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Reproductive Behavior of an Eleotrid Goby *Odontobutis obscurus* in Aquaria

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Abstract Frequency observation on 5 essential movements of the reproductive behavior of an eleotrid goby, *Odontobutis obscurus*, was made in aquaria. The nesting male made a few characteristic movements (fanning, upside-down movement, and beating) before the female's entrance into his nest. After the entrance of a female in the nest, the male's beating disappeared; weaving, the upside-down movement, and quivering were observed frequently in the two sexes at prespawning and in spawning. Weaving and fanning by the egg-guarding male were frequent at the time immediately after the spawning as well as hatching of larvae. Dead eggs infected by aquatic fungi were not observed in the egg mass guarded by the male, in contrast with the unguarded egg mass. In addition, more dead eggs were dropped during 48 hr-experiment from the guarded egg mass than from that unguarded. It is suggested that the dead eggs were shaken out of the nest by such movements of the egg-guarding male as weaving and fanning, before the fungal infection spreads over the whole egg mass.

Introduction

Odontobutis obscurus (Temminck and Schlegel) is an eleotrid goby, about 15 cm in body length, which is distributed in western parts of Japan. The fish prefers the sandy bottom of stagnant waters in the middle and lower reaches of rivers. They feed on small fishes and crustaceans (Okada, 1960). Dôtu and Tsukahara (1964) reported their breeding habits in the field and in an aquarium. The breeding season of the fish in Kyushu is between April and June when water temperature ranges from 15 to 20°C. The egg mass is found under stones, concrete blocks and other fixed substances on the stream bed as well as in nest-shelters artificially introduced to an aquarium, and guarded by the male. However, the reproductive behavior of this fish has not yet been described in detail.

In the present report, the reproductive behavior of this fish is described along with a frequency record of some essential movements in the respective stages of its reproductive behavior. In addition, the role of parental behavior in preventing aquatic fungi from spreading over the egg mass is also discussed. The breeding ecology of *O. obscurus* in captivity will be reported in another paper by the present author.

Material and Methods

1. Observation of reproductive behavior

Newly hatched larvae of *O. obscurus* were obtained by large round polycarbonate tank (1000 *l* in volume) in 1973 and 1974. They were reared in glass aquaria for a year or more, and their reproductive behaviors were observed from April to July in 1974 and 1975. Water in aquaria was circulated through the layers of gravel, active charcoal, and glass wool in a filter box placed above the aquaria. Water temperature was regulated at 18±1°C from October to April and at 20±1°C from May to September in 1973 and 1974. In 1975, water temperature was not regulated and ranged from 8°C in January to 24°C in the breeding season. Several sets of shelters composed of piled opaque hard vinyl pipes and/or black vinyl mesh (4 mm) pipe (15 cm in length and 5 cm in diameter) were introduced on the gravelled bottom of the aquaria. The fish were fed in excess on oligochaet *Tubifex* before maturation, and on small live loaches during and after the breeding season.

Table 1 shows the date of spawning and aquarium conditions. The frequencies of several essential movements of reproductive behavior, excepting parental behavior, were checked at observation No. 5 for 30 min by the tally system.

Table 1. Date, body length of *O. obscurus* and aquarium condition in the observations of reproductive behavior.

Observation No.	Date of spawning	Body length of paired fish in cm (age in years) ♀	♂	Water temperature (°C)	Aquarium size (cm)	Number of fish in the aquarium ♀	♂
1	May 28, '74	8.5 (1)	9.5 (1)	20	30×90×45	3	10
2	Jul. 2	7.5 (1)	10.0 (1)	20	30×90×45	3	10
3	Apr. 7, '75	11.2 (2) 8.0 (1)	14.8 (2)	16	30×120×45	2	2
4	Apr. 30	9.5 (2)	13.0 (2)	19	30×60×45	1	1
5	May 21	7.7 (1)	10.4 (2)	18	30×60×30	1	1
6	Jun. 9	9.7 (1)	12.0 (2)	21	30×60×45	1	1

