UNDERWATER OBSERVATIONS AND EXPERIMENTS ON PAIR FORMATION AND RELATED BEHAVIOURS OF THE APOGONID FISH, APOGON NOTATUS (HOUTTUYN)¹⁾

HIDEAKI USUKI

4-10-36, Mukodai-Machi, Tanashi City, Tokyo

With Text-figures 1-6

Abstract

(1) Underwater observations and experiments on pair formation in Apogon notatus were conducted almost every morning in June to July, 1976 in a rocky region north of the Seto Marine Biological Laboratory. (2) Experiments manifested that homing of this fish at least in the rocky region can be referred to the "pharotaxis". But homing in the sandy area remains still unexplained. (3) The usual sex recognition of this fish is thought to be based primarily on the differences in behavioural patterns between the sexes, while the mate identification in paired fish is supposed to be closely related to their determined attitude at the nest site. (4) Defended space, or individual space of paired fish is regarded as territory from the viewpoints of territory definition and its functional significance. (5) The smaller aggregations formed mostly in the season of pair formation is comparable with "the club" of the herring gull, *Larus argentatus*, from the viewpoint of animal sociology. As the aggregated fish maintain their restricted area for the time, the term "home site" may be used in explaining the behaviours of this fish. This seemingly accords with the results of studies on other fishes.

Introduction

Various cardinal fishes of the family Apogonidae are known for their habit of oral brooding (Tanaka, 1915; Sakamoto, 1930; Ebina, 1932; Amemiya, 1934; Garnaud, 1950, 1962; Hobson, 1965; Tanase, 1968; Fishelson, 1970; Smith, 1971 and others) as in the cichlid fishes (Baerends *et al*, 1950; Show *et al*, 1954; Fryer *et al*, 1972 and others). As to the one of them, *Apogon notatus* (Houttuyn) that is met with very commonly in dense aggregation in the vicinity of the Seto Marine Biological Laboratory, the spawning behaviour was observed and described by Nakahara (1962). Generally the pair formation by a male and a female precedes to the oviposition and mouth incubation of eggs in oral-brooding fishes, though the pair is kept for the time of different length in respective species. Thus, the pair formation is indispensable in the process of their reproduction. Further, it not only implies the maintenance of a couple by a definite male and a definite female but also includes some ethological problems in the natural circumstances, such as the homing behaviour

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to the nest or home site, orientation for domiciliation, selection and identification of the partner, and the territorial aggression to others. Although many observations have been published on the oral-brooding habit, feeding habit (Vivien, 1975; Hobson, 1974), production ecology (Yamada, 1957) and the circadian rhythm (Livingston, 1971) of various cardinal fishes, information is still hardly available as to those ethological problems mentioned above. The present paper is to record the field underwater observations on the pair formation of *Apogon notatus* and the results of some experiments designed to analyse this behaviour. In addition, on the basis of new findings obtained during the present study, some points in the social organization of this fish such as the territory, aggregation, individual space, home site, etc. are discussed.

Methods of Observation and Experiment

In the nearshore waters, north of the Seto Marine Biological Laboratory in Shirahama, Wakayama prefecture, *Apogon notatus* occurs in numerous small aggregations each consisting usually 50 to 500 fish over shallow rocky floors in the breeding season from June to August, but in several much bigger aggregations respectively consisting of a tremendous number of fish over rocky reefs in the other season. For the present study, the region around a rocky outcrop about 50 m off the north ccast of the laboratory ground and the neighbouring area over the sandy or boulder floor were selected (Fig. 1 & 2) and most of observations using scuba were conducted by the three specific rocks, named during the study tentatively "Three Rocks", at the depth of 4–5 m on the southeast margin of this rocky region at least for 40 minutes at a time almost every morning in June and July, 1976. General observations on



Fig. 1. The study area, from the north coast of the Laboratory ground. Arrows a, b and c show respectively the site of each of the "Three Rocks", the point for releasings (XVI and XVII) and the releasing point (XVIII). See Text -figure 2.

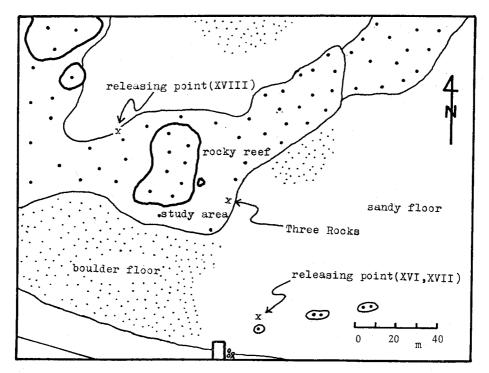


Fig. 2. Bottom topography around the rocky area studied, indicating the sites of "Three Rocks" and the releasing points XVI to XVIII. Hatched are the raised rocks.

behaviours of various fishes of course inclusive of *Apogon notatus*, lasted from March 17 to December 30 of the same year, were made by about 220 dives in total.

During the observations, several experiments were made in order to confirm what were actually seen or to analyse the observed behaviours of the fish. Those experiments are classified as follows:

(1) Expelling experiment. In order to learn more exactly the homing behaviour, domiciliation, mate recognition and some other habits, that are respectively important constituent factors of the social organization of this fish, it was tried to expel either of a pair or any one of aggregating fish out of the living space in the rocky region. This was achieved rather easily by expelling an aimed fish by a plastic sheet for underwater recording as seen in Fig. 3. Subsequent experiments in each observation were usually started soon after the former experiment was ended.

(2) Covering experiment of nest site. To learn how a couple of this fish recognize each other without fail, their nest site was covered by the author's body and the behaviours of these shut out fish were traced carefully.

(3) Driving-in experiment. For the same purpose as in the covering experiment, it was tried to drive another fish into the nest site of a certain couple of this fish and the behaviours in these fish were closely observed. Driving was done as in the expelling experiment.

