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Spawning and biparental egg-care in a temperate filefish, *Paramonacanthus japonicus* (Monacanthidae)

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Synopsis

Reproductive habits of a temperate filefish, *Paramonacanthus japonicus*, were studied on a rocky reef at Tsuyazaki, Fukuoka, Japan, from 1989 through 1990. Males had territories of 30–70 m^2 and defended them from conspecific males and potential egg predators such as another filefish, *Stephanolepis cirrhifer.* Egg masses were found on the sandy bottom in male territories. Individual discrimination of males and females occurring in three male territories revealed that males and females stayed in stable pairs during one month of observation in 1989. In these stable pairs, males fed only within their territories, but females occasionally foraged outside. The occurrence of egg masses within male territories and biparental egg care showed that fish were reproducing as monogamous pairs. Contrary to this, males tagged in 1990 changed their territories after the disappearance of females, and males and females mated polygamously. Spawning was observed only four times during the study period, between 1633 and 1754 h. Prior to spawning, the female prepared a spawning bed on the sandy bottom. The male nuzzled the female and the pair spawned, touching their gonopores on the spawning bed. Spawning was very quick and took only 1–3 seconds. The adhesive eggs were spherical with a diameter of 0.56 mm. They were mixed with sand particles and formed a doughnut-shaped mass of about 4 cm in diameter. One egg mass contained 3300–3800 embryos of similar developmental stage, which hatched 2–3 days later. *P. japonicus* appears to be monogamous but may also practice polygamy when pair-bonds are unstable.

Introduction

In spite of their common occurrence on coral and rocky reefs of tropical and temperate regions, studies of the reproductive ecology of the Monacanthidae are rare (Thresher 1984, Barlow 1987). As far as we know, they spawn adhesive eggs, on the tufts of fine blue-green algae or on the surface of larger brown algae, in a mass or in a locally scattered condition (Nakamura 1942, Murakami & Onbe 1967, Barlow 1987). The mating system, known in only one species, *Oxymonacanthus longirostris*, is monogamy (Barlow 1987). Because many species of the Monacanthidae are known from shallow waters, and many of them are commercially caught in large numbers, further knowledge of their reproductive ecology is urgently needed. The aim of this study is to describe the reproductive biology and behavioral ecology of *Paramonacanthus japonicus* (Monacanthidae). We consider the spawning site, courtship and spawning behavior, spawning frequency, egg mass shape, egg size, egg care by both sexes, male territorial behavior, female home range sizes, and differences in levels of feeding and aggression between the sexes. We also describe change in this species' mating system from monogamy to polygamy with the disappearance of females from the population. A remarkable feature of *P. japonicus* reproduction is that the female extrudes all her eggs in a quick spurt. This quick spawning behavior is compared with that of several other demersal egg spawners.

Materials and methods

Underwater observations were carried out at the rocky reef surrounding Tsutsumi-island, Tsuyazaki (33°47′N, 130°29′E), Fukuoka, Japan. This location seems to be about the northern distributional limit of *Paramonacanthus japonicus*. This species is not a permanent resident there, occurring only in the warm months from May to October. The number of fish appearing at the study area differs markedly from year to year; there were very few before 1989 and they were not found on and after 1991.

This study started in June 1989, when the fish were relatively abundant. Egg masses were first found on the sandy bottom near the reef in early August 1989. After finding the egg masses, we studied the behavior of *P. japonicus* near the egg mass. Soon it became clear that only two individuals were appearing near a given egg mass and were taking care of them. Four neighboring pairs (pair A–D) were netted, tagged and released. Standard length (SL) was measured underwater to the nearest 1 mm and acrylic paint was injected beneath the skin slightly below the 2nd dorsal fin for individual discrimination (Thresher & Gronell 1978). The place of capture was marked with a small underwater buoy connected to an anchor nail with a short rope. One pair (D) disappeared after tagging. The remaining three pairs (A–C) were regularly observed during the rest of the spawning season at or near the place at which they were originally caught.

Behavioral observations of tagged fish were made in two ways. First, the observer stayed near the egg mass and recorded behavior, such as aggression toward conspecifics and other species of reef fishes, feeding and egg-care. This method, however, did not show the entire range of their movements. We therefore followed each individual of a pair and placed numbered metal plates on the substratum as they moved from one point to another. The positions of the metal plates were determined by measuring the distances and compass directions from the anchor nail after an observation period ended. Sizes of the male territories were determined by connecting the outermost points at which territorial defense was observed.

For both methods, the occurrence of each behavior pattern was recorded as one event, because we found no differences in the duration of these patterns.

Spawning sites were visited as frequently as possible between early August and late September, to determine the presence of egg masses, tagged fish, and duration of pair-bonding. As occasion demanded, a small part or the entire egg mass was brought back to the laboratory to observe the size and developmental stages of the embryos and their number. Two additional pairs of fish were collected near the study reef, and each pair was kept in a 60 l tank. One of these pairs spawned once in the tank. The eggs, scattered on the glass bottom, were photographed and counted. After the spawning season ended, 6 specimens of *P. japonicus* were collected outside the study area to analyze their food habits.

Because the 1989 observations did not detect the beginning of the spawning season and spawning behavior, additional observations were made at the same locality in 1990, when the fish were found in nearly the same numbers as in the previous year. Since the mating system used varied between 1989 and 1990, we shall describe 1989 results first, followed by those for 1990.