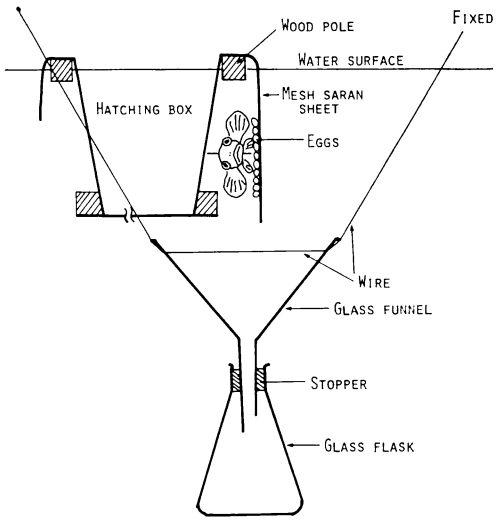

Fig. 1. The apparatus for the collection of eggs dropped from the egg mass which was deposited on saran sheet, and an egg-guarding male. The apparatus was composed of a glass funnel (20 cm in diameter at the upper margin) and a triangular glass flask (1 *l* in volume), and was set up one day before the first 48 hr-collection. The saran sheet was part of a hatching box floated near the water surface in the 1000 *l* tank.

In this case, a gravid female was introduced into an aquarium where a ripe male had been kept alone for two weeks. The frequencies of essential movements in parental behavior were checked at observation No. 6 for 30 min twice a day. The first observation was made at any 30 min between 10: 30 and 11: 30 hr and the second one between 13: 00 and 15: 00 hr.

2. Role of parental behavior

Two kinds of observations were made of the egg masses deposited in the large round tank. First, the degree of infection by aquatic fungi was compared between two egg masses, (a) one guarded by a male and (b) one unguarded, for about 2 weeks after spawning. Secondly, the eggs dropped from the nest in such two cases were examined (Fig. 1). The experiment was done using a single egg mass, which was guarded by a male for 13 days after spawning, during successive 96 hr; (1) during the first half (48 hr) the eggs were guarded as usual, and (2) during the latter half (48 hr) the male was removed and the eggs were left unguarded. Water temperature in the large round tank was regulated at 20±1°C by a water cooler.

Results

Reproductive behavior was divided into three parts: prespawning, spawning, and parental behaviors, according to Liley (1969). Most of the essential movements of each behavioral stage are named after Tavolga (1954, 1956) and Winn (1958).

1. Prespawning behavior

The body color of *O. obscurus* is monochromatic, and little sexual dimorphorism is apparent in non-breeding season. But in breeding season, the outer margins of the male's ventral, pelvic and anal fins including ventral side of caudal fin thicken and become tubercled with some semi-transparent secretive substance. Such an estrous male emits yellow sperm by pushing the basic part of its urogenital papilla. The male is apt to stay in and near the specific nest-shelter during most of the day. The nest-shelter is defended against intruders by a series of aggres-

sive behaviors as described by Yamagishi et al. (1974).

The entire procedure of nest preparation was accomplished by a male, and the nest was used for the spawning site. The nest preparation was composed of two main movements, i.e., carrying gravel into the nest-shelter mainly with the mouth, and fanning in it. A small amount of gravel was carried into the nest-shelter of mesh vinyl pipe where the inner surface was rough. On the contrary, much gravel was gathered and flattened on the floor in the nest-shelter of hard vinyl pipe where the inner surface was smooth. But this action was not so frequent as fanning. Fanning