(4) Release of marked fish. In order to analyse the orientation of the fish in the

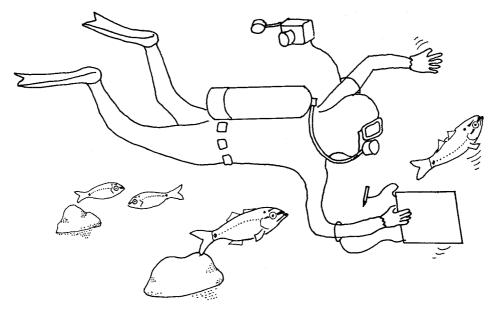


Fig. 3. Any aimed fish, paired or in aggregations, could be expelled very easily to any desirable places by using a plastic sheet of underwater recording, though this was limited within the rocky region.

sandy region, some marked fish were released there and traced as far as possible. Collecting and marking of the fish and release of marked fish were all done as underwater works and during a single dive in most cases, except only marking on July 28, that was done on land. Aimed fish were collected from around the "Three Rocks" by underwater angling and respectively marked by hypodermic injection of Chinese ink and vermillion while they were still hooked. These marked fish were measured and stored in a nylon bag till an enough number of fish were secured, when they were released at selected points in the sandy region and then traced (Experiments XVI and XVII). Identification of the experimented fish was made distinctly by combination of black and red spots at different positions. The marking positions are shown in Fig. 4. For instance, a fish marked with vermillion at two points 1 and 5 was defined as "No. r (red) 1–5". In addition, tagging with a piece

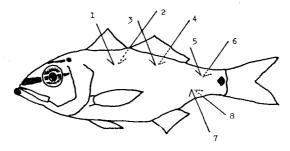


Fig. 4. Marking points were set and numbered as shown above, odd numbers on the left, while even numbers on the right side.

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of red nylon line on the dorsal part of the body was tried in some cases.

The sex of this fish could not be confirmed by external appearance unless they were already ready to spawn. However, females of pairs present, sometimes even in a preceding state to breeding, a "lateral display" by showing her curved body. Such a "lateral display" was usually observed frequently in pairs, but also in aggregations though rarely. Against that the fish presenting a "lateral display" were defined as females, those accepting the display were identified as males.

All the fish observed during these experiments could be divisible into two size groups, the larger fish group consisting of 8 to 9.5 cm long fish and the smaller fish group including 5 to 8 cm long fish. And most of the fish experimented with belonged to the latter group. Observation records were put immediately on a plastic sheet during diving, and an underwater SLR camera and an 8 mm underwater cine camera were used for registering the fish behaviours. The water temperature, transparency, swells and waves were checked regularly at every observation and experiment.

Record of Observations and Experiments

As known well already in other cardinal fishes, *Apogon notatus* are observed aggregating in the rocky region to take shelter in the daytime and go out from to the open water at night. In their reproductive period, many pairs are formed in various spaces in the rocky region so densely that some fish might touch one another. In such cases they attack and expel those approaching so closely their nest site to keep the small space around them. The following observations and experiments were made in such conditions.

Observations mainly on the behaviours of the expelled fish and remaining one of pairs

Observation I. On June 26, at the southeast margin of the rocky region, water temperature 22° C. A preliminary observation was made on an aimed pair. Two other pairs were found 50–60 cm apart from this pair and an aggregation of this fish consisting of more than 300 individuals was staying 0.5–1.5 m above the pair during the observation. The female of the pair presented the "lateral display" to the male 24 times in five minutes.

Expelling Experiment I-a. The male of this pair was moved 4 m apart from the nest site and then released. He soon began to swim very slowly but straight towards the nest site and coupled with his former female partner without hesitation.

Expelling Experiment I-b. The same male was moved again to a distance of 4 m and there released. He behaved just the same as in I-a.

Expelling Experiment I-c. The same male was moved 4 m apart once more and released. He returned to the nest site as in two previous experiments. This time, however, his female partner had already formed a new pair with another mate and attacked her former mate partner fiercely. He tried to couple with her again eight times in about 5 minutes, but in vain. Observation II. On June 27, at the south east margin of the rocky region, water temperature 23°C. The female of an aimed pair presented the "lateral display" to the male and an aggressive behaviour to others three times respectively in 5 minutes.

Expelling Experiment II-a. The female of this pair was moved to a distance of 5 metres from the nest site and released. She immediately started to return slowly to the site. She showed an aggressive behaviour to another fish at the distance of 40 cm to her male partner and then coupled with him presenting the "lateral display".

Expelling Experiment II-b. The male of the same pair was moved 5 m apart from the nest site and there released. But he remained there still. Five minutes later, he was urged to move and began to swim slowly towards the nest site. He made speed at a distance of 50 cm to his female partner and was accepted by her with her "lateral display".

Observation III. On June 28, at the southeast margin of the rocky region, water temperature 22.5°C. The female of an aimed pair presented the "lateral display" to the male eight times and an aggressive behaviour to others six times in 5 minutes.

Expelling Experiment III-a. The female of this pair was moved 3 m apart from the nest site and released. She returned to the site straightly, but approaching slowly her male partner. She attacked one of aggregating fish before she coupled with her former partner, presenting the "lateral display".

Expelling Experiment III-b. The male of the same pair was moved to a distance of 3 m to the nest site. The male began to swim towards the site 30 seconds after the release. When he approached his female partner staying 40 cm apart from the nest site, she shivered as if in preparation for attack. But this was not done, and she moved to the regular nest site being accompanied by her male partner.

Observation IV. On June 29, at the south east margin of the rocky region, 22°C. The female of an aimed pair attacked others 22 times and presented the "lateral display" to her male partner twice in 5 minutes.

Expelling Experiment IV-a. The female of this pair was moved 25 m apart from the nest site and released. She returned, slowly but straight, to the site in 3 minutes and 45 seconds.

Expelling Experiment IV-b. The male of the same pair was moved about 25 m, but in a course with a right turn on the way. When released, he returned slowly but almost directly to the nest site to couple with his female partner in 4 minutes and 15 seconds, but stopping two times on the way.

Expelling Experiment IV-c. A fish of an aggregation consisting of about 100 unpaired fish hovering near above this pair was moved into another adjacent aggregation 5 m apart from the former aggregation. When released it returned slowly but directly to its former aggregation.

Expelling Experiment IV-d. A fish of the same aggregation was moved into the next aggregation but one 10 m apart from its own aggregation. When released it returned to the former aggregation through the adjacent aggregation.

