Two alternative female tactics in the polygynous mating system of the threadsail filefish, *Stephanolepis cirrhifer* (Monacanthidae)

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Abstract Reproductive behavior of the threadsail filefish *Stephanolepis cirrhifer* was studied at Kashiwajima, southern Shikoku, Japan. This species spawned in pairs on the sandy bottom, the eggs being scattered over an area of about 15 cm in diameter and attached to sand particles. After spawning, males departed immediately, while the females remained at the site to guard the eggs for a few minutes. Thereafter the eggs were left unguarded for three days until hatching. Females spawned only once daily, whereas males mated with multiple females in succession. The reproductive males established territories, in which 1–4 resident females defended smaller territories from each other. The harem size changed according to some ecological conditions, such as population density. Moreover, the males also mated with visiting non-resident females. Thus, the two alternative tactics of females resulted in two mating patterns, haremic polygyny and female visiting of male territories, in a single population of *S. cirrhifer*.

Key words. — Spawning; demersal eggs; territoriality; haremic polygyny; visiting females.

Filefishes (family Monacanthidae) are reported by 95 species distributed widely in temperate and tropical seas (Nelson, 1994). Studies of their reproductive ecology based upon field observations have been limited to several species, but are sufficient to suggest that a high degree of variability within the family exists. *Oxymonacanthus longirostris* spawns on algae in monogamous pairs and shows no parental egg care (Barlow, 1987). *Paramonacanthus japonicus* spawns on sandy bottoms in monogamous pairs and shows biparental egg care (Nakazono and Kawase, 1993). *Cantherhines pardalis* spawns on algae and shows no parental care (Kawase and Nakazono, 1994a). *Brachaluteres ulvarum* spawns into sponge cavities in promiscuous pairs and shows no parental care (Akagawa et al., 1995). *Rudarius ercodes* spawns promiscuously on algae and usually shows maternal egg care (Akagawa and Okiyama, 1995; Kawase and Nakazono, 1995), but occasionally biparental or paternal care (Kawase and Nakazono, 1995).

Little is known about the reproductive ecology of the threadsail filefish, *Stephanolepis cirrhifer* (Temminck & Schlegel). The species is distributed in temperate waters of Japan, and is commonly found on rocky reefs and sandy bottoms to depths of 100 m (Matsuura, 1984). Adults attain 25–30 cm total length (TL), the body color usually being brown, but varying with motivational and social state. Sexual dimorphism in males exists as a filamentous extension of the second ray of the second dorsal fin (Fujita, 1955).

In this paper, we report reproductive behavior of *S. cirrhifer*, as well as territoriality, aggressive interactions, courtship behavior, and features of eggs and larvae based on field observations. We found that this species spawned on the sandy bottom in pairs, and showed maternal egg care, lasting only for a few minutes. Furthermore, two mating patterns, haremic polygyny and female visiting of male territories, were observed in a population. The two alternative tactics of females are discussed.

Materials and Methods

Underwater observations of *Stephanolepis cirrhifer* were made at Kashiwajima, southern Shikoku, Japan (32°46′N, 132°37′E). Preliminary observations (about 630 min in total) were carried out on seven occasions in four areas on 8–9 November 1990 and 12–14 May 1991. After the first observation of spawning, on the sandy bottom in 11 m depth at the northern side of Kashiwajima on 14 May 1991, detailed observations were made in that vicinity from 18 June to 17 August 1991 and from 22 June to 21 July 1993.

The study area of 40 m×30 m (10–13 m depth) was characterized by a sandy bottom with scattered boulders and rocks. The area was mapped with the aid of a grid utilizing ropes, measuring tapes, numbered sticks and nails driven in at 5 m intervals. At the beginning of the 1991 observations, three males and 10 females were caught by a barrier net (1.5 m×10 m; 5 mm mesh), measured (mm TL) and each tagged by affixing a colored rubber tube to its first dorsal spine. None of these tagged individuals were found at the beginning of the 1993 observations, eight males and 11 females being newly tagged. Additionally, two females ("x" and "y") were discriminated by a spilt in the fins and their TL was estimated by eye.

