Japanese Journal of Ichthyology
Vol. 28, No. 4 1982

魚類学雑誌
28巻4号 1982年

Social Behaviour and Mating System of the Gobiid Fish *Amblyeleotris japonica*

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(Received March 26, 1981)

Abstract The behaviour, social interactions and mating system of the gobiid fish *Amblyeleotris japonica*, that utilize the burrows dug by the snapping shrimp *Alpheus bellulus* as a sheltering and nesting site, were investigated at two localities on the southern coast of Japan. The fish spent most of their time in the area near the entrance of the burrow in daytime. Movements were limited to an area of about three metres in radius from the entrance. Aggressive encounters occurred between adjacent individuals sometimes resulting in changes of occupation of burrows. Males were more active in pair formation, whereas females were rather passive. Paris were usually maintained for several days or more, but some of them broke up without spawning. All the males that successfully spawned were larger ones that were socially dominant, and they remained within the burrow for four to seven days after spawning to care for a clutch of eggs. Variation in social interactions and burrow-use was recognized between two study populations and was attributed to the differences in predation pressure and density of burrows.

A number of species of Gobiidae are known to live in the burrows of alpheid shrimps in tropical and subtropical waters (Luther, 1958; Klausewitz, 1960, 1969, 1974a, b; Palmer, 1963; Karplus et al., 1972a, b; Magnus, 1967; Harada, 1969; Yanagisawa, 1976, 1978; Polunin and Lubbock, 1977; Lubbock and Polunin, 1977; Hoese and Steene, 1978). It is widely admitted that the association is a mutually beneficial partnership (Magnus, 1967). For the fish the burrows are indispensable as shelter and for nesting. For the shrimps the tactile alarm communication developed between them and the fish serves to avoid predation. Shrimps that emerge from the burrow maintain antennal contact with a fish posted at the entrance. The shrimp detects the quivering motion of the goby's caudal part during unusual situations and reacts by immediate withdrawal into the burrow.

Recently, considerable information has been accumulated on the behaviour of the partner animals associated in one burrow and the communication between them (Preston, 1978; Karplus, 1979; Karplus et al., 1979), but no investigation has been carried out on the associated lives of these animals from populational and developmental aspects.

In another paper (Yanagisawa, MS.), the life history and pair formation of the shrimp *Alpheus bellulus* are described. In this study, the behaviour, social interactions and mating system of its partner fish *Amblyeleotris japonica* are investigated and analyzed.

* Studies on the Interspecific Relationship between Gobiid Fish and Snapping Shrimp. III.

Materials and methods

Study area. Field work was carried out at Rinkai Beach, Tanabe Bay (33°41′N, 135°20′E), the Kii Peninsula and at Murote Beach, Uchiumi Bay (33°00′N, 132°30′E), Shikoku Island. Both coasts are exposed to the Kuroshio Current and their faunas are similar. Sea surface temperatures at both coasts are between 25°C and 28°C in summer and seldom fall below 12°C in winter. At Rinkai Beach, the gobiid fish *A. japonica* is abundantly found on the sandy bottom that borders the rocky reefs. A 9 m×9 m quadrat was set on the sandy bottom at 4 m depth for repeated observations. At Murote Beach, *A. japonica* occurs in the relatively narrow area lying between the sand floor and the submerged rocks extending from cliffs. A 15 m×40 m quadrat, divided into 5 m×5 m sub-quadrats, was set on the bottom at the depths from 5 m to 8 m.

Field observations and collections. At Murote Beach, the positions of the opened entrances of the burrows of the shrimp in the quadrat and the approximate sizes of fish that occupied the

entrances were recorded monthly on a map during the period from September 1978 to August 1980 in order to obtain information on the seasonal fluctuations of the population, the growth rate of individuals and the frequency of paired fish. A detailed census was also made in a narrow zone within the quadrat (2.5 m×40 m) to find even smaller entrances which were apt to be overlooked in the whole quadrat census.