Expelling Experiment IV-e. A fish in the same aggregation was moved 5 m but in the direction opposite to that in two previous experiments. Released fish

returned slowly to its former aggregation.

Observation V. On July 4, at the south east margin of the rocky region, water temperature 21.5° C. This time, three pairs (a, b, c) and a single domiciliating female (d) were aimed. All these fish were found located 20 to 30 cm apart from one another and any other hovering aggregations were not observed in the neighbourhood. Only an attack of the female of the pair c against a fish of the pair a was recorded. The "lateral display" was observed twice in the pair a, eight times in the pair b, and twice in the pair c in 5 minutes respectively.

Expelling Experiment V-a. The male of the pair a was moved 6 m apart from his nest site and arrested there for 5 minutes. When released, he soon started to return to the nest site. His female partner noticed him when he reached 20 cm above the nest site and attacked on his belly. However he didn't wear to go forward to the nest site and when he attained there the female presented the "lateral display" to him.

Expelling Experiment V-b. The female of the pair a was moved 6 m apart from the nest site and arrested there for 5 minutes. When released, she began to swim slowly towards the nest site after about a minute. When she reached there, she presented the "lateral display" to her male partner staying 20 cm above the site.

Expelling Experiment V-c. The female of the pair c, situated 30 cm apart from the solitary domiciliated female (d), was moved 6 m apart from her nest site and arrested there for 5 minutes. When released, she soon returned to the site and coupled again with her former partner that remained solitary without forming a pair with the female d living just near.

Removing Experiment of a possible sign from the nest site V-d. A small stone, about 15 cm in diameter and laid on the floor below the living space of the pair a, was removed. However, the pair remained still there, though exactly moved about 10 cm apart from the former site. No special changes were noticed in their appearance.

Removing Experiment of a possible sign from the nest site V-e. A stone, about 25 cm in diameter and laid on the bottom below the nest space of the pair b, was removed. The pair seeked refuge during this action, but soon returned exactly to the former site when the turbid water cleared up and remained there without showing any change in their appearance.

Observation VI. On July 6, at the south east margin of the rocky region, water temperature 21.5° C. In this observation, three pairs (a, b, c) were aimed. Four other pairs were domiciliated near by 40–50 cm apart from one another and nearly 50 fish were aggregating 50–100 cm above the bottom. One of the aggregated fish, that had been tagged with a piece of red nylon line by a big rock about 10 m west of the "Three Rocks", was defined as 5-R. No positive "lateral display" was presented in the aimed pairs in 5 minutes of observation, although a few attacks were made by some of these pairs against some fish of the aggregation.

Expelling Experiment VI-a. The male of the pair c was moved 10 m apart

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from his nest site. When released he soon returned to the nest site. When he noticed his female partner, however, he approached her bending his head sidewise.

Expelling Experiment VI-b. The male of the pair b was moved in a zigzag course to a distance of about 15 m from his nest site. When released he soon began to proceed in the direction to his nest site, stopped three times on the way, but advanced almost straight towards the site, and made speed to pair with his female partner female, however, presented only simply her "lateral display" to him.

Expelling Experiment VI-c. The fish 5-R was moved in a zigzag course to a distance of 15 m from its former site. When released, it started immediately to proceed slowly towards the site of aggregation and was included in that aggregation.

Expelling Experiment VI-d. The female of the pair a was moved 10 m apart from her site. When released she remained there still for about a minute. Then, she began to swim slowly towards her nest site. The male accepted his female partner approached him with her head bending sidewise, but without any special expressions in his appearance.

Expelling Experiment VI-e. The male of the pair a was moved 10 m apart from his nest site to just the same point as in the experiment VI-d. When released, he soon returned to the nest site.

Observation VII. On July 7, at the same place as in the Experiment VI, water temperature 22°C. Two pairs (a, b) were aimed in this observation. Eight other pairs were domiciliated near these and about fifty fish were aggregating only 10–20 cm above the bottom. The "lateral display" and aggressive behaviour were recorded in these pairs, but not so often in 5 minutes of observation.

Expelling Experiment VII-a. The male of the pair a was moved 10 m apart from his nest site and his return was awiated at the nest site, where his female partner remained still without any particular changes in her appearance. In 50 seconds after releasing, he came home and approached the female swiftly at the angle of 45° to her body axis. The female advanced 2–3 cm slightly bending her head sideways and presented the "lateral display" to him.

Expelling Experiment VII-b. The male of the pair b was moved 15 m apart from his nest site and his retrun was awiated at the nest site, there the remaining female made a violent attack against the adjacent pairs four times and against a fish of the aggregation twice in a minute till the male came home and approached her swiftly. This time the female accepted the male almost motionlessly.

For the results of further expelling experiments see Expelling Experiment XIV-a (p.).

Observations mainly on the behaviours of the fish shut out of their nest site Observation VIII. On July 9, at the south east margin of the rocky region, water temperature 24°C. During five minutes' observation, only a single pair was aimed, of which the female was discriminated by a natural cut at the lower tip of the tail fin, while the male by a short black streak on the second dorsal fin, thus the former was recorded as "Cut Tail" and the latter as "Black Streak" (Fig. 5). Three other pairs were found around this pair and about 80 fish were aggregating more than 50

Pair Formation of Apogon notatus

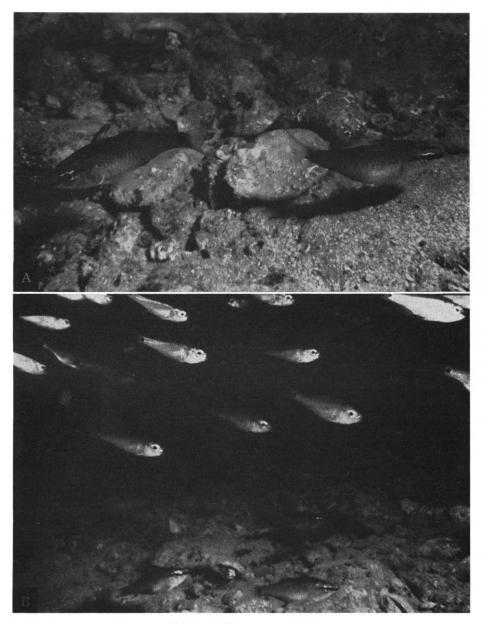


Fig. 5. Appearances of the pair of "Cut Tail" and "Black Streak". Above (a) Cut Tail on the right is presenting the "lateral display" to "Black Streak" on the left by curving her body. Note the cut lower tail tip of the former and a black short streak on the second dorsal fin of the latter (photographed on July 9). Below (b) About 80 fish are agregating above the pair of "Cut Tail" on the left and "Black Streak".