Results

Sexual dimorphism and dichromatism

Paramonacanthus japonicus is so sexually dimorphic and dichromatic that the male and female were considered different species until Matsuura (1984) redescribed them. Usually, females are smaller than males although the body is deeper in females. The dorsal and anal fins are higher in males, and their

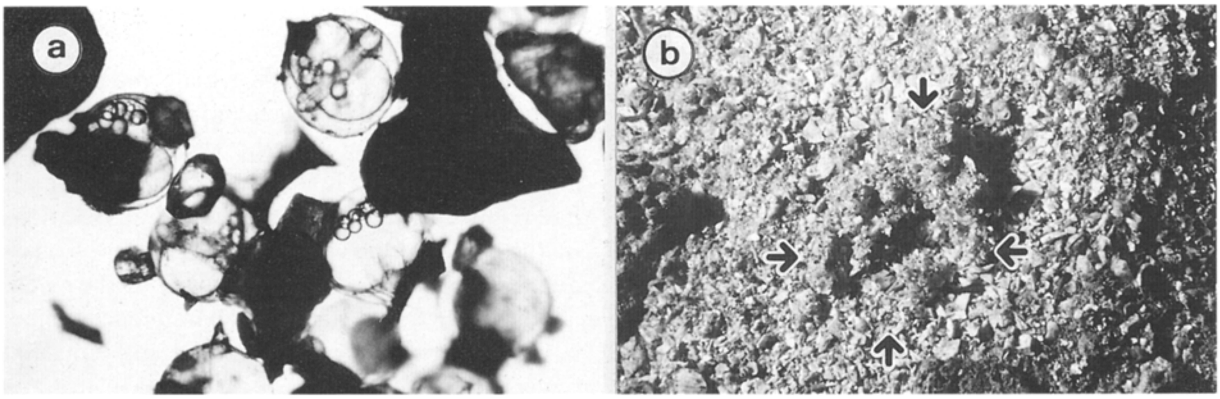

Fig. 1. a-Photomicrograph of *Paramonacanthus japonicus* eggs entangled with sand particles, b-An egg mass on the sandy bottom. Arrows show outer margin of the egg mass.

upper, lower-most, and median caudal fin rays extend as filaments. They are frequently torn off, probably during aggressive encounters. The spine of the 1st dorsal fin is stronger and higher in females. The body color of males is conspicuous compared with that of females. The female body color is dull with the upper half usually dark brown and the lower half whitish. Body color of both sexes varies with motivational and social state.

Seasonal occurrence of fish in the study area

By late May 1989 we found *P. japonicus* at depths of 10–16 m where the substratum changed from rocky reef to sand. We frequently observed 2–4 males aggressively displaying close to one another by late May-early June.

Body sizes of the fish observed at the study site were relatively uniform. In 1989, tagged males ranged in size from 76–85 mm SL and females from 61–72 mm SL. During the ensuing spawning season, territorial males were limited to one female per territory. Untagged fishes of both sexes were also observed in the area and their body sizes were similar to those which were tagged. Later, in September 1989, young of the year, measuring about 10 mm SL, appeared in the same habitat. These fish did not reproduce during the season of recruitment. Overall, the size composition of the stock lost uniformity and the number of individuals decreased gradually after this time. On and after 1991, they were not found in or around the study area at all.

Examination of stomach contents showed that *P. japonicus* fed upon various small benthic animals such as sponges, isopods, amphipods, and medusae. Small fragments of algae were also found in their stomachs.

Spawning site, egg size, and shape of egg mass

We determined that eggs were present on the sandy bottom when we observed a male positioned, with head lowered, about 20 cm above the substratum. The male maintained this position, looking at a point below him, for several seconds before swimming away. Departure from this point was usually associated with aggression or searching for food. The point of the substratum consisted of a patch, about 4 cm in diameter, that was colored differently from that of the sand. We collected sand from this patch for microscopic examination in the laboratory. We found many eggs entangled with the sand particles (Fig. 1a). The eggs were spherical with a diameter of 0.56± 0.02 mm ($\bar{x}$ and SD, $n = 20$). They had 4–5 large, and many small, oil globules and were similar to those of other Monacanthidae (Nakamura 1942, Murakami & Onbe 1967). The developmental state of the eggs in the same mass was uniform (Fig. 1a).

Although the small translucent eggs were hardly visible through a diving mask, repeated underwater observations revealed that eggs adhering to sand particles formed a distinct shape that was recognizable on the sandy bottom. The egg mass was somewhat round at first, but it became shaped like a 'doughnut', measuring 43.6 ± 5.0 × 40.3 ± 5.3 mm (the longest and shortest diameters to the outer margins of the doughnut, $\bar{x}$ and SD, n = 16); this shape resulted from the parents ejecting (blowing) water at the central part of the egg mass (Fig. 1b). Just before hatching, the egg envelopes seemed to lose their adhesiveness and the egg mass became thinner. Embryos from eggs spawned in the tank and in the field hatched within 2–3 days depending upon ambient water temperature. The clutch spawned in the tank by a female measuring 75 mm SL contained nearly 3300 eggs. One egg mass of average size contained 3800 eggs. The maximum number of egg masses found in a territory was 3 (10 August 1989, pair B, but fish were not tagged yet). The shortest distance between the egg masses was about 100 cm, but the longest was more than 500 cm. The egg masses occurred anywhere on the sandy bottom of male territories suggesting that the fish do not have a particular spawning site.