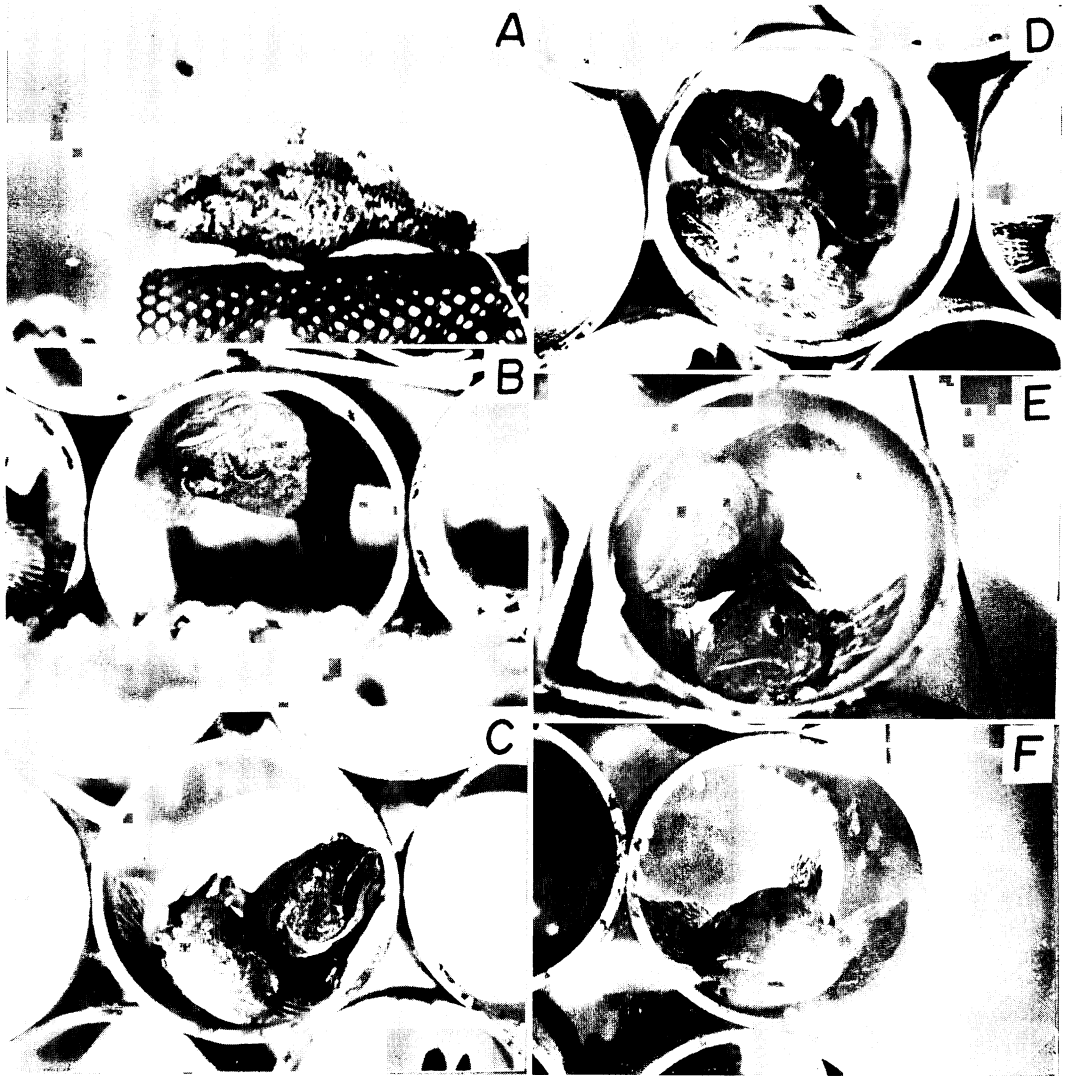

Fig. 2. Reproductive behavior of *Odontobutis obscurus*.
(A) A gravid female out of a mesh nest-shelter. (B) Upside-down movement of an estrous male in his nest-shelter. (C) Pairing immediately after the female's entrance into the male's nest-shelter (male-beside-female position). The female (at left, lighter) pushed her body closely to the male's body against butting of the male. (D) Pairing (male-on-female position). Butting and other aggressive signs disappeared in the male (the upper and darker) and the two sexes repeated fanning and weaving. (E) Spawning. The fish in upside-down position is male. Female darkened as the male. (F) Egg-guarding male after spawning.

Table 2. Frequencies per 30 min of each essential movement and staying time in nest-shelter per 30 min, of estrous female and male in two cases; when the two sexes were isolated in different aquaria (30 min), and when the female was introduced into the male's aquarium (1 hr).

Condition (Observation time)	Isolated (15: 00–15: 30)		(15: 30–16: 00)		Male and female together (16: 10–16: 40)		(16: 40–17: 10)	
Sex	♀	♂	♀	♂	♀	♂	♀	♂
Fanning	3	10	10	22	3	14		
Upside-down movement	0	0	0	6	0	8		
Beating	0	0	0	46	0	51		
Attacking to the opposite sex	—	—	0	0	0	1		
Weaving	0	1	0	3	0	1		
Quivering	0	0	0	4	0	9		
Occurrence of swimming out of nest-shelter	18	1	5	3	9	4		
Staying time in nest-shelter (min)	0	29.5	2.0	29.5	0	28.0		