Below (b) About 80 fish are aggregating above the pair of "Cut Tail" on the left and "Black Streak" on the right (photographed on July 9)

cm apart from these pairs.

Covering Experiment VIII-a. When the nest site was perfectly covered by the observer's body and Cut Tail and Black Streak were shut out of the site they flew into the aggregation of fish, that was remaining in a metre or more from the observer. The two discriminated fish in the aggregation were quite indifferent to other fish and no interference was observed between these two and other fish of the aggregation in 10 minutes of observation. However, sometimes the two fish approached the observer to return to their nest site but in vain, being expelled by the observer. When the observer raised his body about 30 cm above the site so that the two fish might be able to return to their nest site below the observer's body, Cut Tail presented the "lateral display" to Black Streak eleven times in 2 minutes even at a distance of more than 40 cm to the site. As soon as the site was evacuated entirely, they came home and there the former presented the "lateral display" to the latter. Immediately they became self-possessed, without any sign of particular appearance.

Note VIII-b. Shortly later a fish happened to approach close to this pair. Cut Tail immediately presented the "lateral display" to the stranger in spite of the presence of Black Streak just by her, stayed there still for a while and left the site slowly. No attack against this stranger was made by the pair.

Observation IX. On July 10, at the same place as in Observation VIII, water temperature 23.5°C. Observations were made on Cut Tail and Black Streak. This time an aggregation of 25 fish was found near by this pair. The male made an attack against some fish of adjoining pairs five times, while the female twice in 5 minutes. Cut Tail presented the "lateral display" to Black Streak only once.

Covering Experiment IX-a. When the nest site was covered by the observer's body, both fish flew into the aggregation but then crept in beneath the body to reach the nest site. Cut Tail approached Black Streak positively six times in 15 minutes, the complete "lateral display" was manifested twice, but in four other cases the male avoided her display. In addition, Cut Tail approached other males thirteen times, but the complete display was manifested only once, while in twelve other cases males avoided her display. When the nest site was uncovered, Cut Tail presented a great display to Black Streak at the site.

Observation X. On July 11, at the same place as in Observation VIII, water temperature 24°C.

Covering Experiment X-a. When the nest site of Cut Tail and Black Streak was covered by the observer's body, they flew into an aggregation of more than 200 fish staying near by the site but then crept in beneath the observer's body in trying to reach nearer to the nest site. In 10 minutes of observation, Cut Tail made 7 approaches positively to Black Streak, inclusive of two perfect "lateral displays" and 5 positive approaches to other males, inclusive of a complete "lateral display".

Observations on the relation between a certain pair and the strangers driven into the nest site of that pair

Observation XI. On July 12, at the same place as in Observation VIII, water temperature 24°C. Driving of a single fish into the nest site of Cut Tail and Black Streak by using the plastic sheet for underwater recording was tried twenty-three times and succeeded in two cases.

Driving-in Experiment XI-a. A fish of unknown sex, that was driven into the site of the pair, remained still there for a while. At this fish Cut Tail shivered for 3 to 4 seconds. Immediately after this act by Cut Tail, the stranger flew away, being pursued by the hostess of the nest. She came home soon.

Driving-in Experiment XI-b. When the male of an adjoining pair was driven into the nest site of Cut Tail and Black Streak, the hostess of the nest shivered at the male driven in there, and the latter flew away in a second, being pursued by the former.

Miscellaneous observations on the discriminated male (Black Streak) and female (Cut Tail)

Observation XII. On July 15, at the same place as in Observation VIII, water temperature 25°C.

Early morning observation XII-a. The observation was made from 5:00 to 5:40. An aggregation of 250–270 fish was hovering about 2 m above the bottom feeding planktonic matters. The pair of Cut Tail and Black Streak and 5 other neighbouring pairs were found domiciliated at their respective nest sites. Males of these pairs sometimes swam up slowly to feed and hurriedly came down to their nest sites. In such cases, females followed their male partners respectively as far as 70–100 cm from the bottom. In doing this Cut Tail presented the "lateral display" even to another male else than her partner three times, but every time she was immediately attacked by the female partner of the male that she allured. On the other hand, Black Streak was once presented the "lateral display" by another female else than Cut Tail.

Observation XIII. On July 16, at the same place as in Observation VIII, water temperature 25°C.

Note XIII-a. The sea was rough for a typhoon drawing near, and all the fish, paired or in aggregations, were being swung for 1 to 2 m. While the water swing was less than 1 m, Cut Tail and Black Streak could maintain the pair keeping themselves close to each other 40 to 60 cm above the floor, and Cut Tail made even an attack against the neighbouring fish. But, when the water swing was over 2 m, the pair collapsed and respective fish entered the adjacent aggregation; the pair was formed again, however, when the swing dropped somewhat.

Observation XIV. On July 20, at the same place as in Observation VIII, water temperature 25°C. This day, it was found that the male partner of Cut Tail, namely Black Streak, was replaced by another male. Black Streak himself was observed endeavouring to couple with Cut Tail again but in vain on account of fierce attacks against him of his former female partner and her new mate.

Expelling Experiment XIV-a. The new male partner of Cut Tail was moved at a distance of 15 m from the nest site and behaviours of Cut Tail and Black Streak during his absence were observed at the nest site. Black Streak approached Cut Tail but was attacked by her four times in 80 seconds, when the expelled male returned there and coupled with her.

On July 21 Cut Tail was observed keeping a pair with an undiscriminated male, but Black Streak could not be found in the neighbourhood of her nest site. *Observation XV.* On July, 22, at the same place as in Observation VIII, water temperature 26° C.