Behavior of the parents near the egg mass

Usually only two individuals, a male and a female, were observed near the egg mass in 1989. These two individuals were the same between 12 August–15 September, 1989 (cf. Table 1). Both male and female had relatively large home ranges and observations on the pair in turbid water was not possible. Consequently, we watched the pair only when they were near the egg mass to compare the frequencies of behavioral patterns between the male and female at the nest site.

During 162 min of observations of three pairs (Fig. 2, I–IV), most of the behavioral events of the parent recorded near the egg mass were egg-care and aggressive displays. One of the findings was that both parents cared for the egg mass. When multiple egg masses were in the same territory, the male and female cared for them equally (Fig. 2, I–II). Parental care consisted of two types of activities. One was watching the egg from the above (broken arrow pointing to egg masses in Fig. 2) and the other was ejecting water at the egg mass (solid arrow). When looking down, the fish came to within 10–20 cm of the egg mass, looked at the eggs and left within 2–3 seconds. When 'blowing' at the eggs, the fish pointed its snout at the egg mass and blew at the center (Fig. 3a, b). 'Blowing' was so strong that the egg mass was pushed up and held briefly above the sand

Table 1. Occurrence of tagged fish and egg masses in the territories.

		1989													
		Aug					Sep								
		12	22	23	25	29	2	4	6	7	9	14	15	24	27
Territory A	♂ 85 mm SL	+	+	+	+	+	+	+	+	+			+	−	−
	♀ 72 mm SL	+	+	+	+	+	+	+	+	+			+	−	+
	Egg mass	−	+	+	−	+	+	+	+	+			+	−	−
Territory B	♂ 82 mm SL	+	+	+	+	−	+	+	+	−			+	+	+
	♀ 61 mm SL	+	+	+	+	+	+	+	+	+			+	+	+
	Egg mass	+	−	−	−	−	−	+	−	−			+	−	−
Territory C	♂ 82 mm SL	+	+	+	+	+	+	+		+	+	+	+	+	−
	♀ 69 mm SL	+	+	+	+	+	−	+		+	+	+	+	−	−
	Egg mass	+	+	+	+	+	+	+		+	+	+	+	−	−

Standard length of the pair D was ♂ 76 mm, ♀ 70 mm. + = tagged fish and egg masses were found, − = not found, blank = observation was not made.