90-min observations were made 1–3 times a day almost every day for a total of 124 observation periods. Observations were made at various times from dawn to dusk (05:05–19:55 h) in 1991, but mostly during the morning (when spawning occurred) in 1993. Locations, swimming tracks and feeding sites of each fish were recorded on a field map for territory determination. When aggressive, courtship and spawning behaviors were observed, the locations and bouts were recorded. Such behavioral bouts were also photographed with an underwater camera, Nikonos V camera with Nikkor 35 mm lens and SB-103 strobe light.

For the determination of clutch size and embryonic development, a dome-shaped colander was placed on each of 8 egg masses just after spawning on 5–9 July 1993, the eggs being collected 1–26 hrs later. After fixing the eggs of each mass in 10% formalin in a 300 ml plastic bottle, the latter was agitated so as to separate the eggs from the sand particles. The liquid and separated eggs were then poured into a second container, and the procedure repeated several times until all of the eggs had been separated from the sand and removed. The container was then shaken so as to distribute the eggs evenly, and a sample poured into a shallow counting dish with a 1 cm×1 cm grid. The number of eggs on the grid was counted under a binocular microscope and the total number per egg mass calculated from the sample. About 200 eggs from each clutch were examined in order to determine the embryonic developmental rate and stages attained.

To determine if predation occurred, two egg masses spawned by different females on 9 and 10 July 1993, were checked daily along with the condition of the sandy bottom. When the two egg masses were collected three days after spawning, they immediately began to hatch in a plastic bottle. The larvae were fixed in 95% alcohol, and those hatched on 12 July were measured TL under a binocular microscope.

A male (208 mm TL) and female (158 mm TL) were collected from the sandy bottom about 100 m west of the study site on 5 August, 1991. After fixation in 10% formalin, their stomach contents were examined under a binocular microscope.

Results

Activity pattern and feeding ecology

Stephanolepis cirrhifer became active about 10 min before sunrise, foraging individually during the day. Their activity tapered off after sunset, the fish going to sleep on the sandy bottom or beside rocks. Feeding was achieved by blowing water strongly at the sandy bottom to expose food items, resulting in characteristic, funnel-shaped holes of about 5 cm diameter. The fish also fed by pecking at food items exposed on rocks. The stomach contents of two specimens consisted of amphipods, barnacles and fragments of sea urchins.

Aggressive and courtship displays

Male *Stephanolepis cirrhifer* showed intense aggressive behavior, especially in intrasexual encounters. When two males came together, each raised its head, expanded its ventral flap and vibrated its first dorsal fin spine 3–4 times/sec ("vibrating," Fig. 1a). Subsequently, reciprocal charging and pecking resulted in rapid whirling about of the two, head to tail ("whirling," Fig. 1b). During such whirling, the two males would slowly ascend in the water column to some 5 m above the bottom. During aggressive encounters, male body color changed from its usual beige or brown to cream with many blackish-brown specks. In male–female and female–female aggressive interactions, charging and pecking occurred, but the remarkable vibrating and whirling were not observed.

Male *S. cirrhifer* showed two types of courtship display: "vibrating" and "nuzzling" (Fig. 2). The former was similar to the vibrating action seen in male-male aggressive encounters. During courtship, male body color was usually bluish-brown with many specks. In response to the male's vibrating behavior, females stayed still or leaned their bodies, marked with two conspicuous blackish-brown specks toward the male (Fig. 2a). The other display, nuzzling of the female's face and flank ("nuzzling," Fig. 2b), was observed only just prior to spawning.