Note XV-a. Cut Tail was found paired with an undiscriminated male and Black Streak was living alone only 50 cm apart from the pair. Four other pairs were found in the neighbourhood and an aggregation of 300–350 fish was formed about 1.5 m above these pairs. When the aggregation moved about 3 m from the mentioned site, the pair of Cut Tail, solitary Black Streak and the other pairs followed it disuniting their pairs that were, however, recovered at the proper positions when the aggregation returned to the former place.

On July 23 and 24 no dive was made as the sea was rough. And after July 25 Cut Tail and Black Streak disappeared from the place of observation and since then the pairs in the area were reduced.

Observations on the behaviours of the fish in the sandy region

It was very easy to move the aimed fish within the same rocky region, the fish could be moved to any desirable place in the region. However, it was practically impossible to expel any fish from the rocky region into the sandy or boulder region. The fish evidently disliked to go out of the rocky region and as soon as dodged the swing of a plastic sheet in expelling experiments they would come back there at full speed. Therefore, in order to learn how the fish keep their orientation in the sandy area, there was no other way else than tracing the marked fish carried to and released in the sandy region.

Releasing Experiment XVI. On July 28, calm water, water temperature 27°C, underwater visible distance 5 m. Twelve single fish of respective pairs were caught around the "Three Rocks" in 10:05–11:00, marked on the land, and released in the shallow sandy region 50 m south of the "Three Rocks" (for the site see Figs. 1 and 2) in 14:00–16:00.

No. bl (8.8 cm) was eaten by a lizardfish, *Trachinocephalus myops*, at the middle on the way from the releasing point to the rocky area where the fish had been living.

No. b2 (7.2 cm) went offshore northerly from the releasing point and was lost out of sight.

No. b3 (9.2 cm) went inshore southerly from the releasing point and domiciliated at the rocky part in the sandy area.

No. b4 (8.9 cm) died during the expreimental operation.

No. b5 (8.7 cm) went offshore 20 m from the releasing point and there seemingly lost its way, only swimming to and fro beneath the water surface.

No. b6 (8.9 cm) went offshore and was soon lost out of sight.

No. b7 (7.6 cm) went straight to the rocky area but could not return to its former nest site.

No. b8 (9.2 cm) went inshore first, but then turned the direction to the rocky area. It was lost out of sight on the way but was observed at its former site at 16:30 of the same day.

No. r1 (8.5 cm) returned almost directly to its former site.

No. r2 (7.5 cm) only wandered about as if in low spirits.

No. r3 (7.5 cm) went offshore and was lost out of sight.

No. r4 (7.5 cm) went offshore meanderingly and was attacked by a *Trachinoce*phalus myops, but barely escaped from this by moving about just beneath the water surface.

Releasing Experiment XVII. On July 30, fine weather and calm water, water temperature 27°C, underwater visible distance 6–7 m. Seven single fish of respective pairs were caught around the "Three Rocks" and marked in the water in 10:00–10:25, and released in the shallow sandy area 50 m south of the "Three Rocks" in 10:30–11:20.

No. b2-4 (7.6 cm) went inshore and domiciliated above a rock in the sandy area, remaining there that afternoon.

No. b2-6 (7.7 cm) went offshore and was lost out of sight.

No. b2–8 (7.5 cm) came back first to the releasing point, but then turned towards the rocky area through the boulder area, though it could not reach the former site.

No. b2–1 (9.4 cm) went north-easterly towards the rocky area through the boulder area.

No. b2–3 (9.7 cm) went towards the rocky area, but was attacked and eaten by *Trachinocephalus myops* on the way.

No. b2-5 (6.7 cm) went straight towards the rocky area after moving around above the releasing point. As soon as it reached the rocky region, it swam along the region to its former nest site.

No. b2–7 (7.5 cm) went straight to the rocky area but could not return to its former site.

Releasing Experiment XVIII. On July 31, calm water, water temperature 27°C, underwater visible distance 6–7 m. Eleven of aggregated (not paired) fish were caught around the "Three Rocks" and marked in the water in 10:00–11:00, and then released at the north-east margin of the rocky region (see Figs. 1 and 2), just opposite the "Three Rocks" across the region, in 11:10–11:25.

All of the specimens released one by one, r2-4 (7.4 cm), r2-5 (6.1 cm) r2-6 (5.5 cm), r2-8 (6.7 cm), r1-2 (6.5 cm), r2-3 (6.2 cm), r2-7 (6.2 cm), r4-6 (7.5 cm), r4-8 (7.2 cm), r1-4 (8.5 cm) and r4-3 (8.4 cm), joined with about 150 fish aggregating at a distance of 1.5 m from the releasing point and remained there that afternoon. Two of them, No. r2-4 and No. r1-4, were however found their former site next morning, on Aug. 1.

Releasing Experiment XIX. On August 1, calm water, water temperature 27.5°C, underwater visible distance 6 m. Twelve of aggregated (not paired) fish were

caught around the "Three Rocks" and marked in the water in 11:10-11:55, and released at the same site as the fishing point in 12:00-12:05.

All of the specimens released one by one, No. r1–3 (6.2 cm), No. r1–3–5 (8.0 cm), No. r1–5 (6.1 cm), No. r1–7 (7.2 cm), No. b3–4 (7.3 cm), No. b3–5 (7.2 cm), No. b3–6 (5.5 cm), No. b3–7 (6.8 cm), No. b3–8 (6.4 cm), No. b4–5 (7.5 cm), No. b4–6 (7.0 cm) and No. b4–7 (6.5 cm), joined with about 200 fish aggregating above the "Three Rocks", and four of them, No. r1–3, No. r1–5, No. r1–7 and No. b4–5, were found near by their former site next morning, on Aug. 2.

Releasing Experiment XX. On August 2, calm water, water temperature 27° C, underwater visible distance more than 10 m. Eight of aggregated (not paired) fish were caught around the "Three Rocks" and marked in the water in 9:50–10:25 and released at the surface over the sandy area 80 m north-east from the "Three Rocks" in 10:30–10:40.

