Mating Strategies and Reproductive Behavior of Ostraciid Fishes at Miyake-jima, Japan

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Abstract Three species of trunkfishes (Ostraciidae) were studied in the waters of Miyake-jima, Izu Islands, Japan. Intensive studies of Lactoria fornasini and less detailed, comparative studies of Lactoria diaphanus and Ostracion cubicus revealed that all three species are haremic and seemingly gonochoristic, although only L. fornasini was examined histologically. Lactoria diaphanus and Ostracion cubicus spawn near the surface in the late afternoon, but Lactoria fornasini spawns 10~20 min after sunset near the substrate. It is hypothesized that predator pressures account for differences between species, and in the female-biased sex ratios of all three species. The role of ostracitoxin, a lethal stress secretion in the mucus of ostraciid fishes, is discussed in relation to predation.

In 1966, Breder and Rosen noted that except for the existence of pelagic eggs in the Atlantic species, Lactophrys quadricornis (Linnaeus), little was known concerning reproduction of trunkfishes (Ostraciidae). Ehrlich's (1975) review of reef fishes stressed the paucity of information on the Tetraodontiformes in general. Mito (1962, 1966), Watson and Leis (1974), Leis and Miller (1976), and Leis (1978) have shown that, like the Atlantic species, all reported Pacific ostraciids spawn pelagic eggs, and that some seem to undergo pelagic juvenile existences (Fujita and Hattori, 1977; Leis, personal communication).

To attempt to add to the growing knowledge of reproductive behavior and mating strategies of reef fishes, an intensive study of the cowfish *Lactoria fornasini* (Bianconi) was undertaken during the summer of 1978 to the early spring of 1979 in the waters of Miyake-jima (34°05′N, 139°30′E), with comparative studies of the related ostraciids, *Lactoria diaphanus* (Bloch et Schneider) and *Ostracion cubicus* Linnaeus. The preliminary results of this continuing research are reported below.

Materials and methods

All observations, amounting to more than 120 hours, were made using SCUBA. Notes were recorded on plastic tablets and trans-

ferred to permanent files immediately upon return to the laboratory. Depths and temperatures were recorded using commercial gauges. Sunset times and tidal fluctuations were taken from official government publications. All underwater photographs were taken by the author using a Nikonos III camera with a 35 mm lense. Specimens were collected using screen nets and multi-pronged spears. Gonads were immediately preserved in Bouin's solution and were later prepared in $7\,\mu{\rm m}$ paraffin sections. Sexes were determined after staining with haematoxylin and eosin.

Results

Lactoria fornasini

This cowfish is the smallest ostraciid appearing in Japanese waters, reaching a maximum size of about 150 mm in total length (TL). Like other members of the genus, it is covered with bony plates, fused into a protective armor. Sharp spines project from the body dorsally, anteriorly, and posteriorly. The mucus is said to be slightly toxic (Thomson, 1964, 1968).

Habitat. At Miyake-jima, Lactoria fornasini is normally associated with an algae-covered boulder substrate or in volcanic rubble in shallow waters. It is one of the characteristic members of the island's ichthyofauna, but frequently goes unnoticed, due partly to

secretive behavior and partly to normally cryptic coloration. Of six harems under observation, four were situated in water from 4 to 6 m in depth and the other two were in less than 15 m (Table 1). Single individuals, probably representing harems, have been found to depths of 30 m. This species rarely, if ever, is found in a coral habitat at Miyakejima.

Population structure, territoriality, and agonistic behavior. At Miyake-jima, L. fornasini occurs in harems consisting of a single sexually functional male and $3\sim4$ females. Females remained with their harems throughout the study, spawning only with the male from their harem. Often, a small, sexually inactive male is present within the feeding range of the harem. This male may range in size from about 70 to 90 mm TL, and is usually smaller than the smallest functional female. The presence of large and small individuals of both sexes suggested gonochorism, which was born out by histological examination (Fig. 1).

Only the functional male defends a territory. Males from four of six harems under study defended adjacent territories, all of which were roughly 20×25 m in size. Agonistic encounters between neighboring males were only rarely observed, and consisted of highly ritualized behavior. This consisted of both fish abruptly darkening and intensifying their color patterns and rushing towards each other to a point 20~30 cm apart. At this point, one fish usually backed up 5~10 cm, while still facing his opponent, turned to one side and rushed a few meters away, where he turned to face his opponent again, perhaps repeating the process before returning to the interior of his territory.