In order to investigate the daily positions and daily changes of the social state of the fish, some of them were tagged in and near the quadrat at Rinkai Beach and in and near a 5 m×5 m subquadrat at a shallower corner of the quadrat at Murote Beach. The fish, caught by underwater fishing with SCUBA, were immediately anesthetized with quinaldine and tagged with a coloured thread and a small coloured bead on the dorsum. Body size was measured and sex was checked by the shape of the anal papillae. Soon after recovery, they were released at the entrance of their burrows. Most of the tagged fish were acting in an ordinary way by the next day. The tag usually lasted for three weeks or more. Twenty-three individuals were tagged during the period from 5 August to 19 August 1978 at Rinkai Beach, and 37 individuals during the period from 12 July to 6 August 1979 at Murote Beach. Daily censuses and observations were carried out during the period from 5 August to 3 September 1978 at the former site and from 12 July to 17 August 1979 at the latter. The degree of gonad maturation of females was roughly recorded by their swollen abdomens only at Murote Beach.

The behaviours of fish and shrimps were observed and recorded in typically densely populated areas within and outside the quadrat at each beach. Fish are alert and ready to withdraw into the burrows when an observer approaches, but become habituated after repeated visits. By keeping motionless, their normal behaviour could be observed from close proximity. Although no perceivable sexual dimorphism exists in this species, the sex of fish in pairs could be determined in the field from the difference in their body sizes and/or the swollen abdomen of the female.

These censuses and observations were usually carried out between 0900 and 1600, and additional dives were made at other hours to observe the diel activity of the fish and the shrimp.

Collections were made at the above two beaches and at other several localities. The body size of the specimens was measured to estimate crude growth pattern and to determine the size correlation between males and females using the same burrow.

Results

Growth. The majority of the gobiid fish *Amblyeleotris japonica* were found inhabiting burrows of the snapping shrimp *Alpheus bellulus* and the rest were seen living in those of another shrimp *A. rapacida*. In addition, other gobiid fishes, *Tomiyamichthys oni*, *Vanderhorstia mertensi*, *Mahidolia mystacina* and *Stonogobiops* sp., were also associated with the shrimps.

The numbers of the above fishes found on the bottom usually decreased during the cold season when water temperatures fell below 15°C. In this period, they were apt to stay within the burrows and rarely appeared on the substrate. Gravid females of all these species appeared from late June to the middle of August and small juveniles were found on the bottom from late July to early October.

Seasonal variation in size-frequency distribution of *A. japonica* observed in the fixed quadrat of 100 m² at Murote Beach is shown in Fig. 1. The number of fish recorded in one census does not necessarily represent the number of the whole population there, since fish in closed burrows, which could not be counted in the census, may be significant, especially during the winter. However, the numbers recorded in the warmer season may safely be taken as a good indication of the numbers of the whole population. Sizes of all the specimens collected are shown in Fig. 2. From these two sources, the crude growth pattern of the fish can be estimated as follows. The smallest juvenile collected was 8.7 mm in standard length and had transparent body with black pigments along the median line of the belly and five clumps of black pigments at the positions where transverse bands of reddish brown will appear in the future. This juvenile, which had presumably settled on the bottom only a few days before, was already in association with a similarly small shrimp in the burrow, and was engaged in tactile alarm communica-