Six of them, No. r5–6 (7.2 cm), No. r5–7 (7.2 cm), No. r6–7 (8.8 cm), No. b5–6 (7.8 cm), No. b5–7 (8.7 cm) and No. b6–7 (6.4 cm), went slowly towards the south, while No. b5–8 (9.5 cm) went slowly towards the north. No. r6–8 (7.1 cm) went down to about 1 m to the bottom and swam northerly 2 m, where it was attacked and eaten by a lizard fish, *Saurida elongata*. None of these released fish was met with around "Three Rocks" in the following dives.

Discussion and Supposition

Homing in the Rocky Region

The results of 24 expelling experiments (I-VII & XIV) indicate that any of paired or aggregating fish are provided with an ability to come back almost straight to their nest site, even when they are moved in a zigzag or turned course. This suggests that the fish of this species possess a good memory of the topographic features of the home area where they are aggregated or keeping a pair in the daytime. Aronson (1951) proposed, after many observations and transfer-experiments of the goby to other various pools, a working hypothesis that a goby, *Bathygobius soporator*, swims over the tide pools at high tide and acquires an effective memory of the general features of the topography of a limited area around the home pool which they are able to utilize when locked in their pools at low tide. The above-mentioned results agree well with what were shown by Aronson in respect of the homing orientation of the goby, in spite of the differences between a tide-pool dweller, the goby, and a rocky-reef dweller in the daytime, the cardinal fish.

According to the results of the covering experiments (VIII-X) and the removing experiments of possible signs (stones in the present case) from the nest site (V-d and e), it is apparent that, the fish approach the nest site by keeping the course by conceiving the whole configuration around the site but not by aiming at some signs in the site. This type of homing has been reported and discussed in the case of the hunting wasp, *Philanthus triangulum*, which is responding not to particular landmarks

but to the pattern of all of them, and defined as "pharotaxis" (Beusekom, 1948; Tinbergen, 1951). Then, homing of this fish may safely be said to belong to the pharotaxis, too, as far as the results presented in this paper are concerned.

Orientation in the Sandy Region

In the releasing experiments of 28 marked specimens in the sandy area (XVI, XVII, XX), three fish were eaten by lizardfishes and one died. And only three of them were found again at their former sites and four were observed in the rocky area. Therefore, seven of 24 live fish could return to the rocky area.

Winn *et al* (1964) demonstrated parrot fishes could utilize their sun-compass in oriented daily movements and escape movements. On the other hand, Nakazono *et al* (1971) reported a wrasse, *Halichoeres tenuispinis*, released on the sandy bottom, swam towards the nearest rocky reef. In discussing the fish orientation in the sandy area, it may be referred to that bees usually use landmarks in flying but over the bare area without any landmarks they decide the course by menotaxis, the sun compass orientation (Tinbergen, 1951).

It has never been observed that *Apogon notatus* are swimming solitarily in the sandy area in the daytime. The fish released in the sandy area looked timorous or frightened and seeking for any shelter. These are probably related to the fact that expelling of this fish into the sandy area could not be succeeded. As the releasing experiments were done under such difficult conditions and the results obtained are rather unsatisfactory, the possession of any orientation ability in the sandy area of this fish remains still suggestive but not conclusive.

Sex Recognition and Mate Identification

Apogon notatus are not sexually dimorphic though the belly swells in females and the mandible becomes protracted in males for oral brooding in the breeding condition. But the female of a pair was observed even on January 10, 1977, seemingly never in the breeding condition, presenting the "lateral display" to the male and making an aggression against other fish. Pairs of this fish were found mostly in June to July, though a few in other warm months and rarely in the winter season. Oehlert (1956) reported that in some cichlid fishes, in which the sexes were not dimorphic, the formation of heterosexual pairs was brought about in different ways by how the three main motivations (aggression, escape and sexuality) inhibited each other in the two sexes. Besides, it was reported even in such sexually dimorphic species as *Hemichromis bimaculatus* that the initial sex recognition was based primarily on the perception of movements but not of colour (Fryer *et al*, 1972). Observations on *Bathygobius soporator* indicate that the male permits the nest entry of a female that resists his nipping, butting and other pugnacious activities (Tavolga, 1954).

Although no attempt is made here to analyse the mechanism of sex recognition in *Apogon notatus*, the following observation made in 14:00–15:30 on July 15 is suggestive of a factor of sex recognition: Two or three females pursued several times a male straight at a considerable speed in an aggregation of 150–170 fish, often presenting the "lateral display" to the male, and then the male went out of the aggregation with one of the females and domiciliated above a small rock. This pursuit and escape display in an aggregation seems to suggest some factors not only of the sex recognition but also of the initiation of pair formation. Anyhow, as far as suggested from many observations and several expreiments, it is likely that the differences in the behavioural patterns between the male and the female in *Apogon notatus* play more important role than any others in sex recognition as in cichlid fishes as well as in permission of the pair formation as in the goby. Anyhow, the sex recognition and the mate identification in *Apogon notatus* can not be discussed separately to thinking of the present author.

Expelling experiments (I-VII and XIV, exclusive of I-c) and observations on Cut Tail and Black Streak manifest that two fishes of respective pairs identify each other in some way. But, it is unnatural that the fish discern their mate from other innumerable fish only by exact individual morphology. The clue to this problem must concern how two fish behave when they meet with each other. According to the results of expelling experiments, however, any explicit behavioural patterns or any ritual displays effective in identifying individuals have not been observed at pair formation, rather the way of pair formation is seemingly various: e.g. a female advanced to present the "lateral display" to an approaching male (VII-a), was almost indifferent to the male (VII-b), or attacked the male (V-a). On the other hand, the expelled males clearly purposed to enter the space of their former nest site even though they had an interference with their female partner. This was demonstrated clearly in the covering experiments, too. Further, it was observed in Note VIII-b and Observations IX, X and XII that Cut Tail presented the "lateral display" by mistake to another fish else than her mate, and in XII that Black Streak was presented the "lateral display" mistakenly by another female else than his mate. These mistakes were made limitedly at a distance of 50-100 cm from their nest site but in the case of VIII-b, that might, however, be treated similarly. Thus, the identification of the mate is seemingly related to the domiciliation of the fish. On the other hand, the approach of a stranger close to the nest site was inhibited by an instant attack of Cut Tail against it (Driving-in Experiments XI-a and b) or stimulated Cut Tail to present the "lateral display" to it (Note VIII-b). Summing up the above-mentioned arguments, the author is inclined to think, that the determined attitude of the fish approaching to the nest site is the most important in the mate identification, on other words for the permission to domiciliation at the nest site and for the pair formation, though some exception were observed as in Expelling Experiment I-c and Observation XIV.