is vigorous alternate strokings of both pectoral fins occasionally accompanied by waving of the caudal fin. The movement continues for 5 to 20 sec in a sequence, and the frequency of the stroking of a pectoral fin is about 1.4 oscillations per sec, though large variability exists. The alternate stroking of pectoral fins in fanning differs from that in swimming. In swimming, pectoral fin stroking is simultaneous and not alternate in most cases. The resultant forward thrust as a reaction to fanning seems to be prevented by using the pelvic fins to stand slightly forward on the gravelled floor in the nest-shelter. Fanning was also observed in the female, but her fanning was not so frequent as in the male's. The female was often observed out of the shelter and frequently swam for about 3 to 10 cm in a sequence (Fig. 2-A).

The response of the estrous male in the nest-shelter to an approaching gravid female was clearly signaled by dark coloration of the body and some characteristic movements, i.e., upside-down movement (Fig. 2-B) and beating. The upside-down movement starts with gradual declining of the body along the inner surface of the nest-shelter and proceeds to an exact upside-down position. Hanging down for several seconds in that state, the male recovers on the floor by two motions, returning back through the same pathway taken just before, and further turning over 180° to 360°. Here the movement when the fish declined its body over 90° was regarded as the upside-down movement even if the fish did not make the further turn over. During this movement, the fish usually strokes its pectoral fins alternately more slowly than in fanning, putting the tip of its snout out of the opening of the nest-shelter. The upside-down movement lasted about 5 to 20 sec in a sequence. Beating is continuously pulsatile shaking of whole body with all fins expanded. Usually beating lasts about 5 to 15 sec in a sequence at the rate of about 1.4 pulsations per sec.

Table 2 shows the change in the frequencies of each movement of the estrous male and female before and after introducing the female into the male's aquarium. In the male, the first beating and upside-down movement occurred at 5 and 9 min respectively after the introduction of the female. The male's fanning speed increased about 2 oscillations per sec when the female approached to his nest. In contrast with the characteristic movements of the male, the female did only occasional short-step swimming. Sometimes the male left a nest-shelter and entered a neighboring one. It is interesting that, in spite of these "attracting" movements, an undeniable attack by the male against the female occurred at 46 min after the introduction of the female. Eventually, the female paired with the male in his nest-shelter.

In many cases, females entered a male's nest-shelter from the back opening, namely from behind the male. Immediately after the entrance

of a female, the male attacked the intruder by butting and pushing with his head against her body side. When he received the intruder during an upside-down position, he quickly returned to his normal position and began to attack. In spite of this attacking by the male, the gravid female did not usually retreat. She pressed her body side against the male's body and tried to sink under the male, waving her pectoral and caudal fins vigorously in the male-beside-female position (Fig. 2-C). Soon after these resistive movements of the female, the male ceased to attack and permitted the female to sink under his body (male-on-female position, Fig. 2-D). Even when the female retreated from a male's nest-shelter because of his attacking, she did not go far, and sometimes entered the neighboring shelter. In this case, the male followed the female and paired with it. Unless the male followed her, the female challenged the next entrance into the male's nest-shelter and usually succeeded in pairing after two or three trials.

Table 3 shows the frequencies of each movement in the two cases; pairing in male's nest-shelter and spawning. Remarkable movements in pairing are weaving and quivering. In weaving, the fish just weaves his body right and left about once or twice per sec accompanied by simultaneous waving of anal and caudal fins. Both pectoral fins stroked alternately according to the weaving of the body. A sequence of weaving usually lasts 3 to 10 sec. Quivering is a fine vibration of the whole body. The vibration is rather noticeable in the caudal and dorsal fins. Quivering lasts also about 3 to 10 sec in a sequence. After the pairing, no more beating occurred. The frequency of fanning increased in comparison with the prior stage of pairing, especially in the female. In fanning and weaving, the male and female frequently rubbed each other's skin with pectoral and caudal fins in male-on-female and male-beside-female positions. During these movements, the male and female erected their urogenital papillae. The female sometimes changed the direction of her body in the nest-shelter and took a reverse orientation against the male (with her head to the male's tail). Their mouths were slightly shut except occasional repeat of opening and shutting. The female sometimes yawned. The paired individuals paid no regard to the movements of other fish in the aquarium. But when another fish approached their nest-shelter too closely, i.e., within less than about 10 cm, the male broke the pair and left the nest-shelter to drive away the intruders. In the progress of courting the male darkened to almost patternless. All expanded fins of the male were also darkened except a few white bars in the dorsal fins and the white margins in the dorsal and caudal fins. The female also gradually darkened but not so much as the male at this stage. The state of pairing usually continued for about a half day, and then spawning began.

