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Spawning Behavior and Timing of Fertilization in the Mouthbrooding Cardinalfish *Apogon notatus*

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Abstract Reproductive ecology and ethology of *Apogon notatus* were studied in the shallow coastal waters of Shirahama and Sakura-jima, southern Japan. Male/female pairs began to separate from large aggregations as early as two months before the beginning of the spawning season. The pair stays at its home site during the daylight hours of each day, attacking and chasing other conspecifics approaching it. The female often displays "warping" to her male partner, but the latter exhibits no active display. In the early morning of the day of spawning, the female initiates the prespawning process, and after "parallel-circling" by the pair an egg mass is spawned in the parallel position between 11: 00 and 15: 00. The male takes the egg mass in his mouth within a few seconds after spawning. External fertilization occurs in the male's mouth within a few minutes after spawning, during the "rapid-circling" by the female. Both conspecifics and other fishes often interfere with the spawning process. Causal factors in the spawning process of *A. notatus* and the sex of the egg-incubating parent in Apogonidae are discussed.

Mouthbrooding or oral incubation of fertilized eggs is well known in many species of cardinalfishes (Apogonidae) (Fowler and Bean, 1930; Nagasaki Aquarium, 1962; Breder and Rosen, 1966; Tanase, 1968; Oppenheimer, 1970; Fishelson, 1970; Charney, 1976; etc.). Among these, courtship and spawning behavior of *Apogon imberbis* has been most precisely studied in the aquarium (Garnaud, 1950, 1962, 1963). In this species a male/female pair is formed prior to spawning, and internal fertilization was suggested to occur during the courtship behavior "rondes nuptiales (nuptial rounds)" of the pair.

The blackspot cardinalfish *Apogon notatus* (Houttuyn), which is dealt with in the present paper, is very common in the coastal waters of southern-middle Japan (Hayashi and Arai, 1980). Its courtship and spawning behavior were observed by Nakahara (1962) in the Sakura-jima Aquarium. He reported that eggs and sperm were released at the same time, when the male was upside down, closely touching his abdomen to that of the female partner.

I have frequently observed the courtship and spawning behavior of *A. notatus* at Shirahama, southern Japan, and experimentally examined the timing of fertilization. My observations differ from those of Nakahara in several points. Also, I have studied its spawning behavior at Sakura-jima, where *A. notatus* was collected for Nakahara's aquarium observations, and found no significant differences in the courtship and spawning behavior of *A. notatus* in Shirahama and Sakura-jima.

In the present paper, I will describe the seasonality of spawning activity in relation to environmental factors, the courtship and spawning behavior, and the timing of fertilization of *A. notatus*.

Study areas and methods

Underwater observations using SCUBA were conducted in the coastal shallow waters (mostly $<$10 m deep) of Shirahama (33°42′N, 135°20′E) and Sakura-jima (31°35′N, 130°36′E) (Fig. 1).

At Shirahama, from 1974 to 1981, the life history and reproductive ecology of *A. notatus* were studied on shallow rocky reefs, mainly Reefs A, B and C in Fig. 1, near the Seto Marine Biological Laboratory of Kyoto University. These reefs were surrounded by sand or pebble bottoms. More detailed description of the study area is given by Kuwamura (1976, 1981).

At least once per month, positions, conditions (either egg-incubating or not) and behavior of pairs were recorded on maps of two study sites: St. 1 (1 × 5 m, at 4 m depth) at the offshore edge of Reef A, observed from March 1975 to