Spacing-out Behaviour

The fish select the nest site along the crack, between the rocks, above a boulder or even around the middle on the vertical face of large rocks for pair formation. Paired fish, especially the females, always defend their ambient space from entering of a neighbouring paired fish or a stranger. This spacing-out is limited usually within a distance of 20-30 cm from respective pairs, though over 50 cm in a few cases, almost independent of fish density around them. And, whenever the site of domiciliation of pairs is shifted in some way, this space will move with the paired fish as seen in Observation XIII, in which the paired fish moved about 100 cm up from the usual nest site for large water swing, presented an aggression to neighbouring pairs. The similar behaviour was observed usually whenever the water swing became larger. Approaches of piscivorous fish (e.g. *Sebastiscus marmoratus*) to the nest site or stays of larger fish (e.g. *Pseudolabrus japonicus, Plectorhyncus pictus*) at the site also brought about a shift of the nest site together with the space. When the water swing diminished or such a fish went away, the paired fish recovered their usual site. This space of the fish, therefore, may be referrable to individual space, that is kept free of other individuals by aggressive or avoidance behaviour. In addition, this spacingout naturally reminds the author of territory, that is generally defined as any defended area.

Here, some discussions will be needed on relations between individual space and territory. Dice (1952) classified home ranges and territories into several types, in which a defense of the winter covey of the California quail and a defended space around the blue-goose family were listed in moving territory. On the other hand, Hinde (1956) defined territory as "a topographically localized defended area" and regions defined by reference to moving datum (e.g. "individual distance", "mated female distance") were excluded from typical territory. Then, can the individual space of Apogon notatus be regarded also as a territory? The domiciliary space of pairs is larger than the defended space as seen in Observation XII and XIII, but preferable sites for the nest may be decided in order in respective domiciliary space (Fig. 6). And pairs of marked fish were observed within 50 cm of the usual nest site except during the period under such bad conditions that they could not remain there in some way. The defended space of this fish is, as a matter of fact, restricted in a definite small space and, strictly speaking, may be called rather a movable space than a moving space as paired fish are never willing to shift their nest site. Therefore, there will be no objection to regarding the space as a topographically localized defended area, apart from the problem whether moving territory listed by Dice belongs to a matter of territory or not. Apogon notatus do not need such food-supplying area as Plecoglossus altivelis or Gerres oyena do, but need a space for pair formation and breeding. From the viewpoint of functional significance, the spacing-out in Apogon notatus seems to be a biological adaptation, as Myrberg et al (1974) mentioned that the major advantages of any territorial system rest with reproductive function and access to food resorces, and may well be called a territory, that is one of important social organizations in advanced animals.

In the author's opinion, problems on complicated relations between territory and individual space seem to occur not only to the fishes that can shift their territory (Apogon notatus) or overrun their territorial boundary in pursuing intruders, such as Eupomacentrus planifrons (Myrberg et al, 1974), Plecoglossus altivelis (Mizuno et al, 1957) and Gerres oyena (in the spring season of 1976, unpublished data), but also to the

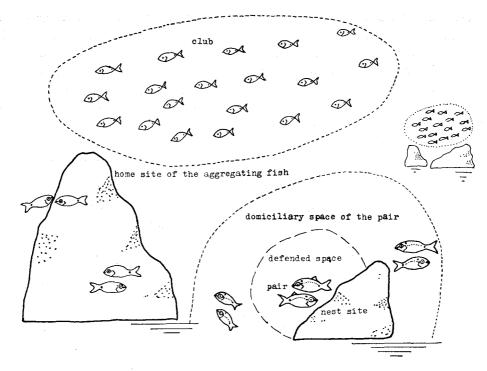


Fig. 6. The social structure of *Apogon notatus* in the daytime in the season of pair formation suspected from the present observations and experiments. For the details of the domiciliary space and the defended space of paired fish and the club of aggregated fish, see the text.

fishes showing well defined territories such as Hypsypops rubicunda (Clarke, 1971), Gerres oyena (Usuki, 1976) and Pomacentrus flavicauda (Low, 1971). Leyhausen (1971) suggested that in sedentary animals, the intolerance toward others expressed as individual distance may increase during the breeding season to the point that it becomes a territory. Such an opinion that individual distance develops into territory in some case may be a possible explanation for the territorial formation of Gerres oyena (this was not discussed in the author's paper of 1976), but not for that of Apogon notatus, in which domiciliation at the nest site and defense of the ambient space coincide with each other. Thus, relations between individual space and territory seem to show complicated and various phases for different species.

Home Site and "Club"

The definition of the home range, that is the area, usually around a home site, over which the animal normally travells in search for food (Burt, 1943) is accepted, though somewhat modified, among zoologists (Hayne, 1949; Stickel, 1954 and others). Gerking (1953), studying the stream fishes, stated that many animals in their breeding conditions had no such attraction as a home site, which implied a nest, a burrow or some other attraction, and yet confined their movements to restricted areas. And then he redefined the home range as the area over which the animal normally travelled. Considering the results of the present study, resting aggregations in Gerres oyena (unpublished data), resting domiciliation in Fugu vermiculare vermiculare (unpublished data) and the maintenance of the home pool in Bathygobius soporator (Aronson, loc. cit.), however, the concept of the home site seems to be rather availbale for these fishes even when not breeding, because such places as they occupy when resting are usually restricted within small limits and seem to be rather attractive and of ecological advatage to them.

The tagged fish R-5 (see VI-c on p.) was observed most days from June 15 to June 29 in a certain definite aggregation settled at a site was displacing day by day but within 5 m. Similar observations were made frequently on other discriminated fish, too. Any fish belonging to an aggregation could never be expelled from it into other aggregations in experiments. From these facts, it seems that this fish possess the home site where the aggregated fish rest or hover around even in the day-time, though this is limited to the time when the planktonic foods are rich. The smaller aggregations found mostly in the season of pair formation may be well said as being located respectively in restricted places in the rocky region for the time.