Table 3. Frequencies of each essential movement in 30 min at two stages of reproductive behavior in one day; after the female's entrance into the male's nest-shelter (pairing), and in spawning. These observations were made on the same individuals shown in Table 2, on the next day.

Condition (Observation time)	Pairing (11: 30-12: 00)		Spawning (17: 30-18: 00)	
Sex	♀	♂	♀	♂
Fanning	42	27	42	38
Upside-down movement	1	6	20	8
Beating	0	2	0	0
Weaving	20	15	84	54
Quivering	30	35	66	28

2. Spawning behavior

In spawning, no different movements from the latter part of prespawning stage were observed. In this stage, the female also darkened until she was almost patternless, as the male, and she made more frequent upside-down movements, weaving, and quivering than in the prior stage (Table 3). Sitting closely to each other side-by-side in several places (on the floor, on the side wall of a nest and on the ceiling), the female and male alternately repeated quivering and weaving (Fig. 2-E). During the female's quivering, the eggs were extruded from the erected and swelled urogenital papilla. Approximately 5 to 10 eggs were extruded in one series. The eggs adhered to the substrate (inner surface of the nest-shelter) as they were extruded. In one case, eggs were deposited on the glass wall of the aquarium (observation No. 3 in Table 1). The spawning continued for about 6 hr to a half

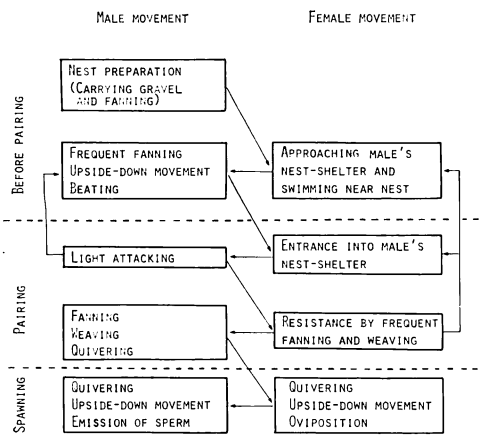

Fig. 3. Ethogram of reproductive behavior up to spawning of *O. obscurus*. The zigzag arrows in the center indicate the order of appearance of each movement. In the case of female's retreat from the male's nest due to attack immediately after her entrance, the movements of the two sexes return to the prior stage as indicated by the arrows on the right and left sides.

day, though large variability seemed to exist depending on the size of the female and the number of eggs extruded. The outline of the reproductive behavior of *O. obscurus* up to spawning is summarized as an ethogram in Fig. 3.

In five cases in Table 1, spawning was done by one male and one female. In one case (observation No. 3), spawning behavior was observed between a male and two females (a large female and a small one). The oviposition of the smaller one was not ascertained, but she acted as if she were a spawner. Female egg extrusion without any pairing was observed in two cases when the water temperature was below 15°C in early April in 1975, when no male made any mating gesture.

3. Parental behavior

After spawning, the female leaves the nest and begins to feed rapaciously. The root of the urogenital papilla of the female was reddish for a day after the oviposition. On the other hand, the male shut himself up in his own nest and guarded the deposited egg mass by aggression against intruders as well as against an observer's hand which was inserted into the aquarium (Fig. 2-F). The male rarely left the nest for feeding and quickly returned after he captured food. Such an egg-guarding male's main movements were fanning and weaving, and the male rubbed the eggs with all his fins except the dorsal fins in these movements. The changes of frequency of the essential movements during the parental behavior are shown in Table 4. Fanning and weaving were extremely frequent on the first day after the spawning, but the frequencies markedly decreased at the next day. These movements became frequent again on the 18th and 19th days, when the larvae hatched. At that time, fanning was not so clearly distinguished from weaving as in the prior stages, because the both movements occurred successively. Beating occurred only on the first and second days after the spawning. This movement was observed especially when the post-ovulatory female approached the nest. Until the 2nd day after spawning, when beating was observed in the male, he did not attack the approaching female.