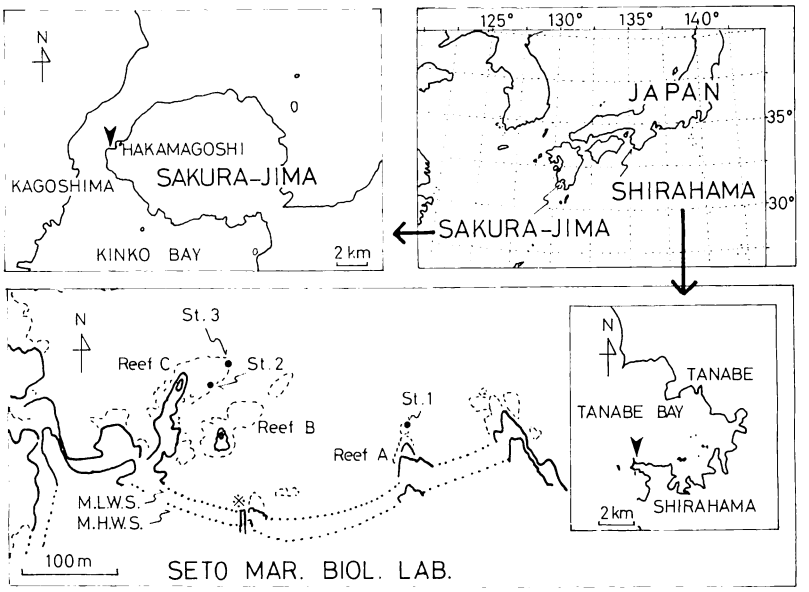

Fig. 1. Maps of Shirahama and Sakura-jima indicating the position of the study areas. Detail of the study area at Shirahama is also illustrated: thick lines indicate rocky (unbroken line) and sandy (dotted line) shores, and profiles of submerged rocky reefs are shown by broken thin lines.

March 1979, and St. 2 (3×5 m, at 5 m depth) at the fringe of Reef C, observed from May 1977 to March 1979. Such records and those of occurrence of spawning were taken everyday for pairs at St. 3 (3×7 m, at 5 m depth) at the offshore edge of Reef C, in August 1980 (16 days) and August 1981 (27 days).

Detailed observations of courtship and spawning behavior were carried out chiefly in the summers of 1977, 1980 and 1981, amounting to more than 100 hrs. Behavior of pairs before, during and after spawning were continuously observed (up to two hours in one survey), and occasionally recorded by 35 mm still and 8 mm movie cameras. Behavior not directly related to spawning was also frequently observed for more than five minutes per survey at various hours of the day.

To examine the timing of fertilization, egg masses were collected from gravid females or from the mouths of males at various stages during the spawning process, in August 1980 at Reefs B and C. The eggs were kept in tanks, and about 200 eggs per egg mass were examined by a stereoscopic microscope between one to seven hours after collection. I regarded the eggs in normal cleavage as fertilized, and calculated the fertilization rate (FR=number of eggs fertilized/total number of eggs examined) for each egg mass. Furthermore, to determine the exact timing of sperm release, egg masses removed from gravid females displaying prespawning behavior and seeming to be about to spawn were immediately (1) placed near, or (2) kept in water scooped from the vicinity of, another pair of fish in various stages of the spawning process. These were examined by the same method as above at times one to seven hours after the experiments.

At Sakura-jima, underwater observations chiefly of courtship and spawning behavior were conducted in the coastal waters near the Sakura-jima Aquarium at Hakamagoshi (Fig. 1), from July 17 to 23, 1981. The study area was composed of lava rocks on which various stony and soft corals were commonly found. The topography of the area was rather more complicated than that of Shirahama. Twenty-one surveys, 34 hrs in total, were made from 09: 00 to 17: 00, but mostly around noon.

Results

I describe the results of observations made at Shirahama at first, and those at Sakura-jima

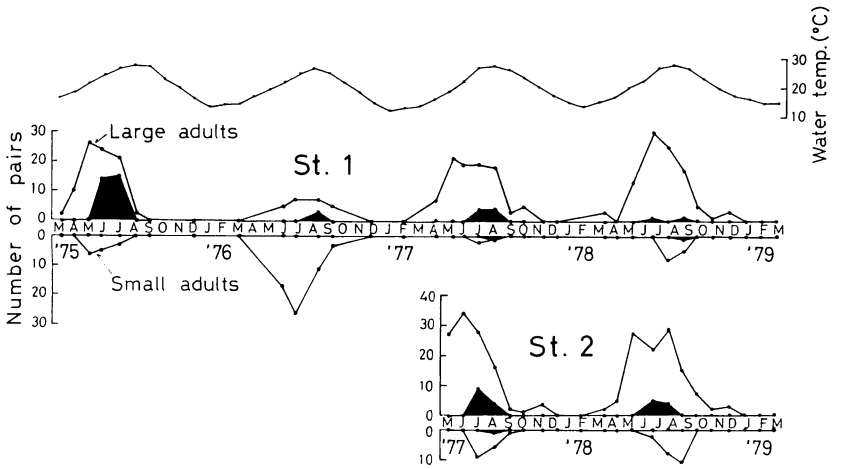

Fig. 2. Monthly fluctuation of the number of pairs at St. 1 and St. 2. When several surveys were made within a month, the data obtained near the middle of the month are shown. Numbers of pairs of large adults (above) and those of small adults (below) are separately shown for each station. Shaded areas indicate the number of pairs in which the male is incubating eggs. Monthly averages of water temperatures, measured at the pier of the laboratory (※ in Fig. 1) at 09: 00 everyday, are also shown.