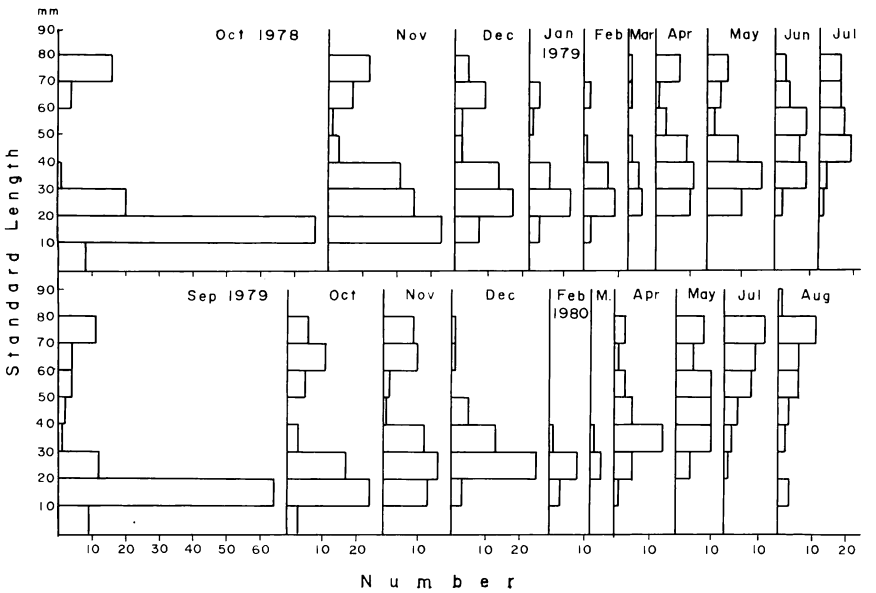

Fig. 1. Monthly size-frequency histogram of *Amblyeleotris japonica* in a 2.5 m×40 m quadrat at Murote Beach.

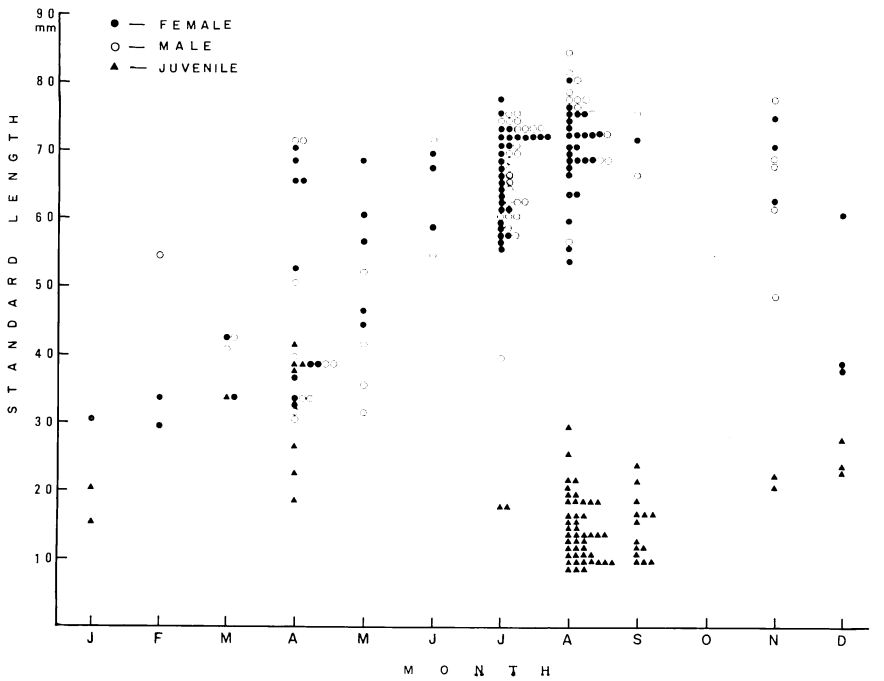

Fig. 2. Sizes of specimens of *Amblyeleotris japonica* collected during the period from 1972 to 1979.

tion with it. Fish grew up to 20 mm to 40 mm by the first winter, and most of them exceeded a size of 50 mm by summer. Individuals with fully developed gonads were found among those of more than 60 mm for females and 65 mm for males. It is presumed from the monthly size-

frequency histogram (Fig. 1) that the number of settled fish decreased by about 80% in one year, both in 1978 and 1979. The adult population must be composed of individuals one and two years old, and those more than two years old are, if any, very rare (Fig. 1).

I have found no egg mass in the field, but in the laboratory a pair of fish (female 77 mm and male 82 mm in standard length) laid eggs on the underside of an evaporation dish placed in an aquarium in July 1973. The egg mass was bunch-like, such as that of the gobiid fish *Sicydium japonicum* (Dôtu and Mito, 1955) and contained about 20,000 eggs. Eggs are ellipsoid in shape and 1.1 mm in length. Newly hatched larvae are 1.5 mm in total length.