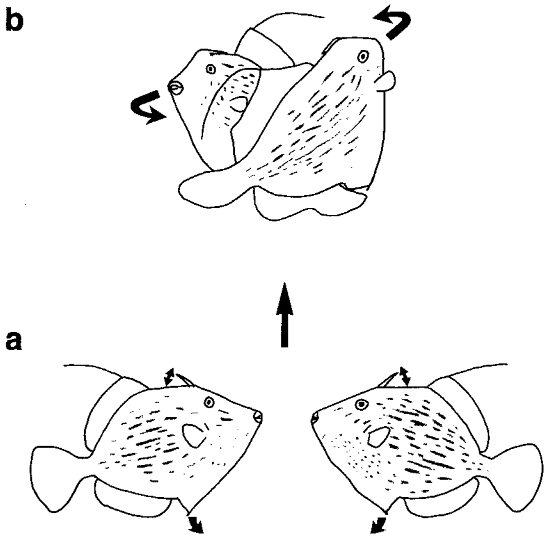

Fig. 1. Aggressive behavior of male *Stephanolepis cirrhifer*. a) Two males face each other, vibrating their first dorsal fins and expanding their ventral flaps ("vibrating"); b) after "vibrating," reciprocal charging and pecking results in whirling about of the two opponents, head to tail ("whirling").

Spawning and maternal egg care

Spawnings of *Stephanolepis cirrhifer* were observed only in the mornings (06:59–12:05 h, $n=47$), all matings being carried out by pairs on the sandy bottom. Males mated daily with up to three females, whereas females mated only once per day.

Within 10–30 min of spawning, each female *S. cirrhifer* thrust her snout repeatedly into the sandy bottom as if loosening the substratum ("thrusting," Fig. 2b). Subsequently, a male repeatedly approached and courted the female. The male, and sometimes the female, drove away other conspecifics of either sex approaching within 5 m of the thrusting site. The female also drove away other fish species, including pomacentrids and gerreids, when they passed nearby. The female conducted thrusting at several sites, often repeatedly visiting the same sites. Later thrusting was concentrated at a single site. From this point the male remained close to the female, courting intently with vibrating and nuzzling.