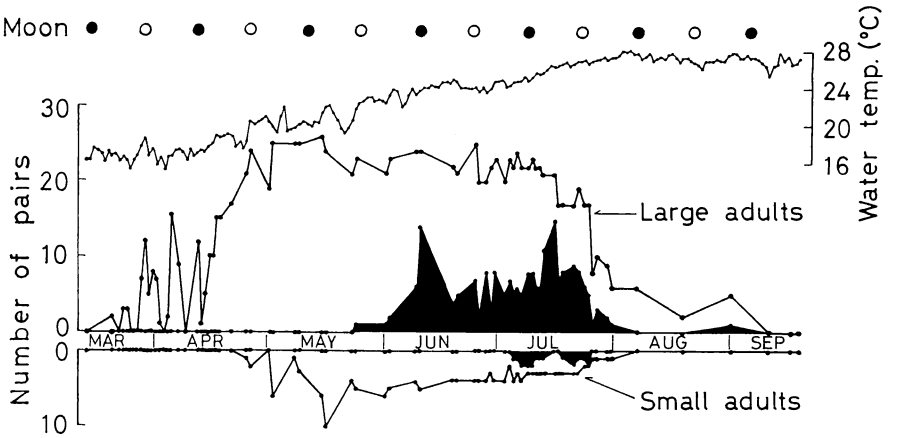

Fig. 3. Daily fluctuation of the number of pairs and egg-incubating males at St. 1 in 1975; illustrated by the same way as in Fig. 2. The moon phase is also shown.

later.

Spawning season. Adults of *A. notatus* usually foraged at night, dispersing in mid-water, and rested in large dense aggregations (see Fig. 5A) in or near rock caves in the daytime. In the spring, the fish began to leave the aggregations and formed male/female pairs. Spawning occurred in those pairs.

Seasonal occurrence of pairs at St. 1 and St. 2 are shown in Fig. 2. Small adults (ca. 7 cm in total length; one year old) and large adults (ca. 9 cm; two or more years old) could be easily discriminated in the field, and pairs were always formed from similar size-classes. Therefore, these are shown separately in the figures. Occasionally small aggregations and hovering solitary fish were also found within the stations, but they are not shown in the figures.

Pairs appeared from late March or April when the water temperature rose over 16°C, and their numbers increased and reached almost a peak in May or June (Fig. 2). The numbers

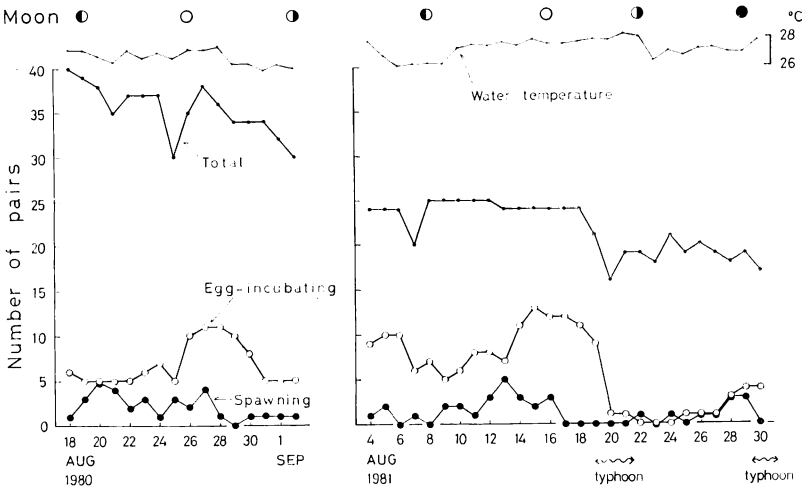

Fig. 4. Daily fluctuation of the number of pairs, egg-incubating males and spawnings at St. 3 in August, 1980 (left) and August, 1981 (right). Water temperatures and phases of moon are also shown.

decreased in August or September although the water temperature was still very high. Pairs of small adults appeared later and disappeared earlier than those of large adults. Egg-incubating males appeared in pairs from late May or June when the water temperature rose over 20°C and about two months later than the beginning of pair formation. They disappeared in early September.

The season of spawning differed to some degree among years. In 1977 spawning began later than in 1975 (Fig. 2). This is probably due to the difference in the water temperature in the two years: in 1977 the average water temperature rose over 20°C in June, while in 1975 it rose over 20°C as early as in May. The large fluctuation in the number of pairs at the beginning of the pair formation period also seems to be partly related to the daily fluctuation of the water temperature (Fig. 3).

During the spawning season, spawnings were observed almost everyday. Spawning does not seem to be related to the moon phase (Fig. 4). When the sea was rough due to the typhoons which often occurred in summer, the number of pairs (and spawnings) also decreased.