Activity and use of burrows. As has been described in another paper (Yanagisawa, MS.), the gobiid fish *A. japonica* and its host snapping shrimps stay within the burrows during the night, the entrances of which are closed with sediments. Soon after dawn, they start to appear on the bottom, the gobiid fish first breaking through the sediment. Each burrow usually has one entrance opened at a time, the position of which changes from day to day. The number of entrances opened fluctuated daily (Fig. 3). The maximum density of the entrances was 0.31/m^2 on 5 August 1978 at Rinkai Beach and 0.84 on 5 August 1979 at Murote Beach. On those days, the average distances from one burrow entrance to the nearest neighbouring ones were 137 cm and 65 cm, with standard deviations of 37 cm and 19 cm, respectively.

The associations of juveniles soon after settlement were composed of one fish and one shrimp and those of young included one fish and one or two shrimps. In the adult associations, the shrimps mostly occurred in pairs, whereas the fish established pairs only in the warmer season. Pairs of fish appeared first in early May at both beaches, about one and a half months before the time when gravid females appeared. The ratio of associations in which two fish were witnessed to the total associations at Rinkai Beach was 7.6% in July, 7.3% in August and 3.6% in September. At Murote Beach, fish in pairs occurred during the same season as at Rinkai Beach and the ratio to the total population was nearly equal to that at Rinkai Beach in each month (Table 1). This is in contrast to the cases of other species, e.g., *T. oni* and *Stonogobiops* sp., that paired in high frequency throughout the year except the months from January to March when only few fishes appeared on the substrate (Table 1). Pairs of *A. japonica* were always composed of heterosexuals and males were usually larger than females by 5～10 mm in standard length (Fig. 4).

It was found from closer observations that some fish utilized two or more adjacent burrows at a time, each of which accommodated a pair

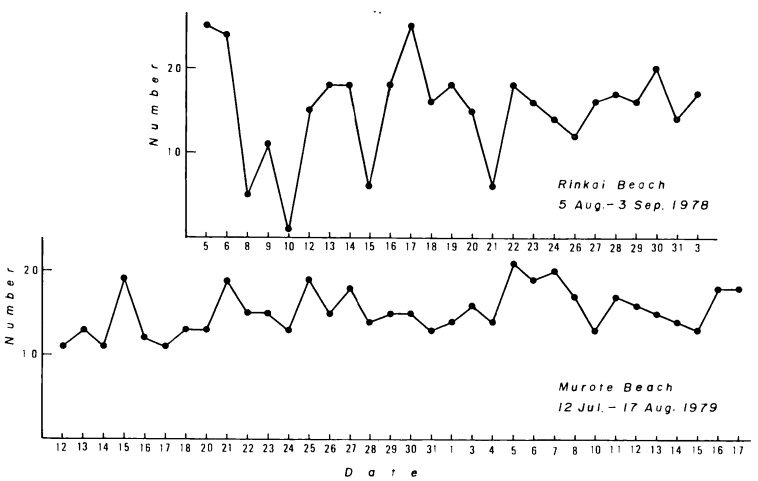

Fig. 3. Number of opened burrow entrances in a 9 m×9 m quadrat at Rinkai Beach and in a 5 m×5 m quadrate at Murote Beach.

Table 1. The proportion of individuals in pairs to the whole population in gobiid fishes associated with snapping shrimps in a 15 m×40 m quadrat at Murote Beach.