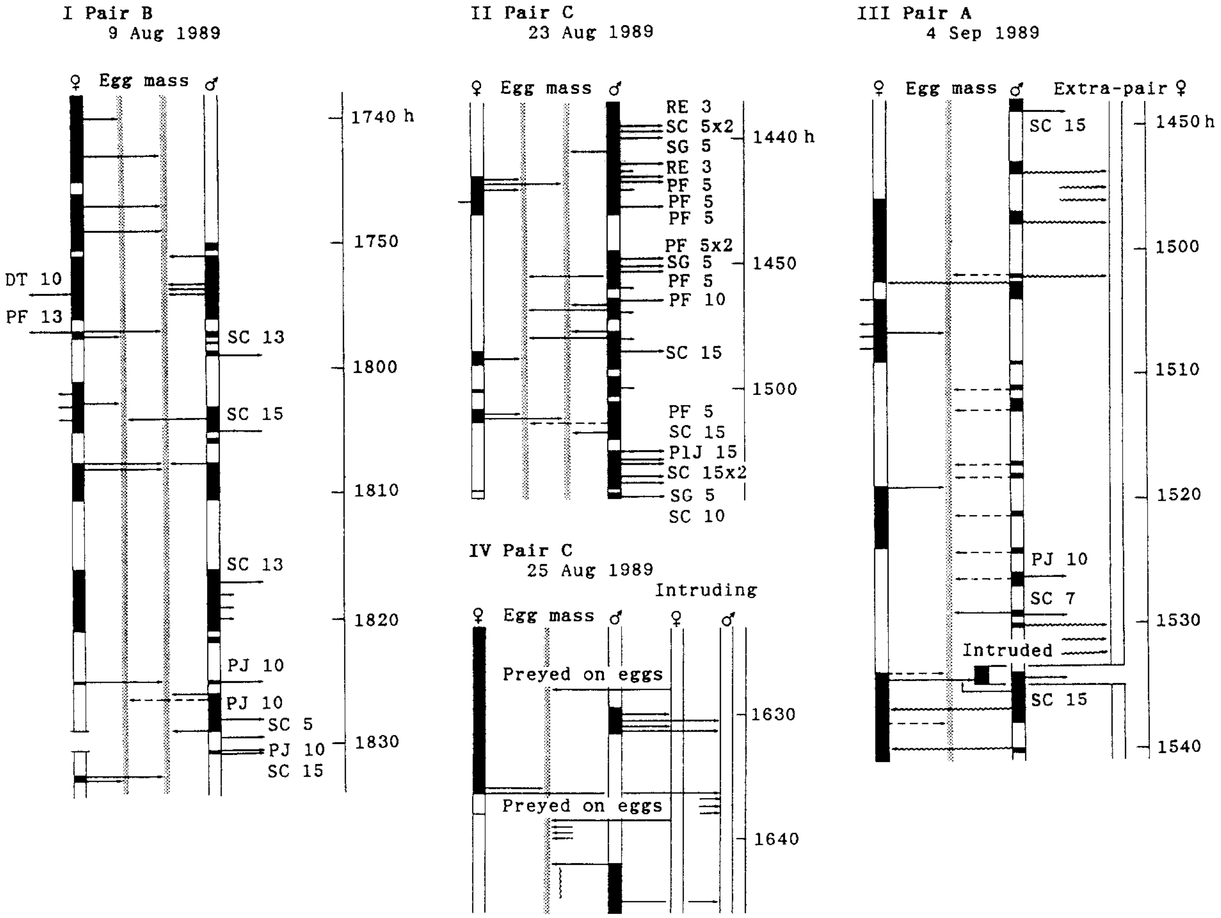

Fig. 2. Behavior of the male and female near the egg mass. Left and right columns correspond to the female and male of the pair, respectively. Black parts of the column show that the fish was seen near the egg masses. Long arrows pointing outside show aggressive displays toward conspecific or other species of reef fishes. Abbreviated names of fishes attacked and approximate total length in cm are shown near the arrow. Short arrows pointing outside indicate feeding. Solid arrows pointing to the egg mass (each stippled column shows one egg mass) show blowing of the parents, arrows with broken line, only watching. Wavy arrows in III show courtship display of the male. Vertical wavy line in IV shows that the male stayed above the egg mass for protection. The fish were not yet tagged when observation I was done. DT = *Ditrema temmincki*, PF = *Pteragogus flagellifera*, SC = *Stephanolepis cirrhifer*, PJ = *Paramonacanthus japonicus*, RE = *Rudarius ercodes*, SG = *Sagamia geneionema*, PlJ = *Pseudolabrus japonicus*.

by the water pressure. The time spent in 'blowing' was brief. The parents left the egg mass after one or a few bouts of watching and 'blowing', leaving the egg masses unguarded. 'Blowing' and watching frequencies (0.20± 0.05 times per min for males and 0.16± 0.07 for females; $\bar{x}$ and SD of I, II, III) did not differ significantly between the male and female of a pair (Mann-Whitney's U-test among I, II, III, two sided, $U_{cal} = 4$, $p > 0.05$). When the male and female approached the same egg mass simultaneously, the female drove the male away.

Fish could have been displaying aggressively when not near egg masses (blank areas of the columns in Fig. 2). Of 33 aggressive displays toward intruders by the male (observation of pair C on 25 August, 1989 is not included), 29 (87.9%) were toward seven other species of reef fishes (Fig. 2), and of these, 51.7% were directed towards another filefish, *Stephanolepis cirrhifer.* Although, *S. cirrhifer* were attacked at various distances from the egg mass, the remaining six species were attacked only when they approached within about 0.5 m of the egg mass. This species usually fed on the bottom by 'blowing' sand and we believe it to be a threat to *P.*

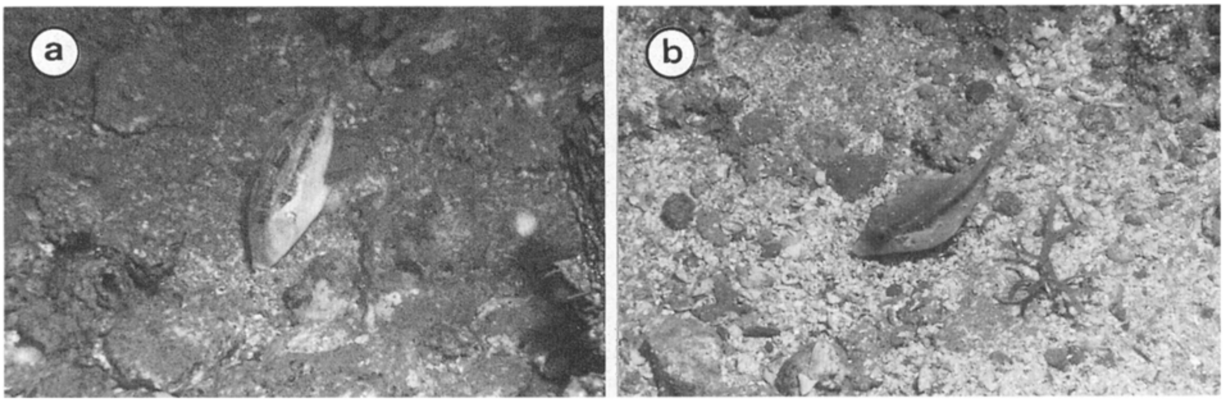

Fig. 3. Egg blowing by *Paramonacanthus japonicus* the male (a) and female (b).

japonicus eggs. Female aggression against other reef fishes was observed only twice, when intruders approached to about 0.5 m from her when she was near the egg mass (1754 & 1758 h in Fig. 2, I). Aggressive displays exhibited by parents near the egg mass seemed to be egg-guarding behavior against potential egg predators. However, egg predation by other species of reef fishes that passed by the egg mass did not occur even when both parents were absent. The only predation on eggs observed was cannibalism by a conspecific female (see further).