With the increase of pairs, the number of fish in aggregations decreased. In the spawning season, most of large adults were found in pairs, but only a part of small adults formed pairs (Table 1). At the middle of the spawning season, aggregations of large adults were com-

Table 1. The proportions of pairing and egg-incubating fish in the breeding season at Shirahama. Fish were counted in the area of 1 m×30 m, near St. 2 in Reef C in 1977. Numbers of large adults (LA) and those of small adults (SA) are shown separately. Solitary fish which could not be determined either a part of a pair or not are included in the numbers of aggregating fish in this table. All surveys were conducted in the afternoon.

Date of survey		Total no. fish (A)	Fish in pairs (B)	B/A%	Egg-incubating fish in pairs (C)	C/(B/2)%	Egg-incubating fish in aggregations (D)	D/(A−B)%	Total (C+D)/A%
June 28	LA	209	108	51.7	22	40.7	92	91.1	54.5
	SA	84	12	14.3	0	0	0	0	0
July 9	LA	155	106	68.4	15	28.3	40	81.6	35.5
	SA	1028	28	2.7	0	0	0	0	0
July 21	LA	158	122	77.2	13	21.3	29	80.6	26.6
	SA	352	24	6.8	1	8.3	18	5.5	5.4

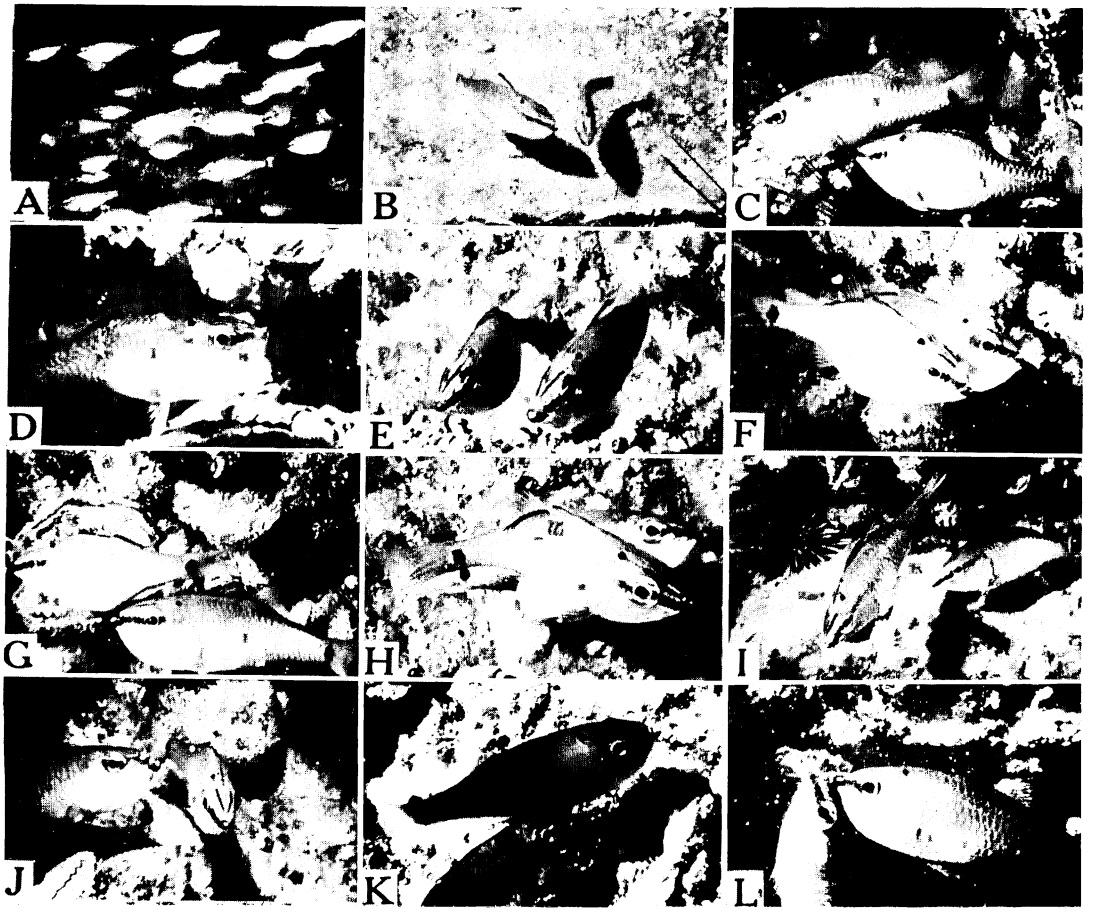

Fig. 5. Behavior of *A. notatus*: underwater photographs taken at Shirahama. A: an aggregation of adults; B: warping by a female (right) to her male partner; C: nuzzling by a female (below); D: mouth-opening by a male (front); E, F: parallel-circling of a pair with the male (right in E and back in F) being outside; G: nuzzling by a male (below); H: spawning in side-to-side position, an egg mass being layed by a female (front); I: mouthing of a male (right) just after spawning; J: rapid-circling by a female (right) around her male partner; K, L: pushing-up by a female (below) from nuzzling position (K) up to the chin of her male partner (L).