Month	Species	*Amblyeleotris japonica*			*Tomiyamichthys oni*			*Vanderhorstia mertensi*			*Stonogobiops* sp.		
		P	W	F	P	W	F	P	W	F	P	W	F
IX	1978	0	72	0	8	14	57	0	1	0	6	6	100
XI		0	130	0	4	11	36	0	4	0	4	11	36
XII		0	110	0	4	13	31	0	5	0	4	9	44
I	1979	0	61	0	4	14	28	2	4	50	0	3	0
II		0	30	0	2	4	50	0	2	0	0	0	—
III		0	20	0	0	8	0	0	1	0	0	0	—
IV		0	155	0	2	35	6	0	2	0	2	5	40
V		14	231	6	4	16	25	0	6	0	6	7	86
VI		4	200	2	20	57	35	4	8	50	8	10	80
VII		8	171	5	12	52	23	6	15	21	10	10	100
IX		2	132	2	16	45	36	2	12	17	2	2	100
X		0	117	0	8	17	47	2	30	7	6	7	86
XI		0	155	0	6	19	32	2	44	5	2	8	25
XII		0	108	0	6	28	21	0	52	0	4	12	33
II	1980	0	8	0	2	3	67	0	15	0	0	0	—
III		0	3	0	0	3	0	0	3	0	0	0	—
IV		0	146	0	6	52	12	0	63	0	0	1	0
V		10	225	4	8	71	11	0	73	0	2	14	14
VII		18	173	10	8	39	21	18	45	40	2	6	33
VIII		12	164	7	28	53	53	10	24	41	8	11	73

Individuals less than 30 mm in standard length are omitted for *A. japonica* and T. *oni* and those less than 20 mm are omitted for *V. mertensi* and *Stonogobiops* sp.

P, the number of paired individuals; W, the number of the whole population; F, P/W×100 (%).

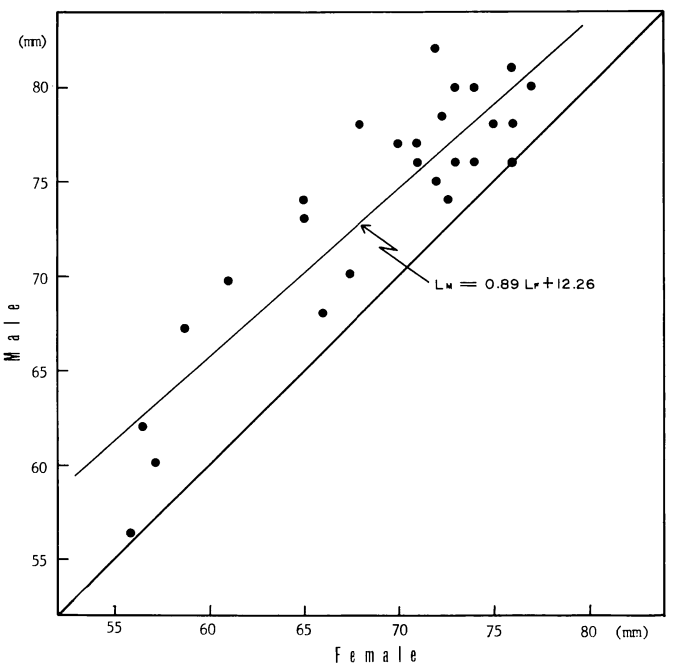

Fig. 4. Relationship between sizes of female and male in a pair.

of shrimp. Such data have never been reported. Such fish travelled at indefinite intervals between or among those burrows and stayed there to take up tactile communication with the shrimp. In solitary fish, individuals that utilized more than one burrow were witnessed only at Murote Beach. Paired fish not rarely used more than one burrow at a time at Murote

Beach. Of 33 pairs observed for 20 to 40 minutes per pair, 9 pairs used one burrow, 21 pairs two burrows and 3 pairs three burrows. At Rinkai Beach, on the contrary, of 19 pairs observed for 30 minutes per pair, 18 pairs used one burrow and 1 pair two burrows.

Three places can be distinguished as having different meanings in the life of the gobiid fish: the inside of the burrow, the entrance of the burrow and the substrate. The inside of the burrow is used as a shelter and nesting place. The entrance and its vicinity are the area from which fish can safely retreat into the burrow when attacked. Their feeding behaviour was mainly seen here. The duration of their stay here has direct significance for the activity of the shrimps outside the burrow, since the shrimps can emerge from the burrow only while they can keep a tactile contact with the fish. The substrate apart from the entrance is the place where fish socially interact with neighbouring conspecifics. The relative duration of time fish spent in each place was compared. At Rinkai Beach, fish spent most of their time in the area near the entrance. Paired fish spent 11.9% of their time within the burrow, 77.4% in the area near the entrance and 10.7% on the substrate apart from the entrance. Observations totalled 570 minutes for 19 individuals. No quantitative observations were made for solitary fish, but they seemed to spend their time in the area near the entrance longer than paired ones. At Murote Beach, fish left their burrows rather frequently. Solitary fish spent 2.0, 75.8 and 22.2% of their time in respective places during observations of 610 minutes for 28 individuals. Those values for paired fish were 2.5, 63.6 and 33.9% respectively in observations of 950 minutes for 40 burrows.