Table 4. Changes of frequency of each essential movement per 30 min in parental behavior of the male fish. The frequencies of these movements are shown as the average of the two 30-min observations except on the 10th, 22nd and 25th days when the observation was made once a day. Water temperature ranged between 21 and 24°C, and hatching of larvae occurred on the 18th and 19th days. The female was removed from the aquarium on the 8th day.

Days after spawning	1	2	4	6	10	14	18	19	22	25
Fanning	78.5	38	27	24	21	26.5	37	34.5	15	2
Upside-down movement	12.5	7	5.5	6.5	2	3	3.5	3.5	0	0
Beating	18	11	0	0.5	0	0	0	0	0	0
Weaving	72	27	24	15	15	23.5	41.5	44	23	2
Attacking to the female	0	0	2	1	—	—	—	—	—	—

Table 5. The degree of infection by aquatic fungi in egg masses under two conditions; being guarded by a male, and not guarded, for about 2 weeks after spawning in the large round tank.

	Total number of eggs in nest	Number of dead eggs	
		Infected by fungi	Uninfected by fungi
Guarded egg mass	960	0	48
Unguarded egg mass	186	86	20

On the contrary, after the 4th day the male's attacks against the female replaced his almost disappearing beating.

Table 5 shows the degree of infection of egg masses by aquatic fungi when they were guarded or not guarded by the male after spawning. In the guarded egg mass, several dead eggs were observed among live eggs, but these eggs were not at all infected by fungi. On the other hand, infected eggs comprised most of the dead eggs in the unguarded egg mass.

Table 6 shows the number of dead eggs dropped from an egg mass in each of two cases in Fig. 1: guarded by a male in the past 48 hr, and not guarded by him in the following 48 hr. In the former 48 hr period, 10 dead eggs and prematurely hatched larvae dropped with a few *Nematoda* and dust, but in the latter 48 hr period few dead eggs and hatched larvae dropped from the nest.

Hatching of larvae succeeded in observations Nos. 3, 4 and 6 shown in Table 1. But in observations Nos. 1, 2, and 5, all eggs were shaken off the nest-shelter before hatching by the rough movements of the male parent fish. After all of larvae hatched from the nest-shelter or all eggs were shaken off, the male fish usually stayed as ever in the nest-shelter.

Discussion

One of the most important problems in the reproductive behavior of fishes, such as *O. obscurus* which show territoriality with secretive habits, seems to be discriminating the estrous partner of the opposite sex from the others. For the *O. obscurus* female, in the discrimination of the male, particular male movements such as the upside-down movement and beating may play a useful role. Both movements seem to comprise courtship behavior in the male. Especially beating was noticeably frequent before pairing of the two sexes. The male of a few gobies, *Parioglossus taeniatus, Pterogobius elapoides,* and *P. zonoleucus*, is known to approach the gravid female and lead her to his nest with immediate interaction such as pecking and rubbing against the female (Dôtu, 1956; Dôtu and Tsutsumi, 1959; Tsutsumi and Dôtu, 1961). But, such an immediate interaction was not observed in the reproductive behavior of *O. obscurus* in the present work, as also reported on this species by Dôtu and Tsukahara (1956), and on other gobies, *Glossogobius olivaceus, Lubricogobius exiguus* and *Gobius gymnauchen* (Senta and Wada, 1970; Dôtu and Fujita, 1963; Nakamura, 1944). Winn (1958) reported that the male of the darter, *Etheostoma nigrum,* performed the upside-down movement in his nest when the gravid female came near. The fact that taxonomically different fishes such as Eleotridae and Percidae have a similar behavior pattern in the prespawning stage is very interesting in considering the origin of the courtship behavior. Tavolga (1955) reported that the courtship behavior of the male of *Bathygobius soporator* was caused by

Table 6. Number of eggs dropped from nest on the saran sheet in two cases; guarded by a male for the first 48 hr, and not guarded for the following 48 hr.

	Number of dead eggs			Number of live eggs and/or hatched larvae	Other dropped substance
	Infected by fungi	Uninfected by fungi	Total		
Guarded	7	3	10	10*	Several *Nematoda* and dust
Unguarded	1	1	2	1	Scanty

* Almost all were larvae hatched prematurely.

the internal fluid of the ovary of a gravid female. During the enthusiastic "attracting" movements such as the upside-down one and beating, the male of *O. obscurus* attacked the female at a later time after the introduction of the female (Table 2). This fact seems to show that the male often regards the female as an intruder when she hesitates to enter the male's nest-shelter even if she is gravid.