Extra-pair courtship display of the male

Three pairs of *P. japonicus* observed in 1989 appeared to be monogamous. However, courtship displays of a male toward an extra-pair female were observed on 4 September 1989 at territory A (Fig. 2, III). An untagged female was seen at the border of the territory. Male A approached the female and displayed, expanding his 1st dorsal and caudal fins rhythmically. He also showed courtship display to his partner several minutes later and took care of the egg mass as usual. About 30 min later, the untagged female entered the territory and the male courted her frequently. Soon after, the resident female discovered her and attacked her fiercely. The male then pecked at the female partner with his snout. Aggression between the two females ended when the intruding female departed. This was the only observation of extra-pair courtship by the male. As will be shown later, females of pairs departed the male's territories, but they usually hid in algae when the male of the neighboring territory approached them. We also observed that an intruding female was aggressively expelled from the territory by the resident male when discovered. The intruding female observed on 4 September 1989 might have been a solitary fish.

Intrusion of another pair and egg cannibalism

A case of intrusion by another pair into the territory of male C is illustrated in Figure 2, IV. The pair, of unknown origin, was seen at 1628 h in the territory, and the intruding female was biting at the egg mass of pair C. Soon male C noticed the intruders and tried to expel them. Then, female C also recognized the intruding male and displayed aggressively to him. Soon thereafter the intruding female approached the egg mass again and bit at it several times. Sand particles fell from her mouth, a behavior not seen in egg blowing by the parents, suggesting egg cannibalism. The intruding female left the egg mass soon, as the territorial male placed himself just above the egg mass and displayed aggressively, expanding his median fins and lowering his head, as if he were guarding the egg mass.

Male territorial behavior and female home range

Male B appeared to have been affected by tagging; he swam weakly and may have had difficulty in defending his territory. On 22 August 1989, we found many depressions in the sand at the spawning site. The presence of these depressions suggested feeding activity by *S. cirrhifer.* The territory and spawning site of males B changed slightly soon afterwards. However, male A and C kept holding the same territories throughout the observation period (Table 1), and provided a chance to study territory and home range sizes. Results of the observations on pairs A and C are shown in Fig. 4. The male territories were drawn by connecting the outermost points to which the males moved (Fig. 4, I, IV), most of which were points of aggression towards conspecific males (open arrows). Size of the territory was 71 m^2 for male A and 34 m^2 for male C. Other behavioral events of the males noted were aggression toward *S. cirrhifer* and other species of reef fishes, egg-care, courtship display and feeding.

The home ranges of females A and C were obtained by the same method (Fig. 4, II, III, IV). Most female behavior was limited to feeding. The female fed principally within the male's territory, swimming cryptically and using algae and the shade of rocks for cover as she moved from one feeding site to the next.

On 9 September 1989, female C fed outside the territory. While she was outside, the male of the neighboring territory swam near her, but neither fish responded to the other, and no marked change in the behavior was seen (Fig. 4, II). Behavior of the same female on 14 September 1989, was almost the same, behavioral events being mostly recorded within the male territory (Fig. 4, III). Around 1722 h, female C went out of the territory for more than 10 m for feeding. On the way, the neighboring male came near to her. This time, the female hid in *Sargassum* and the male passed without responding. Then, another behavioral pattern, spawning bed preparation, was observed before dusk (see spawning behavior).

Sizes of the male's territory and the female's home range in pair A were nearly the same as in pair C (Fig. 4, IV). The male's territory and the female's home range also overlapped widely in pair A. The difference in size between the male's territory and the female's home range in pair A was attributable to female feeding behavior; the female went out and kept feeding upon a ctenophore medusa drifting in the midwater column.

To summarize the above observations, male territories and female home ranges mostly overlapped. Males defended territories and egg masses from conspecific males and from potential egg predators of other reef fishes (0.41 times per min, total of observations I-IV in Fig. 4, same for below), but females showed aggressive displays only in special cases (0.01 times per min). Feeding by females usually took place within the male's territory, but occasionally it was done outside (12/85 = 14% of total observations). Frequencies of egg-care (blowing and watching together) were 0.36 times per min for males and 0.12 times per min for females. The frequency was lower in females, but statistically the difference was not significant (Mann-Whitney's U-test, two sided, $U_{cal} = 0$, $p > 0.05$).

Spawning behavior

Female *P. japonicus* usually occurred in male territories, but pairs did not behave synchronously. Males showed courtship displays only when meeting females, and this was the only recognizable interaction between sexes during daytime (Fig. 4).

Spawning behavior was observed only four times: in pair C, on 14 September 1989 (the pair spawned while observer was out to change his empty SCUBA tank), in an untagged pair on 19 July 1990, and in two untagged pairs on 21 July 1990. The first indication of the spawning behavior was when the female thrust her snout rhythmically into the sandy bottom, a pattern referred to as 'sand digging' (Fig. 5a). This behavior was observed between 1600–1700 h. Early on, she did not use this behavior at a single site but did more so as time passed (solid star in Fig. 4, III). Concentrated sand digging lasted between 15–30 min. The male approached during the latter part of this time interval, placed himself beside her, and nuzzled her belly frequently. Soon thereafter, the pair suddenly touched their gonopores on the