Fish rarely left their burrows for long duration. Rather, they repeatedly returned to the entrances of their burrows. The associated shrimps often appeared from the inside of the burrows as soon as they returned, as if the shrimps had been prepared to do so. The repeated returns of the fish clearly serve to facilitate the activity of shrimps outside the burrows, and consequently may prevent the entrance from being blocked with sediment.

When leaving the burrows, fish usually ranged within a radius of 3 m from the entrance. In an experiment in which fish caught by underwater fishing were released at different sites on the substrate, 1, 2, 3 and 4 m apart from their burrow entrances, those released at the point four metres apart were never able to return directly to their burrows in four observations, while those released at the points 1 to 3 m from their burrow entrances often managed to return to their burrows within a few minutes. In another experiment in which fish were expelled from their burrows and chased persistently by an observer, they fled within a few metres radius of the entrances of their burrows and after short time took refuge in their burrows or rarely in adjacent burrows. Even if the entrances had been broken down beforehand by the observer, the expelled fish succeeded in returning to the right points of their burrows. These observations suggest that fish know and recognize well the bottom topography within some 3 m radius of their burrows.

Food and predators. The fish chiefly fed on benthic organisms on the substrate near the entrances. Examination of stomach and intestinal contents revealed that more than 90% of their food items were corophiid amphipods and other small-sized crustacean species, as already reported by Harada (1969). These animals are abundantly distributed over the sea floor in areas where the burrows are dug and are in easy access by the fish outside their burrows. Occasionally, all fish in a small area were observed feeding on planktonic organisms. In such cases, the fish dashed 1 to 5 cm above the sea floor, performing repeated biting motions. This behaviour was usually observed near their burrow entrances. Young fish exhibited this feeding behaviour more frequently than adult and sub-adult fish (Table 2). The frequency of feeding motions of adult females was significantly greater than that of adult males (Table 2).

Although I have never seen living individuals of *A. japonica* being attacked and eaten by any animals under natural conditions, several times at Rinkai Beach I experienced that a gobiid fish was gulped by the lizardfish *Trachinocephalus myops* or the scorpion fish *Sebastiscus marmoratus* the very moment I hooked it on my underwater fishing line. The fish that escaped after being hooked were also attacked by such

Table 2. The frequency of feeding action of *Amblyeleotris japonica* per 10 minutes.

Standard length (mm)	I	II	III	IV
	<30	30–60	>60 (Female)	>60 (Male)
Number of observations	39	18	32	33
Food item				
Benthos	2.43[1]	2.66	4.08	2.76
	(0~9)[2]	(0~6)	(0~11)	(0~15)
Plankton	10.54	1.50	1.44	2.07
	(0~62)	(0~17)	(0~29)	(0~42)
Mann-Whitney U test	Benthos: III>IV, P<0.05			
	Plankton: I>II, P<0.01			
	I>(III+IV), P<0.01			

1, average; 2, range

predators. The gobiid fish never emerged from their burrows while predatory benthic fishes, such as the stone fish *Inimicus japonicus* and the above two species, were in the vicinity of their burrows. They were also alert against carnivorous fishes patrolling above the bottom, such as *Therapon jarbua*. On one occasion when one *T. jarbua* approached gobiids, it was witnessed that the gobiids in a certain area simultaneously withdrew and took the posture of the posterior half of their body inserted into the burrow or retreated wholly within the burrow. These potential predators were relatively common at Rinkai Beach, and rarer at Murote Beach. The gobiid fish was rather indifferent to the approach of non-predatory fishes, such as *Geres oyena* and *Parapercis snyderi*.