posed mostly of egg-incubating fish, while those of small adults included only a few egg-incubating fish.

Formation and maintenance of pairs. Observations on the process of formation of new pairs were limited. A female initiated display similar to "warping" (mentioned later) to a male in an aggregation, and chased him toward a site distant from it. A pair resided at the same site from dawn to dusk everyday. The site will be called the "home site" of the pair. Fish in pairs left their home sites to feed at night along with those in aggregations. A female probably resides at the same site throughout the pair formation season, while sometimes a male may leave the site and move into an aggregation, especially after spawning, and later form a pair with another female at another site (Kuwamura, in preparation).

A male and a female in a pair were usually seen in a side-to-side position. When other conspecifics approached them, they attacked and chased them. A female exhibited attacks about twice as frequently as a male.

A female of a pair often displayed "warping" to her male partner (Fig. 5B). After she swims

away from her male partner, the female swims back to him, warping the body laterally with the abdomen pointed towards him. Then, immediately or after swimming around him, she becomes situated alongside of him. Warping behavior was often seen after the female chased conspecifics. Warping was observed as frequently as 25 bouts per 5 min.

The male did not respond to the warping behavior of his female partner, except for slightly warping the body in a few cases. The male never exhibited any other active display to his female partner except on the day of spawning.

Both attacking and warping were often seen at various hours of day throughout the pair formation season, regardless of the presence of eggs in a male partner's mouth.

Prespawning behavior. In the early morning of the day of spawning, a female's abdomen was observed to be swollen with eggs, and a male's lower jaw was somewhat expanded (though in a few cases these changes were already seen on the previous day). Behavior of a pair also changed, although attacking and warping were still seen.

About 5 hrs before spawning, a female began "nuzzling" at the abdomen close to the genital pore of her male partner (Fig. 5C). The male began to open his mouth widely ("mouth-opening", Fig. 5D). This behavior was repeated intermittently.

Within two hours before spawning, active prespawning behavior began to occur. A female and a male of a pair closely touched the abdomens in a side-to-side position, and slowly moved in circles of about 10 cm in diameter ("parallel-circling", Fig. 5E, F). During circling, the female often took a slightly head-down position, and sometimes hit her abdomen against that of her male partner, or both bumped. The male continued mouth-opening, and his jaw became gradually more expanded. Nuzzling by the female ceased in this phase, instead, the male began nuzzling at the abdomen close to the genital pore of his female partner (Fig. 5G). The prespawning behavior continued intermittently until spawning. However, the order of displays and their frequencies were not constant among pairs. For example, some pairs did not display parallel-circling before spawning during one-hour observations.

Spawning. A female spawns an egg mass, about 2 cm in diameter which contains several thousands of eggs, abruptly without any definite preceding act. I have seen 43 spawning acts at Shirahama, between 11: 35 and 14: 47 (Table 2).

The release of an egg mass occurred mostly in the side-to-side postition with abdomens closely touching (Fig. 5H). However, in two cases the male was situated several centimeters ahead of his female partner, and in one case spawning took place when the male was nuzzling at his female partner. Immediately after spawning, the male turned about or swam back to take the egg mass in his mouth in a single gulp ("mouthing", Fig. 5 I). The egg mass was transferred from the female into the male's mouth within a few seconds.

In 9 out of 46 postspawning cases, a small part of an egg mass (<5 mm in diameter) was left attached to the genital pore of the female. However, the male never tried to take the remaining eggs in his mouth. In 9 out of 78 prespawning cases, a small part of an egg mass was exposed from the genital pore of the female before true spawning, but the male did not try to take these eggs either. In one of these cases, a male "fed" on such eggs (but he later incubated the rest of eggs spawned by the same female).

Postspawning behavior. Just after an egg mass was removed by the male, the female began to go rapidly around him ("rapid-circling", Fig. 5 J) for a few minutes. She exhibited vigorous attacks if other conspecifics approached them. During rapid-circling, the egg-incubating male was stationary, and repeated mouth-opening several times to round the egg mass

Table 2. Spawning time of *A. notatus* at Shirahama.