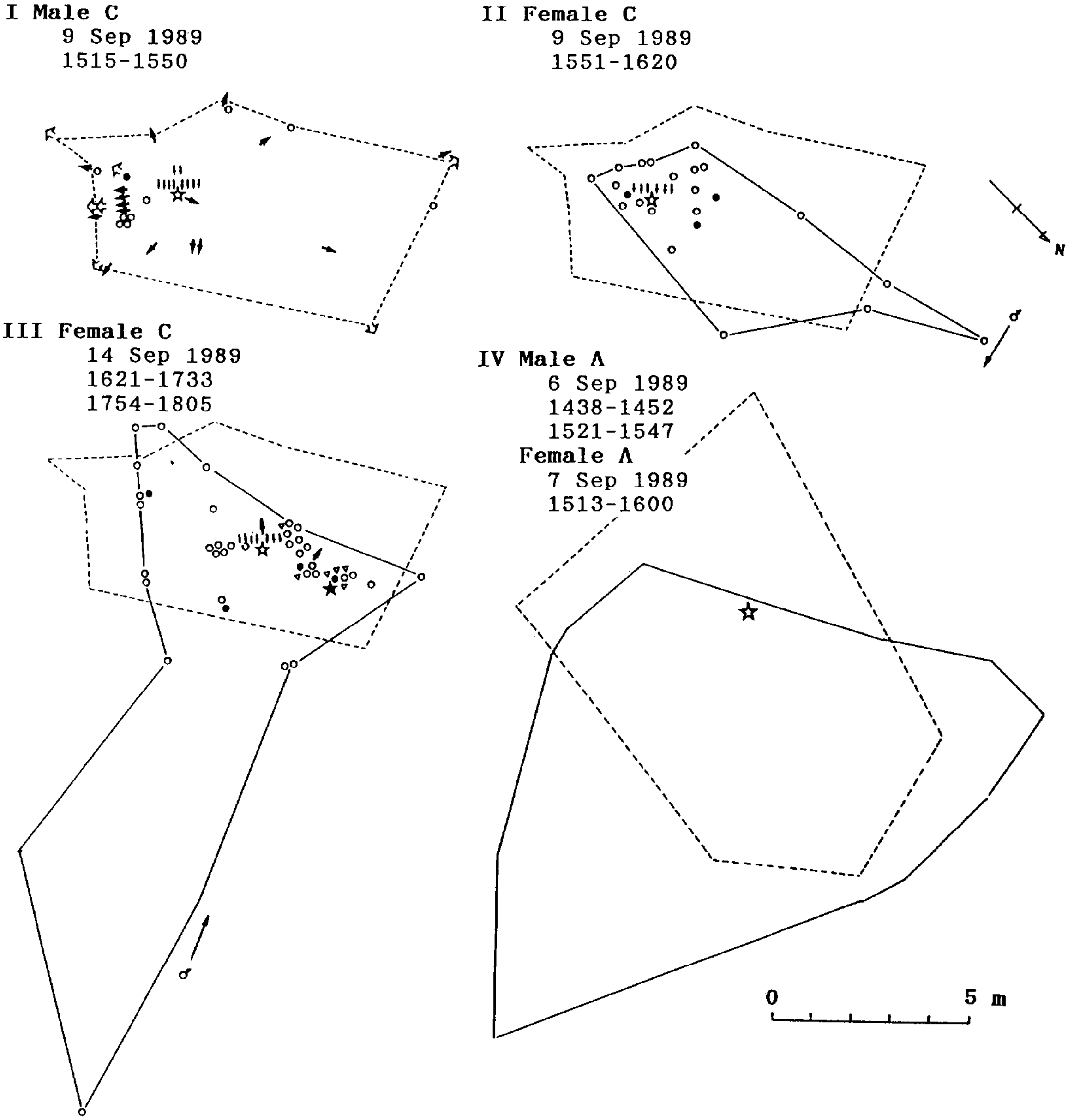

Fig. 4. Male territory (broken line) and female home range (solid line). I, II and III are results for pair C. In IV, only the borders of male territory and female home range of pair A are shown. Each symbol shows one behavior pattern. Arrows with a male symbol = a neighboring territorial male swam near the female, large open arrow = aggressive display towards a conspecific male, large solid arrow = aggressive display towards other reef fish, small solid arrow = egg-care, open circle = feeding, solid circle = courtship display of the male or the female was courted by the male, upside-down triangle = sand digging, open star = egg mass, solid star = newly spawned egg mass.

spawning bed and released gametes (Fig. 5b). Mating lasted only 1-3 seconds, and the male left the site immediately. The female, however, stayed at the spawning bed and kept thrusting her snout into the egg mass. This behavior lasted for several minutes before the female left the spawning site. Spawning was observed between 1633 and 1754h. In spite of intense observations during afternoons of the 1990 season, and frequent observations of egg masses in male territories, spawning behavior was observed only infrequently. The developmental stages of the eggs collected and examined in the laboratory sug-