Spawning occurred on the sandy bottom

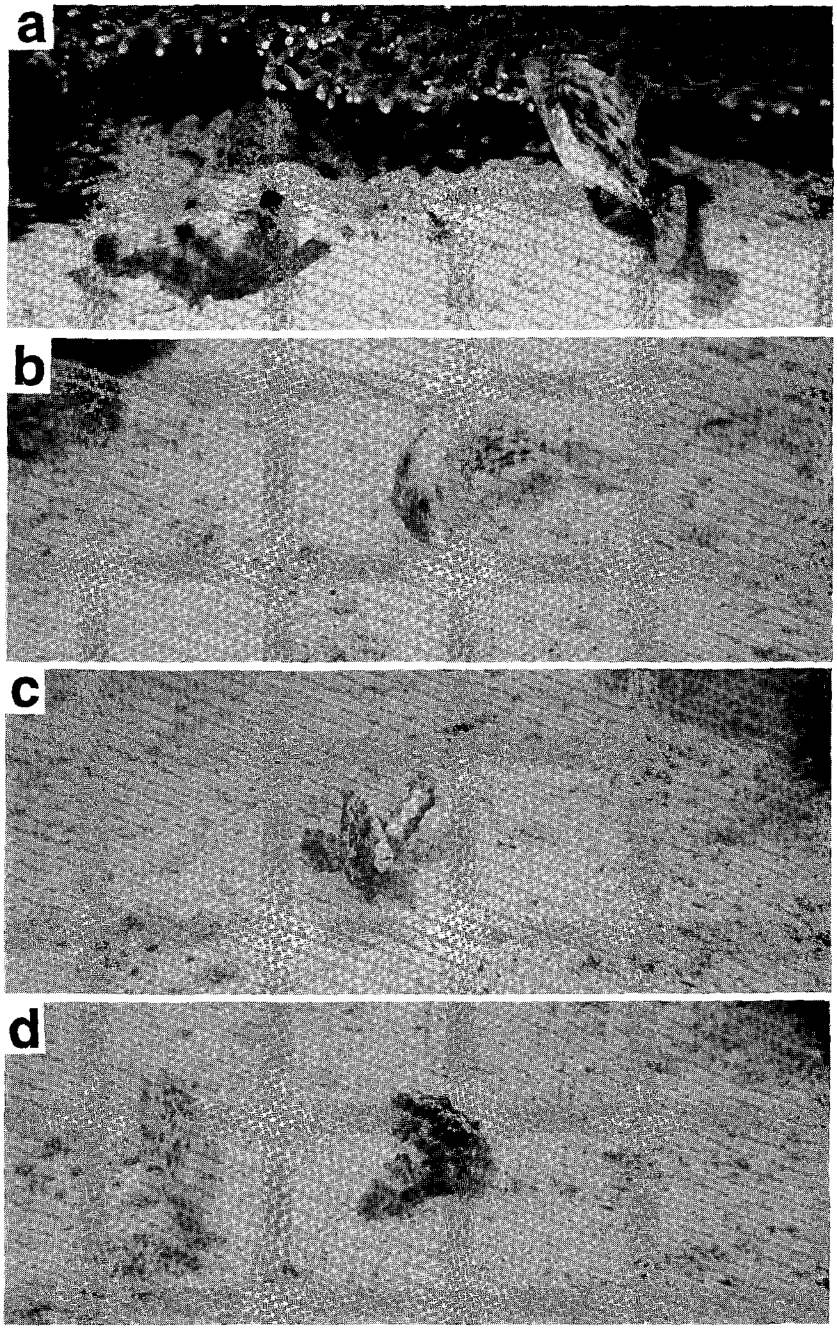

Fig. 2. Mating behavior of *Stephanolepis cirrhifer*. a) Courtship behavior, "vibrating," of the male (*right*). The female (*left*) stays still or inclines her body; b) pre-spawning behavior: "nuzzling" and "thrusting." The male (*right*) nuzzles at the face of his partner, while the female (*left*) is thrusting her snout into the sandy bottom; c) spawning behavior. The male (*right*) and female (*left*) touch their abdomens on the sandy bottom and release gametes; d) post spawning behavior. The female (*right*) turns her body just above eggs, while the male (*left*) departs.

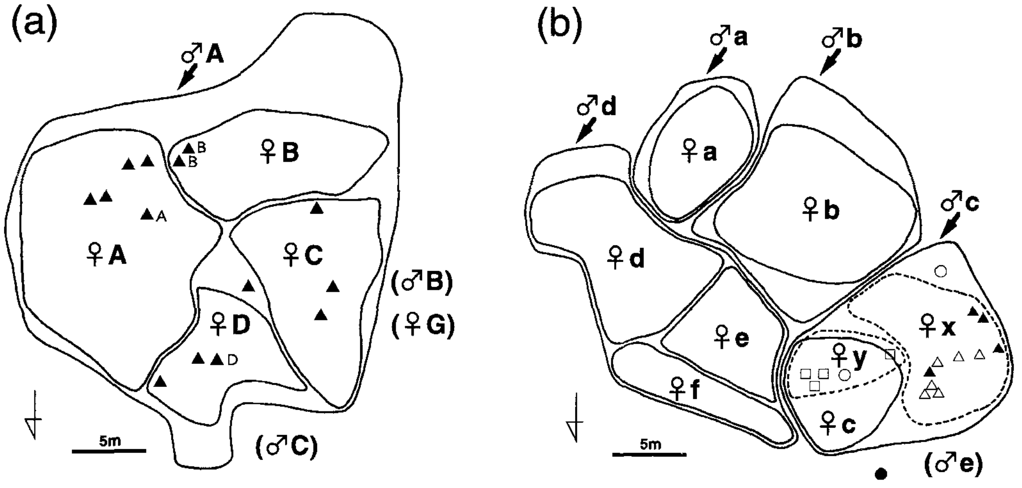

Fig. 3. Territories of *Stephanolepis cirrhifer* in 1991 (a) and 1993 (b) at the same site. The areas surrounded with lines are territories of each individual. Parentheses indicate territorial individuals, whose territorial boundaries were not exactly determined. a) Solid triangles with and without letters indicate the spawning sites where ♂A spawned with the resident and visiting females, respectively; b) the areas surrounded with broken lines are a temporal territory of ♀x and the home range of ♀y. Open triangles, open squares and open circles indicate the spawning sites of ♂c with ♀x, ♀y and untagged visiting females, respectively. Solid triangles and a solid circle indicate the spawning sites of ♀x and an untagged visiting female, respectively, with ♂e that took over a part of ♂c's territory.

where the female had concentrated her thrusting efforts (Fig. 2c). The male and female touched abdomens, with the male slanting his body and slowly moving forward (ca. 10–20 cm). At this point the pair released gametes for a few seconds. During gamete release, the female waved her anal fin on the bottom, scattering sand particles, while the male slowly rose into a head-up position. Immediately after spawning, the male left the site, but the female remained, turning her body alternately to the right and left about 20 times with her anal fin waving just above the egg mass (Fig. 2d). Subsequently, the female remained with the eggs for a few minutes, driving away conspecifics approaching within 2–3 m and other species passing nearby. Afterwards, the female left the site and no further parental care was observed.