It was not clear from the present observations whether the post-ovulatory female leaves the nest because of his attacks or by herself. But the spawning activity of the male seems to continue for a few days after the spawning because the male showed such courtship behavior as beating instead of aggression during 2 days after spawning (Table 4). For this reason, the post-ovulatory female seemed to leave the nest by herself without any attacking by the male. After she leaves the nest, the appearance of the male's aggression against the female (on the 4th day after spawning) instead of courtship behavior may be caused by some change in an inner mechanism of the male, perhaps hormonally as suggested by Aronson (1957) and Liley (1969).

The egg-guarding habit of the male parent fish is known in other many gobies (Dôtu, 1954, 1959, 1961a, 1961b; Dôtu and Fujita, 1963; Dôtu and Tsutsumi, 1959; Shiogaki and Dôtsu, 1971, 1972a, 1972b; Tsutsumi and Dôtu, 1961; Tavolga 1954). However, the detailed role of this parental behavior seems to be unknown due to a lack of quantitative analysis. In the case of *O. obscurus,* this behavior seems to be functional for avoidance of overall infection of eggs by fungi. Dead eggs may be shaken out of the nest mainly by the egg-guarding male's fanning and weaving, before the fungal infection. The thickened and tubercled fins of the male of *O. obscurus* may be related to such parental care of eggs. Not only dead eggs but also prematurely hatched larvae and other substances dropped from the nest guarded by the male. Premature hatching observed here may be promoted by the male's mechanical stimuli. Such premature hatching is not rare in the egg incubation of *O. obscurus* (Mashiko, 1976). Baerends and Baerends Van-Roon (1950) reported that the eggs of cichlid fish die soon after the removal of a parent fish, and pointed out the importance of egg-cleaning behavior by the parent fish. Winn (1958) reported that darter eggs attacked by fungi were eaten by the egg-guarding male, and that eggs were covered with fungi soon after the removal of the male. The treatment of dead eggs and the prevention of fungal infection of the egg mass seems to play an important part in the parental behavior of some kinds of fishes. However, the role of sending a current of fresh water to the egg mass may also be important when the egg mass is deposited in a nest in a stagnant flow as described in stickleback by Rowland (1974).

During the parental behavior of the male of *O. obscurus,* frequent fanning and weaving were recorded twice (Table 4). The first one, on the next day after spawning, may be regarded as an extension of spawning activity. But it is interesting that the second one was observed on the days of larval hatching. Visual stimuli such as wriggling of the larvae in chorions immediately before hatching may be related to the frequent movements of the male. Tail-shaking by the embryo was often observed at that time through the chorion. This frequent fanning and weaving of the male may be effective for the breakage of the chorion in paralleled with action of the hatching enzyme. Tavolga (1954) also noted the presence of such two peaks of the egg-guarding male's activity in *Bathygobius soporator.*

In Table 1, all deposited eggs were shaken out of the nest by the egg-guarding male's rough actions of weaving and fanning in observations Nos. 1, 2, and 5. The age of the parental male in observations Nos. 1 and 2 was one year. The young male may be unskillful at parental care of eggs, and probably prior experience is necessary for skillfulness such as displayed 2-year-old males in observations Nos. 3, 4 and 6.

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ドンコの産卵行動

益子　計夫

ドンコの産卵行動の水槽内観察により，5つの基本的動作を区別し，それらの出現頻度を産卵行動の進行過程に沿って記録した．その結果，営巣中の雄は雌の接近により頻繁な fanning, upside-down movement, beating を行い雌を巣中に誘いこむ．番いを形成すると雌雄は頻繁な upside-down movement, weaving, quivering を行い，産卵する．産卵後の卵を保護中の雄には主に fanning と weaving が認められ，両動作とも産卵後頻度は減少するが，仔魚のふ化時に再度増加

した．雄親魚によって保護されていた卵塊では，そうでない場合と比較して，水生菌に侵された死卵がなく，また多数の死卵が落下することから，雄親魚の巣中での fanning と weaving は死卵を卵塊からかき落すことにより卵全体が水生菌によって侵されるのを防ぐ役割を持っているのではないかと示唆された．

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