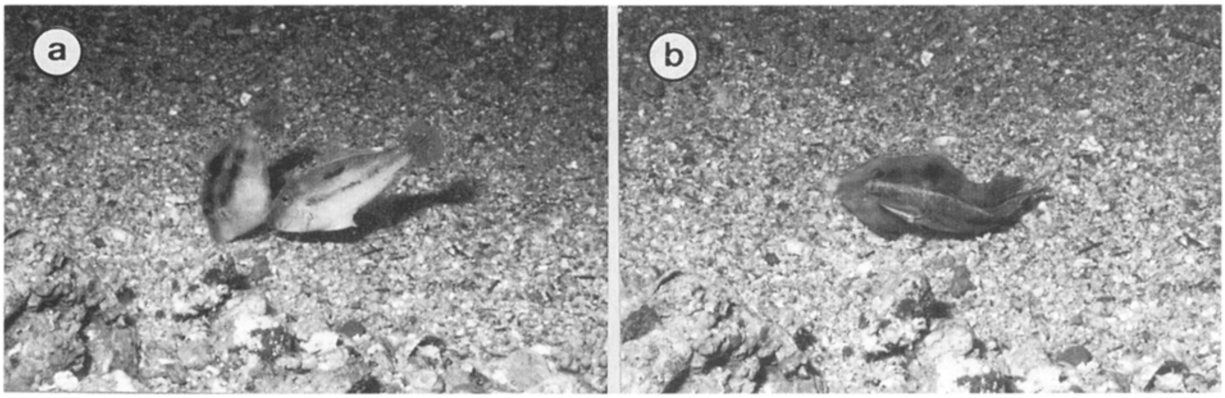

Fig. 5. Spawning behavior of *Paramonacanthus japonicus*: a-sand digging of the female and nuzzling of the male, b-the same pair spawning. The male is at the front and leaning to the left side.

gested that the eggs were also deposited in the morning.

Observations around sunset revealed that fish sought refuge apart from the egg masses and that the egg masses were left unguarded at night.

Pair-bonding and spawning frequency

Observations on the duration of pair-bonding began on 12 August and extended until 27 September 1989 (Table 1). The observations on 15 September showed that three pairs were present and they all had egg masses. We made 31 observation attempts of three pairs from 12 August–15 September 1989. Of these, 28 were successful in seeing the same pairs within their territories. We were unable to find the pairs during the remaining three. The results clearly show that males and females of *P. japonicus* remain as pairs for a long period of time.

Earlier, we stated that male B may have been adversely affected by the tagging process. After 23 August, this male seemed to have changed his spawning site, presumably after an attack by *S. cirrhifer.* We failed to notice this until 4 September 1989. Therefore, egg masses were less frequently found at territory B. Nevertheless, egg masses were found in 22 out of 31 observations which were performed before 24 September. Such a high frequency of occurrence of egg masses at the spawning site in randomly timed observations suggested that the pair spawned nearly every day during this period. After 15 September, however, no egg masses were found, and the number of tagged fish decreased.

Male and female *P. japonicus* remained paired during the spawning season, but it is not known whether they stayed in pairs during non-reproductive periods. They seemed to migrate elsewhere during winter.

Mating system observed in 1990

Observations of biparental egg-care and long lasting pair-bonds in *P. japonicus* at Tsutsumi-island in 1989 suggested that the species is monogamous. In 1990, nearly the same number of *P. japonicus* was found at the same study site. Egg masses were first observed on 5 July. To confirm that the fish were also monogamous in this year, three pairs found near buoys A, D and between B and D were tagged on 23 and 26 July 1990. These pairs are referred to as A', D' and E', hereafter. On 26 July, we observed that the pairs D' (♂ = 89, ♀ = 72 mm SL) and E' (♂ = 85, ♀ = 75 mm SL) were taking care of the same egg masses in the respective territories. Pair A' (♂ = 88, ♀ = 74 mm SL) was tagged on this day, but female A' disappeared and was not found in the territory again until 16 August. Female D' also disappeared on 28 July and did not appear again. On 31 July, male A' intruded into the territory of male D', and male D' moved to territory E'. Male E' was not observed thereafter. Males A' and D' stayed in their neighbor's territories until 6 August. During this period, these two males were observed to have egg masses in their territories, but the females who laid the eggs were not known. These two males returned to their original territories on 7 August and stayed there until observations ended on 31 August. After the males returned to their original territories, male D' displayed to female E' on 16 August and these two fish were later observed caring for the same egg mass on 21 August. On 16 August, female A' appeared and joined male A' in caring for the egg mass. On 31 August, we found male D' jointly caring for three egg masses, sharing two of them with female E' and one with a female (70mm SL) which was recently tagged (16 August) near the territory of male D'. Although these two females were observed within the territory at different times, egg-care of female E' with male E' (26 July) and later egg-caring with male D' and that of male D' with a newly tagged female confirmed that female E' and male D' were polygamous. Polygamous mating observed in 1990 probably resulted from the disappearance of two females from the territories of two males.

Discussion

Sexual dimorphism

Although sexual dimorphism is not rare in the Monacanthidae (Clark 1950), it is manifested differently among species. *Paramonacanthus japonicus* had striking dimorphic features compared with another monogamous filefish, *Oxymonacanthus longirostris,* in which sexual dimorphism was subtle (Barlow 1987). Barlow suggested that females did not exercise mate choice, although salient dimorphism in *P. japonicus* may be an indication of female mate choice (Krebs & Davies 1981). Fierce aggressive displays among males observed at the beginning of the spawning season suggested that female mate choice can be possible in monogamous *P. japonicus.* Furthermore, it is unlikely that the pairs remain together during winter after they disappear from the spawning territories. The dissolution of pairs at the end of the season may offer females an opportunity to exercise mate choice at the beginning of the following year's spawning season, thus increasing their fitness.