Eggs and larvae

Eggs of *Stephanolepis cirrhifer* were adhesive and nearly spherical in shape, measuring 0.62±0.08 mm ($\bar{x}$±SD, n=10). They had 5–6 oil globules of 0.10–0.15 mm diameter and numerous globules less than 0.02 mm. The eggs were attached to sand particles, in many small patches, within an overall area of about 15 cm diameter. The estimated clutch size ranged from 2100–36,700 (mean=17,500, n=6). As the eggs were small and translucent, and were camouflaged with sand particles, they were difficult to find unless the exact spawning location had been recorded. No predation occurred on the two egg masses left exposed, during the three days of subsequent observations.

Embryonic development of *S. cirrhifer* at 19.4–21.1°C was as follows: two-cell stage was reached at 1 h 58 min, early blastula stage at 7 h 50 min, and elevation of the embryo at 21 h 59 min. The proportion of normally developing eggs between 2–26 h ranged between 91.2–100% (n=8). Hatching occurred when egg masses were collected 73–74 h after spawning (n=2), probably triggered by stimulation during the collection. The total length of newly-hatched larvae was 2.13±0.03 mm ($\bar{x}$±SD, n=10).

Territorial behavior and mating system

Observations in 1991. — The three tagged males "A"–"C" (205–219 mm TL) and seven of the 10 females "A"–"G" (184–216 mm TL) were seen in the study area until the end of the 2-month study period. The remaining three females "H"–"J" (165–183 mm TL) disappeared 2–5 days after being marked.

Territory boundaries and sizes were recorded for one male and four females (Fig. 3a). Male "A" (205 mm TL) had a territory (648 m^2) within which each female "A"–"D" (184–216 mm TL) had a separate territory (61–197 m^2). Male "A" showed aggressive interactions against the adjacent territorial males "B" (219 mm TL) and "C" (210 mm TL). Male "A" was also aggressive towards female "G" (200 mm TL), which was resident in the territory of male "B". Females "A"–"D" were aggressive towards each other, and also towards males and females of adjacent territories.

Both male "A" and females "A"–"D" usually foraged solitarily within their territories. Male "A" often approached the resident females for courtship, and also courted other females visiting his territory, such females appearing to be of similar size to the resident females. The latter severely attacked visiting females in defense of their territories, whereupon they themselves suffered aggressive attacks from male "A."

Only four of 14 observed matings of male "A" were conducted with the resident females, all in their respective territories (Fig. 3A), once with female "A," twice with female "B," and once with female "D" (Table 1). The ten observed matings of male "A" with visiting females all occurred in the former's overall territory (Table 1; Fig. 3a). After spawning and guarding the egg mass for a few minutes, the visiting females left the territory.

Observations in 1993. — Out of eight males (194–226 mm) and 11 females (167–230 mm) tagged, five males "a"–"e" and six females "a"–"f" were seen in the study area until the end of the 1-month study period. Males "f" and "g" had territories which bordered male "b"'s on the east and male "c"'s on the west, respectively. They engaged in intense interactions along the borders, but disappeared from the study area after 27 June. Male "h," and females "g" and "h" were occasionally observed in the study area, but