Time of day	No. spawnings observed
~11:00	0
~12:00	5
~13:00	9
~14:00	21
~15:00	8
15:00~	0
Total	43

which became completely hidden within his mouth.

Then the female began to hit the face of her male partner with her snout. Within two to four minutes after spawning, the female began to take position under her male partner, as in the "nuzzling" position, and moved forwards and upwards pushing the ventral side of his chin up ("pushing-up", Fig. 5K, L). At the end of pushing-up, the female often opened her mouth slightly and hit the male's snout. Pushing-up was repeated, even till dusk in some pairs, although its intensity and frequency gradually decreased. The female also again commenced warping as early as 10 min after spawning, but it was less ferquently exhibited than during prespawning or on other days.

The male did not exhibit any territorial attack after spawning on that day. During the female's pushing-up, the male often began to leave the home site as early as three minutes after spawning, and most males left at least once within 15 min. In a single case out of 31 observations, the male stayed at the home site for more than 30 min after spawning. When a male left the home site, his female partner always followed him, and they sometimes returned together. However, when the male entered an aggregation, the female often lost him, and returned to her home site alone or with another male (either egg-incubating or not) of the aggregation. The female continued pushing-up at the new male partner as well as the original one, either in an aggregation or at the home site. Such leaving and returning of the female and her partner or new male were often repeated several times.

Table 3. Interference of spawning acts by other fishes. Numbers of spawning pairs which were interfered with by respective species are shown.

Species	Pre-spawning phase	Post-spawning phase
A. notatus	1	5
Thalassoma cupido	34	11
Halichoeres tenuispinis	2	3
Pseudolabrus japanicus	0	5
Total	37	24

From the day after spawning, whether the male partner of a pair was egg-incubating or not, territorial attacks by both sexes and warpings by the female were often seen in the pair, the same as on the days before spawning. On the other hand, egg-incubating males which had entered aggregations were inactive and never attacked conspecifics around him.

Interference of spawning. During the spawning process, pairs were often approached by conspecifics or other fishes, and their behavior was disturbed: in 37 out of 78 cases in the prespawning phase, and in 21 out of 46 cases in the postspawning phase. Such interference often occurred especially when a small part of an egg mass was exposed on the belly of the female (8 out of 9 cases, for both phases).

Wrasses (Labridae), especially *Thalassoma cupido*, often chased the female and picked at her genital pore (Table 3). If there were exposed eggs, they fed on them. The male was sometimes chased after spawning, but I have never seen predation on eggs in the male's mouth. Conspecifics also fed on exposed eggs from the female. In one case in which the male opened his mouth to rearrange the egg mass soon after spawning, his female partner took and "fed" on a part of the egg mass.

An egg-incubating male rather easily vomited his egg mass, when he was collected. In such cases, conspecifics including his female partner and other fishes soon came to eat the egg mass. Eggs were often found in the stomachs of collected specimens of *A. notatus* including egg-incubating males.

Timing of fertilization. During the field observations, sperm release could not be visually seen. The timing of sperm release and fertilization was estimated by comparing the fertilization rates (FR) of different egg masses collected at various stages of the spawning process (Table 4). Fertilized eggs kept in a tank were not in cleavage within one hour after spawning. The most developed eggs of an egg mass reached the 4-cell stage in 2 hrs after spawning; 8-cell stage, 3 hrs; 16~32-cell stage, 4 hrs; 64-cell stage, 5 hrs. Even in 4 hrs after spawning some eggs of an egg mass were still at 2-cell stage. Probably due to such difference in development among eggs of an egg mass, the FR of an egg mass kept in a tank sometimes increased slightly

with the lapse of time: e.g., from 83.0% (3 hrs after spawning) to 86.8% (8 hrs); from 79.4% (4 hrs) to 91.6% (8 hrs); from 13.3% (3 hrs) to 16.7% (8 hrs). The figures of FR shown in Table 4 were obtained in three to five hours after spawning, and may sometimes be slightly underestimated values of the true FR of the egg mass; but comparison between different egg masses is possible.

Eggs removed from the body of females, which were displaying prespawning behavior and were collected just before spawning, were not fertilized (Table 4), nor were two small egg masses exposed prior to true spawning. The FR of the egg masses collected just after spawning and before rapid-circling of the female was considerably lower than that of those collected on or after the rapid-circling. Thus, fertilization began just after spawning and was almost complete within a few minutes, during the rapid-circling and before pushing-up of the female. The experiments to time sperm release (putting an egg mass from another gravid female into the water near a pair) did not prove this, since none of the eggs used in the experiments were fertilized. However, it can be estimated that the male begins to release sperm just after spawning, when he tries to take an egg mass in his mouth, and that he continues to release sperm during rapid-circling of the female.