Egg mass and egg size

The present study revealed that the eggs of *P. japonicus* are deposited on sand. The eggs were adhesive and mixed with sand particles to form the egg mass. The egg mass was unlike that reported for *Rudarius ercodes,* whose egg mass consisted solely of eggs (Nakamura 1942). The mixture formed a definite shape, referred to as 'doughnut', because the central part is concave as a result of parents' blowing seawater into the mass. The diameter of the egg mass was about 4cm and was relatively easily found by careful observations on egg-care by the male and female.

Known egg diameters of monacanthid fishes are 0.52mm for *Rudarius ercodes,* 0.64mm for *Thamnaconus* (formerly *Navodon*) *modestus* and 0.7mm for *Oxymonacanthus longirostris.* Clutch sizes are 1840–5380, 30 000–190 000, and about 200 eggs, respectively (Nakamura 1942, Takami & Utsunomiya 1969, Barlow 1987). Barlow (1981) indicated that small coral reef fishes (<100mm SL) invest more per egg by laying larger demersal eggs. This investment in larger egg size would favor lower mortality during planktonic larval stages. The eggs of *P. japonicus* were spherical with a mean diameter of 0.56mm. This size is very small for demersal eggs and is amongst the smallest known for pelagically-spawned eggs (Ahlstrom & Moser 1980). Clutch sizes ranged from 3300–3800 eggs, far larger than those reported for *O. longirostris.* Egg sizes of this species are also smaller than those predicted by Barlow (1981). Smaller egg sizes may be advantageous for survival in that small size may decrease the chance of discovery by predators when left unguarded.

Male territorial behavior and female foraging

Male *P. japonicus* were territorial. Aggression was directed mainly at conspecific males and potential egg predators. Among egg predators, *Stephanolepis cirrhifer* was chased most frequently and fiercely, suggesting that this species, when near the spawning sites, was a major threat to *P. japonicus* eggs. Egg predation attempts by *S. cirrhifer*, as seen in the territory of male B, probably provoke aggression from territorial *P. japonicus* males.

Females were less aggressive compared to males, and attacked other species only when caring for eggs. These differential behavior patterns between sexes may be advantageous for the pair, because well-fed females can produce more eggs.

Spawning behavior

P. japonicus mated in pairs. Interference by other males was not observed. When polygamous, as was observed in 1990, two females were considered to have mated with the same male at different times.

A typical feature of the spawning behavior of *P. japonicus* was that eggs were deposited by means of a very short spurt compared to many other demersal egg spawners, in which egg-laying takes a relatively long period of time (Thresher 1984). *Oxymonacanthus longirostris* also deposits eggs quickly (within 2–3 seconds, Barlow 1987). Other quick demersal egg layers are the balistids. Although spawning duration was not reported, Kawabe (1984) observed that female *Sufflamen fraenatus* mated immediately after pair formation.

The same quick mating of demersal eggs occurs in the Tetraodontidae. For example, Gladstone (1987) observed that mating in *Canthigaster valentini* lasted only 5–10 sec. Sikkel (1990) also showed that *C. rostrata* mated very quickly.

Thresher (1984) was the first to point out that the newly hatched embryos of siganids and balistids are more similar to those of pelagic egg spawners than they are to other demersal spawners. The spawning behaviors of the above three groups, monacanthids, balistids, and tetraodontids, are similar to these of pelagic egg spawners in that the eggs are extruded very quickly.

Biparental egg-care and mating system

Male and female *P. japonicus* visited and cared for egg masses. Two types of egg-care, watching and blowing, were recognized in the present study. During watching, the fish only looked at the egg mass. During blowing, the fish blew water at the center of the egg mass. Blowing must be effective not only for supplying oxygen to the eggs, but also for preventing the egg mass from being buried in the sand. Total frequencies of watching and blowing behaviors did not differ significantly between males and females. These results shows that egg-care is apparently biparental in *P. japonicus*. Biparental egg care and territorial defense by males, both important for egg survival, is also known for the balistids (Fricke 1980, Clutton-Brock 1991).

Biparental egg-care is considered to be common in monogamous species, although it is rare in marine reef fishes (Barlow 1984, Gross & Sargent 1985, Kuwamura 1987, Clutton-Brock 1991). Observations in 1989 revealed that *P. japonicus* was monogamous, that pairs remained together and mated with each other repeatedly. Biparental egg-care and other behaviors, such as female aggression toward other females, and mutual egg protection against an intruding pair, support monogamy in the present species. Barlow (1987) suggested that monogamy in another filefish, *O. longirostris*, was the result of pair territoriality in which the female benefited from the reduced cost of defense and increased fecundity. In *P. japonicus*, the male defended the territory and the female principally foraged. These results suggest that the scenario for *O. longirostris* is applicable to the present species as well.

Observations made in 1990, however, revealed that *P. japonicus* was polygamous, in that two females spawned in the same territory and one female spawned in the different territories successively. The existence of variable mating systems in the same species is not unusual, as was reported for hawkfishes (Donaldson 1989). A shift from monogamy to polygamy, observed in *P. japonicus*, was preceded by the disappearance of females. It is probable that this disappearance disrupted an otherwise monogamous system. Monogamy appears to be the principal mating system operating in *P. japonicus*, but this species may adopt an alternate mating system, polygamy, if local population sizes are unstable.

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