More intensive aggression began similarly, but if neither fish backed away, the confrontation resulted in both individuals pointing their bodies upward toward the surface, displaying their broad, pale ventral surfaces towards each other. On one occasion a particularly aggressive male rammed his opponent with the horny spines that project anteriorly from above the eyes.

Functional males were consistently aggressive towards the smaller sexually inactive male

Table 1. Composition of harems of Lactoria fornasini under study at Miyake-jima, Japan, 1978.

Harem	No. of functional males	No. of non-functional, sub-adult males	No. of females
A	1	1	4
В	1	1	4
C	1	1	3
D	1	0	4
E	1	1	3
F	1	0	3

within their harem. Agonistic display was identical to that described above, and ramming was occasionally observed. The smaller male invariably appeased by assuming the upturned position, showing the ventral surface (similar to the above-mentioned threat display) and rising high into the water column, often nearly to the surface in $4\sim6$ m water. The dominant male often followed 2~3 m upward, but seemed reluctant to stay in the water column, suggesting possible fear of predation (see Discussion). Repeated encounters of this nature were seen in three harems, but in no case was the dominant male successful in driving the small male from the territory.

Females showed no noticeable territoriality but seemed to have definite home ranges which tended to exert a strong influence on the size of the male's territory, which always extended beyond the limits of his females' home ranges. Females were never observed to display agonistically toward either males or other females, and in fact showed an obvious gregariousness. Usually, $2 \sim 3$ females were seen feeding together. This gregariousness undoubtedly contributes to the male's success in locating all of his mates during the short spawning period.

During daylight hours, the dominant male displayed towards each of his females when chance meetings occurred during feeding. This display was similar to the agonistic frontal thrust used against other males, except that he did not pursue the female, who immediately took cover behind or under a boulder. L. fornasini can take on cryptic coloration, and a hiding female could and often did lose her mate.

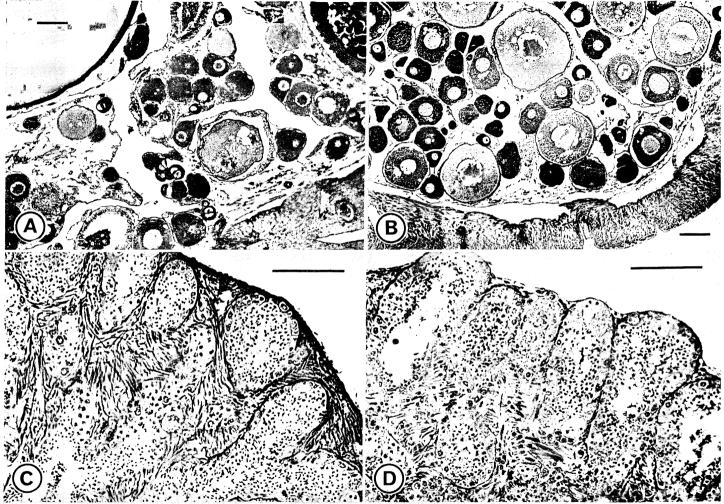


Fig. 1. Photomicrographs of the gonads of Lactoria fornasini. Scales show 100 μ . A: Ovary of female 84 mm in SL. B: Ovary of female 64 mm in SL. C: Testis of male 89 mm in SL. D: Testis of male 66 mm in SL. Photomicrographs by A. Nakazono.

Spawning behavior. Of 79 spawnings observed, only five occurred before sunset, three of them on the same dark, rainy evening in erosion-clouded waters. Sixty-three % of all spawnings occurred between 10~20 min after sunset. Earlier spawnings were usually associated with cloudy skies and/or turbid waters (Fig. 2). Spawnings were observed almost daily, and showed no relationship to tides or moon phases. The spawning season began in early April, 1979. A false spawning, with no gametes, was observed in 19°C waters on Apr. 9, and true spawnings were observed on Apr. 13 and 14, in 16°C waters. Spawning continued until early October in water temperatures ranging from 15°C to 29.5°C. Courtship and spawning were characterized by the following actions:

1) Searching: As the waters darken at sunset, the dominant male begins to move around his territory, apparently searching for females. At this time, the blue lines on his body appear distinct, compared to more drably-colored females. He swims fairly rapidly throughout his territory, at a distance of about 20 cm~1 m above the substrate. Occasionally he stops and pivots from side

to side, as if searching for his females.