Table 1. Spawning dates, times and mates of three male *Stephanolepis cirrhifer*

♂A, 1991			♂c, 1993			♂e, 1993		
Date	Time	Female	Date	Time	Female	Date	Time	Female
1 July	11:30	♀A	27 June	8:05	vf	9 July	9:59	vf
	11:36	♀D	28 June	9:04	vf	11 July	9:16	♀x
	11:40	vf	3 July	9:16	♀y	12 July	9:40	♀x
3 July	11:09	vf	5 July	10:01	♀x	13 July	8:50	♀x
6 July	8:20	vf		10:29	♀y	18 July	7:35	♀x
	8:50	vf	6 July	9:54	♀x			
7 July	7:59	vf		10:51	♀y			
	8:54	vf	7 July	9:10	♀y			
8 July	7:12	vf		9:58	♀x			
	8:47	vf	8 July	10:08	♀x			
9 July	10:42	vf	9 July	9:52	♀x			
11 July	10:18	♀B	10 July	9:15	♀x			
12 July	10:18	♀B						
17 July	7:41	vf						

vf: untagged visiting female.

were driven away by the territory holders. Three females "i"–"k" disappeared from the study area a day after they were tagged.

Four males "a"–"d" (194–218 mm TL) established territories (70–217 m^2) in the area formerly controlled by male "A" in 1991 (Fig. 3). The mean territory size of the four males was 159 m^2, about one fourth of male "A"'s former holding (648 m^2). Three males "a"–"c" contained only one female territory (females "a"–"c," respectively), and male "d" enclosed three female territories (females "d"–"f"). The mean territory size for the six females was 62.6 m^2 (range=36–114 m^2), about half that of females "A"–"D" in 1991 (112 m^2, range=61–197 m^2).

The males and females foraged solitarily within their territories, but sometimes departed briefly for a point about 20 m away for feeding and cleaning by a cleaner wrasse, *Labroides dimidiatus*. When they foraged in other territories, they were driven away by the territory owners.

Observations of matings were focused on males "c" and "e" and related females. Male "c" mated with visiting females "x" (ca. 230 mm TL) and "y" (ca. 220 mm TL), as well as untagged ones, but not with resident female "c" although courtship was observed (Table 1). When female "x" entered male "c"'s territory, females "c" and "x" fought severely, and female "x" finally succeeding in establishing a temporal territory (75 m^2) in which she spawned (Fig. 3b). When female "y" visited male "c"'s territory for spawning, male "c" drove away females "c" and "x" which had severely threatened and attacked female "y." Male "e," occupying a territory adjacent to that of male "c"'s, had intense aggressive interactions with the latter territory holder. The two males were observed following female "x" on their territorial boundary on 4 July. Subsequently, male "e" occupied a portion of male "c"'s territory and mated with female "x" from 11 July onward (Table 1; Fig. 3b).

The visiting females "x" and "y" left the male territory after spawning and a few minutes of egg guarding, and reappeared in the study area on the following morning. On 11 July, female "x" left male "e"'s (formerly male "c"'s) territory, but returned to her spawning site within 8 min. After a 5 min period of egg guarding, she again departed, moving in a south westerly direction, at an angle of about 45° toward the shore. During the next 26 min, she was approached or attacked by two male *S. cirrhifer* and stopped 8 times to be cleaned by *L. dimidiatus*, but did not forage. Feeding commenced at the final destination, about 200 m from the spawning site and 20 m from the shore in 3 m depth. She pecked on the surface of rocks and boulders in an area of about 10 m×10 m, but did not meet conspecifics during the next 30 min of observation. Female "x" showed similar behavior, leaving spawning site but returning there soon, swimming straight to the south westerly direction, on 7 and 12 July.

Incidental observations outside the study area revealed that a male and female (both about 200 mm TL) shared a territory some 50 m from the shore, in 5 m depth. The territory included rocks, boulders and a shallow area of sand. Mating of the pair was observed on 1 July and prespawning behavior the next day.