This problem may be treated in another explanation as follows. From the viewpoint of its biological significance, the aggregation of this fish in the season of pair formation is seemingly comparable with the "club" of the herring gull, *Larus argentatus*, in that a group is formed in the area in the breeding season for the unpaired birds for their meeting place in addition to usual pairs (Tinbergen, 1953). The term "club" is proposed here to express the smaller aggregations of this fish more exactly in animal sociology. However, the club of this fish is seemingly less steady and more primitive in some respects than that of the gull. The aggregation of this fish is supposed to be a group resting and preparing for breeding. It was often observed that pairs slipped out to their nearby domiciliary sites all in good time; yet these did not seem to imply the initiation of pair formation, rather they might be pair re-formation.

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LITERATURE CITED

Amemiya, I. 1934. Which is the oral brooder in Apogon lineatus, a male or a female?. Proc. Sci. Fish. Assoc. 5(4): 392.

Aronson, L.R. 1951. Orientation and jumping behavior in the gobiid fish Bathygobius soporator. Amer. Mus. Novitates. No. 1486.

Baerends, G.P. and J.M. Baerends. 1950. An introduction to the study of the ethology of cichlid fishes. Behaviour, Supplement, I: 1-242.

Beusekom, G. Van. 1948. Some experiments on the optical orientation in *Philanthus triangulum* Fabr. Behaviour, 1: 195-225.

Burt, W.H. 1943. Territoriality and home range concepts as applied to mammals. Jour. Mamm. 24: 346-352.

Clarke, T.A. 1971. Territory boundaries, courtship, and social behaviour in the Garibaldi, Hypsypops rubicunda. Copeia, no. 2: 295–299.

Dice, L.R. 1952. Natural communities. Univ. of Mich. Press.

Ebina, K. 1932. Buccal incubation in the two sexes of a Percoid fish, Apogon semilineatus. J. Fish. Inst. Tokyo, 27: 19-21.

Fishelson, L. 1970. Spawning behavior of the cardinal fish, *Cheilodipterus lineatus*, in Eilat (gulf of Aqaba, Red Sea.). Copeia, no. 2, 370-371.

Fryer, G. and T.D. Iles. The cichlid fishes of the great lakes of Africa. Neptune City, t.f.h. Publication.

Garnaud, J. 1950. La reproduction et l'incubation branchiale chez Apogon imberbis. Bull. Institut Oceanographique, No. 977.

Gerking S.D. 1953. Evidence for the concepts of home range and territory in stream fishes, Ecology: 34: 347-365.

Hayne, D.W. 1949. Calculation of size of home range. Jour. Mamm., 30: 1-18.

Hinde, R.A. 1956. The biological significance of the territories of birds. Ibis., 98: 340-369.

Hobson, E.S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. Copeia, no. 2, 291–302.

Leyhausen, P. 1971. Dominance and territoriality as complemented in mammalian social structure. In A.H. Esser (ed.), The Use of Space by Animals and Men. New York, Plenum Press.

Livingston, R.J. 1971. Circadian rhythms in the respiration of eight species of cardinal fishes: comparative analysis and adaptive significance. Marine Biology, 9: 253-266.

Low, R.M. 1971. Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. Ecology, 52: no. 4.

Mizuno, N. and H. Kawanabe. 1957. Behaviour of salmon-like fish "ayu" in an area with closely established territories. Jap. J. Ecol., 7: 26-30.

Myrberg, A.A. Jr. and R.E. Thresher. 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. Amer. Zool. 14: 81–96.

Nakahara, K. 1962. On the spawning behavior of a cardinal fish, *Apogon notatus* (Houttuyn). Mem. Fac. Fish. Kagoshima Univ. 11(1): 14-17.

Nakazono, A. and H. Tsukahara. 1971. On the swimming direction of the wrasse, *Halichoeres tenui-spinis* (Günther), released on a sandy bottom. Rep. Fish. Res. Lab., Kyushu Univ., No. 1: 1-7.

Oehlert, B. 1956. Kampf und Paarbildung einiger Cichliden. Z. Tierpsychol. 15: 141-174.

Sakamoto, K. 1930. Buccal incubation in the Percoid fish, Apogon lineatus. J. Fish. inst. Tokyo, 26: 9-10.

Shaw, E.S. and L.R. Aronson. 1954. Oral incubation in *Tilapia macrocephala*. Bull. Amer. Mus. Nat. Hist. 103: 379-415.

Smith, C.L., E.H. Atz and J.C. Tayler. 1971. Aspects of oral brooding in the cardinalfish *Cheilodipterus affinis* Poey. Amer. Mus. Novitates. No. 2456.

Stickel, L.F. 1954. A comparison of certain methods of measuring ranges of small mammals. Jour. Mamm. 35: 1-15.

Tanaka, S. 1915. On brooding of a cardinal fish. Zool. Mag. (Tokyo), 27: 501-502.

- Tanase, H. 1968. Observation on spawning behavior of Apogon niger. Nankiseibutsu, 10: 16-18.
- Tavolga, W.N. 1954. Reproductive behavior in the gobiid fish *Bathygobius soporotor*. Bull. Amer. Nat. Hist., 104: 427-460.
- Tinbergen, N. 1951. The study of instinct. Oxford, Clarendon Press.
- ———— 1953. The herring gull's world. London, Collins.
- Usuki, H. 1976. Observations on the territorial behaviour of Japanese majarra, *Gerres oyena* (Forsskål), in the vicinity of Publ. Seto. Mar. Biol. Lab., 23: 105–118.
- Vivien, M.L. 1975. Place of apogonid fish in the food webs of a Malagasy coral reef. Micronesica, 11: 185-198.
- Winn, H.E., M. Salmon and N. Roberts. 1964. Sun-compass orientation by parrot fishes. Z. Tierpsychol. 21: 798-812.
- Yamada, T. 1957. Studies on morphometry and bionomics of Indian-Perch Apogon lineatus (Temmink et Schlegel) in Õmura Bay. Bull. Fac. Fish. Nagasaki Univ. No. 5: 80-90.