Aggressive behaviour. The encounter between individuals of this gobiid species on the bottom raised one sided or mutual aggressive behaviour. Four distinct types of aggressive behaviour were observed: chasing, lateral display, mutual lateral display and circling. "Chasing" is essentially the same as seen in any species of fish. One fish rushes towards another to drive it away (Fig. 5b). In "lateral display", one fish approaches the other with the unpaired fins fully expanded and held stiffly, lifts the head with the mouth and the gill-opening widely opened, and slowly undulates the body (Fig. 5c). At the same time, the five transverse brown bands on the body almost fade away. Lateral display is frequently followed by chasing. In "mutual lateral display", two fish place themselves side by side, spreading their fins and opening their mouths in the same fashion as in lateral display, with head-to-tail or head-to-head orientation (Fig. 5d). This display continues for several seconds or more, and occasionally leads to circling. In "circling", the two aggressive individuals intermittently circle each other, head-to-tail, each trying to attack the caudal part of the opponent with its mouth. During fighting, bands on their bodies fade away. This behaviour lasts for a long time, up to 30 minutes. A scene of biting has not been observed, but there is no doubt that it actually occurs, since the individuals whose caudal fin or dorsal fins were partially torn off were not rare. Such individuals were mostly males.

Fish staying near their burrows were aggressive against conspecifics invading their proximity. The residents approached the invaders and exhibited lateral display and/or chasing to drive them away. Fish using more than one burrow were aggressive to the individuals that intruded into any of their burrows. Mutual lateral display and circling occurred between two fish of similar body size, and the resident fish often won in the fighting. Aggressive encounters were frequently observed between males and prolonged fighting and circling were executed only by males, whereas such encounters between females were relatively rare (Table 3).

Table 3. Intersexual and intrasexual aggressive encounters in *Amblyeleotris japonica*.

Receiver / Attacker	Female	Male	X	Total
Female	5	11	18	34
Male	8	18	21	47
X	1	1	7	9
Total	14	30	46	90