- 2) Attraction: Upon sighting a female, the male rapidly rushes towards her, abruptly changing into a vividly contrasting black and yellowish-brown color pattern. He stops motionless about 60 cm from her, apparently attempting to attract her attention only by his contrasting colors. If she is unwilling to spawn, she moves behind a rock or clump of seaweed, taking on cryptic colors, and the male swims off in search of another female.
- 3) Rising and following: When a female is ready to spawn, she rises slowly up in the water column. The male follows closely behind, his snout $1\sim3\,\mathrm{cm}$ from her caudal fin, his color gradually fading (Figs. 3A, B; 4A). Often the female initiates "following behavior" by rising up even before the male He then quickly intensifies his colors, rushes foreward, and follows her up in the water column. Occasionally, $2\sim3$ females may rise up at the same time, but the male usually notices only one of them. The others return to the substrate and wait for him to complete spawning and return to search for another female.
 - 4) Turning away: At a distance of 60 cm~

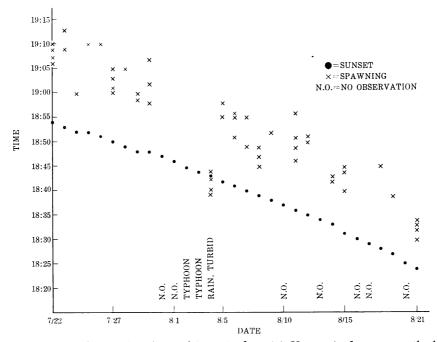


Fig. 2. Sunset and spawning times of Lactoria fornasini, Harem A, for one month, 1978.

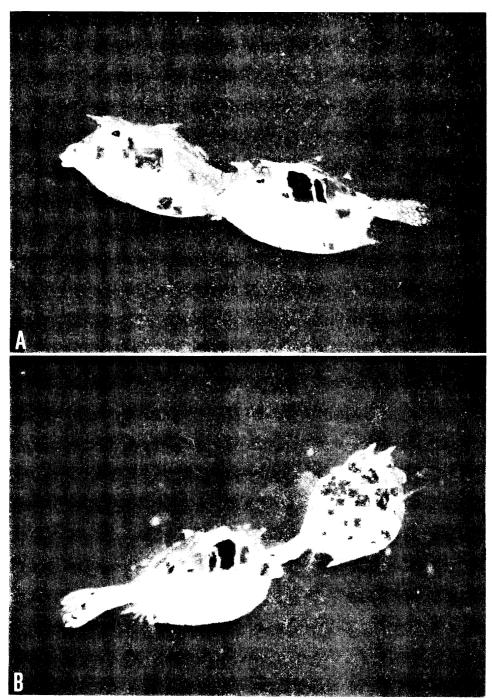


Fig. 3A. Lactoria fornasini rising and following. Note contrasting "signalling coloration" of male. 3B. Lactoria fornasini rising and following. Male's colors begin to fade.

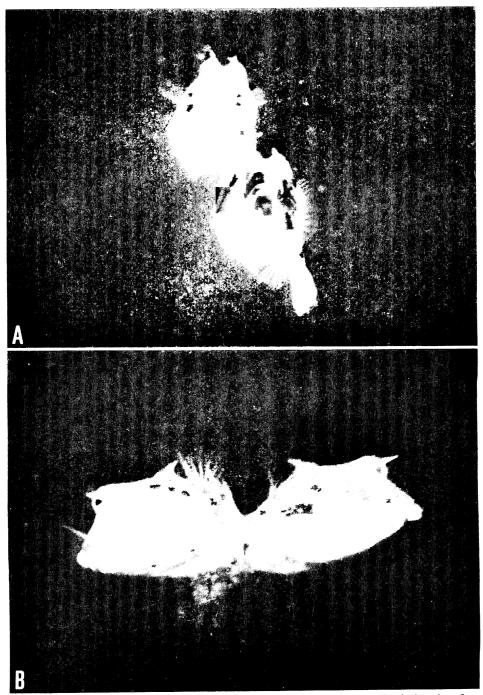


Fig. 4A. Lactoria fornasini rising and following. Male's colors only slightly darker than female's.

4B. Lactoria fornasini turning away. Sound signalling has begun and gametes are appearing.

Male and female colors are almost identical.