Courtship and spawning behavior at Sakura-jima. Large adults (ca. 9 cm in total length) and small adults (ca. 6 cm) could be also easily discriminated in the field at Sakura-jima in July, 1981. However, small adults were very rare as compared with Shirahama. Most fish formed pairs, although some fish were found in small aggregations (Table 5). Egg-incubating males were also seen both in pairs and aggregations.

Spawning acts were observed in 12 cases, between 12: 18 and 14: 41. The increase in the proportion of the egg-incubating fish from morning to afternoon (Table 5) also suggests that spawning usually occurred in the early afternoon like at Shirahama. Spawning postures in all cases were the same as the common position observed at Shirahama. Courtship, prespawning and postspawning behavior were also similar to those at Shirahama. Some males also began to leave their home sites after spawning, and on the day after spawning the male had changed in one case out of 11.

Table 4. Fertilization rates of egg masses collected at various stages of the spawning process. See text for the method in detail.

Stage	Fertilization rate (%)	No. egg masses examined
Before spawning	0	13
After spawning		
Before or just on male's mouthing the egg-mass	7.1～ 59.7	4
On female's rapid-circling (within 4 min after spawning)	87.1～100.0	6
On female's pushing-up (5 min to 3 hrs after spawning)	79.4～100.0	13

Table 5. The proportions of pairing and egg-incubating fish at Sakura-jima on July 21, 1981. Fish were counted in the area of 1 m×30 m. Numbers of large adults (LA) and small adults (SA) are shown separately.

Time of survey		Total no. fish (A)	Fish in pairs (B)	B/A%	Egg-incubating fish in pairs (C)	C/(B/2)%	Egg-incubating fish in aggregations (D)	D/(A−B)%	Total (C+D)/A%
09:40～10:12	LA	150	126	84.0	24	38.1	3	12.5	18.0
	SA	4	4	100	0	0	0	—	0
16:18～16:03	LA	171	144	84.2	34	47.2	7	25.9	24.0
	SA	0	0	—	0	—	0	—	—

Thus, I was unable to find any significant difference in the reproductive behavior between *A. notatus* at Sakura-jima and Shirahama during the present study.

Discussion

Spawning behavior and timing of fertilization. Nakahara (1962) observed spawning behavior of *A. notatus* in the Sakura-jima Aquarium, and reported that spawning occurred with bellies touching and the male being upside down. However, in the present field study both at Shirahama and Sakura-jima, such posture was not seen. The aquarium observations on *A. notatus* collected from Suruga Bay (Suzuki et al., in preparation) and field observations in Murote Bay of the Uwa Sea, Shikoku Island (Hiromi, unpublished) also support the results of the present study. The spawning posture reported by Nakahara seems to be a variation of the normal belly-touching position, or to be an unusual behavior due to aquarium conditions.

Nakahara (1962) also reported that eggs and sperm were released at the same time, although no experimental evidence was shown. However, detailed examination of egg masses at various stages of the spawning process in the present study shows that the sperm release began a few seconds later than egg release, i.e., at the time when the male tried to take eggs in his mouth, and that eggs were mostly fertilized within a few minutes after spawning, during rapid-circling and before pushing-up of the female.

In another species *A. imberbis*, the occurrence of internal fertilization during "nuptial rounds", which is very similar to "parallel-circling" of *A. notatus*, of pairs was suggested (Garnaud, 1962). However, the evidence of internal fertilization given by Garnaud seems to be insufficient, as was already pointed out by Breder and Rosen (1966: 405). At least in one species of genus *Apogon*, i.e., *A. kallopterus* (=*snyderi*), in Hawaii, internal fertilization does occur during the spawning process somewhat different from that of *A. notatus* and *A. imberbis* (Chave, 1971 after Barlow, 1981; Chave, personal communication).

Causal analysis of reproductive behavior. Reproductive activity of *A. notatus* at Shirahama was related to the rise of the water temperature. Pair formation began when the water temperature rose over 16°C, and spawning began when it rose over 20°C (Figs. 2, 3). Nakahara (1962) described that spawning activity of *A. notatus* at Sakura-jima had its peak in the season of highest water temperatures, from late July to early August. However, at Shirahama the peak of spawning activity occurred, strictly speaking, just before the period of highest water temperatures (Fig. 3). That is, spawning activity decreased prior to the fall of the water temperature, being affected probably by day length and typhoons, as was suggested in the sympatric labrid *Labroides dimidiatus* (see Kuwamura, 1981).

