1). This suggests that both participants may release eggs.

When we returned males to their respective harems 2–10 min after the F-F spawning, there was no obvious agonistic interaction between the male and the largest female, and they spawned within 1–20 min (median=4) in seven of eight experiments (Fig. 2). The largest female always took the female position in these cases. Although no gamete cloud was visible nor were eggs collected, the abdomen of the largest female became smaller in two cases (Table 1), in which we may have failed to catch any released eggs.

In the supplementary male-removal experiments just after the largest female spawned with the male (n=2), the abdomen of the largest female was observed shrank in size, and fertilized eggs were collected after the M-F spawning in both cases. F-F spawning occurred 16 and 53 min after male removal with the largest female taking the male position. In both cases, abdominal shrinkage was apparent only in the smaller female, and unfertilized eggs were collected. Thus, the largest female participated in F-F spawning just after true (M-F) spawning, i.e., even if she had no ovulated eggs.

When the male was removed from a harem of two females and never returned, fertilized eggs were collected 17 days after. During that period the largest fish performed spawning rush with the smaller one on 9 of 11 observation days, on 8 of which unfertilized eggs released by the smaller female were collected. That is, the largest fish had repeated mating behavior in the male role almost every day before it could actually release sperm, and the smaller female continued to produce new eggs during the period.

DISCUSSION

The present study revealed that eggs were released in the female-female spawning of *Labroides dimidiatus*, suggesting that the largest females performed complete male sexual behavior to induce the smaller to spawn. In another protogynous wrasse *Thalassoma bifasciatum*, after removal of all males from a patch reef, behavioral sex change occurred in the largest females whose ovaries had been previously removed by surgical manipulation (Godwin *et al*., 1996). The authors of that study concluded that testes are not necessary for the performance of male sexual behavior (Godwin *et al*., 1996). On the other hand, it is known that prostaglandins produced just after ovulation may induce female spawning behavior in some fish (Stacey, 1987). The present study, however, confirmed that even if ovulated eggs are present, they do not prevent the owners from performing complete male spawning behavior. It is interesting that the largest females often released their own eggs while playing the male role. Moreover, the largest females could perform spawning in the female role again when the male was returned soon. That is, behavioral sex is changeable according to social status, independent of gonad condition.

We might wonder why the smaller females of *L. dimidiatus* engage in such fruitless spawning rush by releasing eggs that will not be fertilized. Are they deceived by the male-like behavior of the largest female? This question seems to be related to the criteria for female mate choice, which have been recently studied in various animals (Andersson, 1994; Karino, 1996). In *L. dimidiatus* larger body size is favored in male-male competition for acquiring mates (Robertson, 1972; Kuwamura, 1984). In the present experiments, smaller females often approached, followed and displayed the female courtship behavior (sigmoid posture) toward the largest female even before the latter began male courtship, suggesting that females may select their mate according to body size. That is, when the male disappears from a harem, females should choose the largest fish among the remaining members as their mate. Such behavior is exactly in accordance with their natural criterion for mate choice though the selected mate is of the same sex.

Then, why should the largest female begin to manifest male sexual behavior so soon after male disappearance? Males of *L. dimidiatus* establish territories to defend their mates, but smaller females may sometimes move into territories of other males (Robertson, 1974; Kuwamura, 1981, 1984; Y. Sakai, unpublished data). Although females may choose the largest fish as their mate, if the latter does not perform male spawning behavior, smaller females cannot spawn, and may leave the harem to seek another mate. Therefore, the largest female will adopt male sexual behavior as soon as possible, in order to retain the smaller females as future mates. Moreover, while repeating spawning with egg release, the smaller females will continue to develop the next clutches until the largest fish is able to release sperm. Thus, it seems adaptive for the largest fish to perform male spawning behavior even before completion of gonadal sex change. This will be the case also in other protogynous fishes.

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