Discussion

Parental egg care and egg condition

The Monacanthid fishes exhibit various patterns of parental egg care: maternal, paternal, or biparental care, or no care at all (Barlow, 1987; Nakazono and Kawase, 1993, Kawase and Nakazono, 1994a; Akagawa and Okiyama, 1995; Kawase and Nakazono, 1995; Akagawa et al., 1995). However, those species which do not provide egg care, nevertheless show some alternative contrivances that seem to offer protection from egg predation and promote the survival rate of the eggs. For example, *Oxymonacanthus longirostris* and *Cantherhines pardalis* both lay eggs on toxic algae, which affords protection against predation (Barlow, 1987; Kawase and Nakazono, 1994a). *Brachaluteres ulvarum* spawns into the exhalant canal of a calcareous sponge, thus protecting the eggs from predation while exposing them to a steady current of oxygenated water (Akagawa et al., 1995). The present study revealed that *Stephanolepis cirrhifer* showed maternal care only for a few minutes after spawning, and that the eggs were left uncared-for for three days until hatching, while other care-giving monacanthids, *Paramonacanthus japonicus* and *Rudarius ercodes*, continue parental care for a few days until hatching (Nakazono and Kawase, 1993; Akagawa and Okiyama, 1995; Kawase and Nakazono, 1995). *S. cirrhifer* spawned in pairs on the sandy bottom, eggs being scattered over an area of about 15 cm diameter, and attached to sand particles as a result of the female's waving of the anal fin on the bottom during spawning. This egg laying practice seems to have two advantages in promoting the survival of eggs without further care. First, attaching eggs to sand particles creates interstices through which oxygenated water may pass. Second, the apparently low visibility of the eggs may confer protection from potential predators, since no predation was observed in this study.

Mating system: two alternative tactics of females

Territorial male *Stephanolepis cirrhifer* mated with resident haremic females and also with visiting females. Thus two types of mating patterns, haremic polygyny and female visiting of male territories, were detected in the population.

Haremic polygyny, in which females are territorial in a male's territory, is known in the related family of balistid fishes; *Pseudobalistes fuscus*, *Sufflamen chrysopterus*, *S. verres* and *Rhinecanthus aculeatus* (Fricke, 1980; Thresher, 1984; T. Kuwamura, pers. comm.). The number of females in a harem varies and monogamous mating is also known under some ecological conditions (Fricke, 1980; Kawase and Nakazono, 1994b). Such changes in harem size were also observed in *S. cirrhifer*, in the same study area in different years. A greater number of territorial males and females were found in 1993 than 1991, and the male territory size and harem size decreased in 1993. Thus, the population density affected the harem size in this case.

The territorial males of *S. cirrhifer* also mated with females visiting their territories. Such a mating pattern is very common in reef fishes (e.g. Thresher, 1984; Kuwamura, 1988). In most cases, females leave male territories after spawning and either paternal egg care or no care is exhibited. For example, females of the damselfish, *Chromis notatus notatus*, visit male territories and spawn adhesive eggs onto the males' nest, the males thereafter caring for the eggs until hatching (Nakazono et al., 1979; Ochi, 1986); in the wrasse, *Halichoeres tenuispinis* females visit territorial males and spawn in the water column (Nakazono, 1979). In case of *S. cirrhifer*, however, females cared for the eggs after spawning, although they soon left the male territories. Females of *Pseudobalistes flavimarginatus* stay in male territories after spawning and care for the eggs until hatching (Gladstone, 1994).

As the two mating patterns were present in a single population of *S. cirrhifer*, male territories (and also resident female territories) were used for spawning sites by both resident and visiting females. Thus, resident females had eggs of their own and visiting females' in their territories. We believe that the resident females could detect the eggs, which were well camouflaged with sand particles, as the sandy bottom was their main feeding place. However, it is possible that they could not distinguish between their own eggs and those from other females, as is the case in another filefish, *P. japonicus*, a pair of which began to care for eggs not their own, that were placed in their territory (Nakazono, pers. obs.).

Female *S. cirrhifer* should choose one of the two alternative tactics; to be resident in a male's territory or to visit such for spawning. Resident females may have advantages in securing a mate and spawning sites at the cost of defending their territories. Visiting females do not spend energy on territorial defense, but have an additional cost of traveling a long distance for every spawning. The lack of sandy bottoms suitable for spawning in shallower areas was probably a factor necessitating extensive traveling.

The present study revealed that territorial males mated less frequently with resident females than with visiting females (male "A"=28.6%, $n=14$; male "c"=0%, $n=12$; Table 1), although incidental observations outside the study area (5 m depth) suggested that a territorial male mated with a resident female on successive days. How females choose between the two tactics, and the relative costs and benefits of the choice, remain unknown at present.

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