Behavior of a pair changed only on the day of spawning. The female's display on usual days, i.e., warping, seems to have an effect to keep her male partner stationary at their home site but is not directly related to spawning. When her eggs became ripe, the female initiated the prespawning process by nuzzling at her male partner. However, prespawning behavior, i.e., parallel-circling and others, did not occur in a definite order or frequency, and spawning took place abruptly without any definite preceding act. This may be a strategy to choose a safe time to spawn, because other fishes often interfered with the prespawning pairs.

In contrast to this, the postspawning process progressed always in a definite order. The male's mouthing behavior seems to be released by both chemical and visual stimuli. Even the male in a position of several centimeters ahead of his female partner tried to take an egg mass immediately after spawning, although he probably could not see it. However, visual stimulus seems to be also necessary, as the male did not try to take a small egg mass exposed before or after spawning.

Removal of eggs by the male from his female partner seems to cause rapid circling by her. The rapid-circling may facillitate fertilization by making violent water movements around the male which is repeating mouth-opening, for fertilization was mostly completed during this behavior.

During the process of pushing-up of the female, it also seems as if she brought sperm from the genital pore of her male partner to his mouth, in which eggs are carried. However, since

fertilization was mostly completed before this behavior, pushing-up may have only an assisting effect, if any, on fertilization. The alternative effect of this behavior seems to be to drive her male partner out of the home site into an aggregation prior to finding another male (Kuwamura, in preparation).

Sex of mouthbrooding parent in apogonids. In *A. notatus* only males exhibit oral incubation of eggs (present study; Nakahara, 1962; Suzuki et al., 1980; Hirai and Dotsu, 1981; Hiromi, unpublished). Viewed from the process of spawning behavior, mouthbrooding by the female is improbable; for she begins a sequence of behavior only after eggs are removed by the male from her body. Although I once saw a female taking a part of an egg mass from the mouth of her male partner soon after spawning, she ate it and never incubated.

In other species of Apogonidae, mouthbrooding generally occurs only in males (Fowler and Bean, 1930; Breder and Rosen, 1966; Suzuki et al., 1980; etc.). In a few exceptional cases, eggs were found also in a female's mouth: in *Apogon lineatus* (Amamiya, 1934; but see Sakamoto, 1931; Yamada, 1957; Omori and Takahashi, 1980), *Apogon semilineatus* (Ebina, 1932; but see Suzuki et al., 1980), *Cheilodipterus affinis* (Smith et al., 1971), *Foa madagascariensis* (Petit, 1931 after Breder and Rosen, 1966). However, all these reports were based on collected specimens, and actual mouthing behavior of such females in the process of spawning was not observed. Since the egg mass was often vomited by the male and eaten by both sexes when he was disturbed (also see Yamada, 1957; Mine and Dotsu, 1973; Omori and Takahashi, 1980; Hirai and Dotsu, 1981), the eggs in the mouth of the female specimen may have resulted in this way. Moreover, mouthbrooding by the female seems to be improbable from the osteological point of view: structure of the lower jaw of the female differs from that of the male in most apogonids (Hayashi, personal communication).

In contrast to apogonids, oral incubation of eggs is usually done by females, instead of males, in cichlid fishes (Fryer and Iles, 1972; Keenleyside, 1979; etc.). It has been suggested that maternal mouthbrooding in cichlids has evolved from biparental guarding of eggs in substrate spawning ancestors (Baylis, 1981). No such ancestral forms other than mouthbrooders have yet been found in apogonids. In the environment where the predation risk on eggs just after spawning is high, paternal mouthbrooding is obviously more advantageous than that by females, since the exposed time of eggs to predators is shorter when the male takes them than when the female does. In apogonids, the predation risk on exposed eggs is seemingly very high, and therefore, it seems to be one of the most effective factors contributing to the evolution of paternal mouthbrooding.

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クロホシイシモチの産卵行動と受精時期

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雄親が卵の口内保育を行うクロホシイシモチ（テンジクダイ科）の求愛産卵行動を，和歌山県白浜および鹿児島県桜島での潜水観察をもとに記載した．また，様々な時期の卵塊の受精率を調べ，放卵にやや遅れて放精・受精がおこることを明らかにした．産卵期に影響を及ぼす環境要因と，一連の求愛産卵過程における各行動の機能と解発因について論じ，また，テンジクダイ科における口内保育担当者の性についても若干の考察を加えた．

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