X, individuals whose sex was not certain

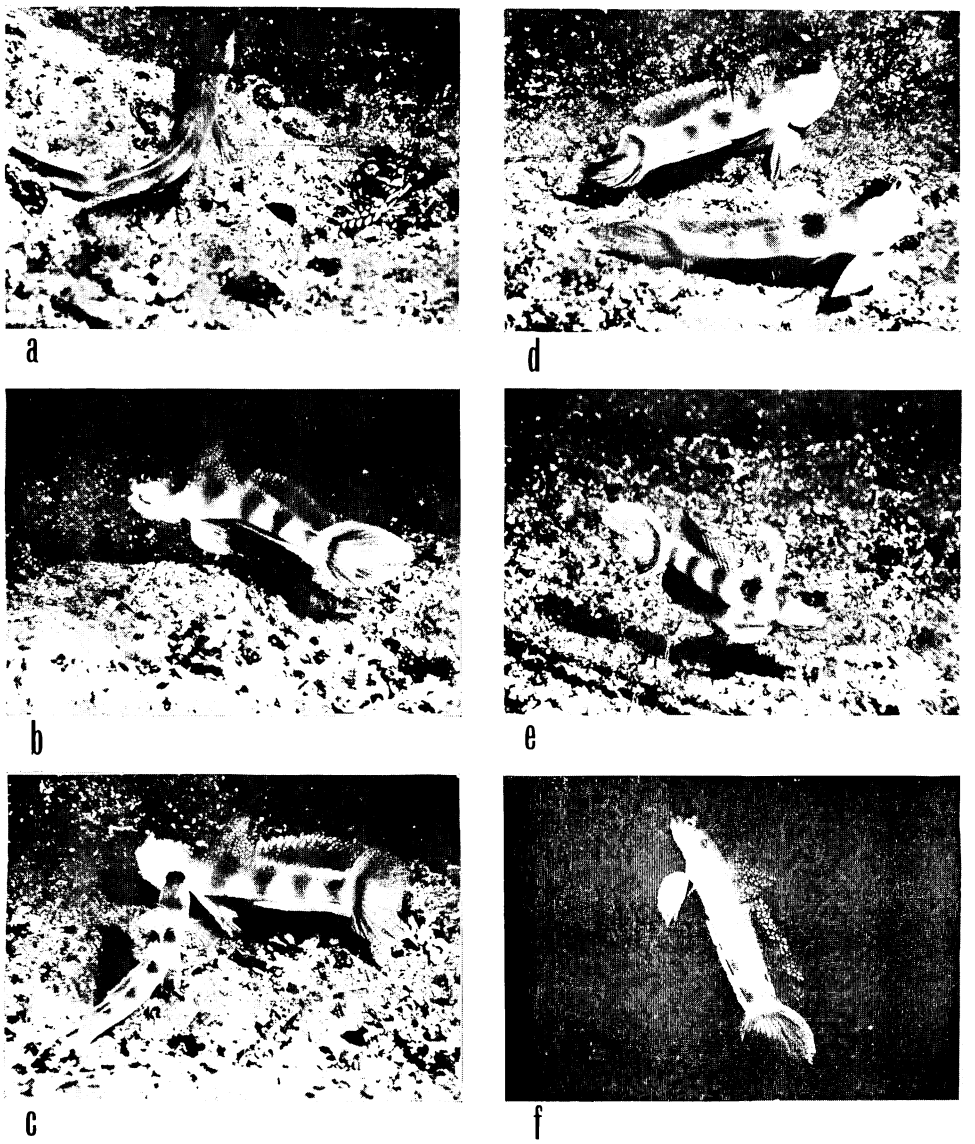

Fig. 5. Behaviours of the fish *Amblyeleotris japonica*. a: a fish staying near the burrow entrance with a shrimp *Alpheus bellulus*; b: a fish preparing to chase another fish; c: a fish exhibiting lateral display to an approaching fish; d: two fish engaged in mutual lateral display; e: a dominant fish returning to its burrow after a fighting with the adjacent fish; f: a fish soaring in the water.

The dominance of the fish was seemingly determined by the body size. Of 90 encounters observed, the apparently smaller individuals defeated the larger ones only in three cases. The dominant fish often intruded into other burrows and stayed there after they chased away the residents, although the occupation was usually temporary. The expelled ones stayed on the substrate nearby or in turn invaded other burrows. The subordinate fish sometimes surrendered their burrows to the approaching dominant ones even without demonstrating any defensive behaviour. The dominance and inferiority of the fish was also discernible from their movement after fighting. The dominant fish returned to their burrows, often swimming

5 to 10 cm above the bottom with their fins expanded and their body swaying (Fig. 5e), whereas the subordinate ones crept on the substrate with their fins folded.

Most of the social behaviours mentioned here were observed at Murote Beach, since the encounters between the individuals were relatively frequent at Murote Beach while such encounters were very rare at Rinkai Beach. A possible reason for this difference may be that potential predators were rare at the former site and relatively common at the latter.

Floaters. Some portion of the population of *A. japonica* do not occupy burrows and wander about on the substrate. These fish, hereafter called "floaters", were apparently smaller than the residents of burrows (χ^2, $P<0.01$) (Table 4). They represented 2.1% of the total population at Rinkai Beach and 5.3% at Murote Beach in summer. The floaters remained usually within a relatively small range on the substrate and showed a tendency to stay at the site nearly equidistant from the adjacent residents, since they received attacks from the residents if they approached nearer the entrances of burrows. Forty-five % of aggressive behaviour of the residents were directed at floaters.

When driven off by an observer, a floater moved about on the floor or took refuge into one of nearby burrows of shrimps. In the latter case, it always entered the burrow after the resident fish of the burrow did first, and then it reemerged from the burrow before the resident did. In 14 cases in which the observer approached a floater and let it retreat into a burrow, the floater stayed within the burrow only for an average of 52 seconds per one retreat, while the resident remained for 91 seconds. It appeared that each floater had a definite burrow into which it temporarily sheltered itself when exposed to danger, and it probably lodges within the burrow during the night, since no individuals remained on the substrate at night.

Floaters were usually very quick to seize an opportunity to occupy vacant burrows. They settled even in the burrow whose resident fish was absent only for a moment, although they were driven away sooner or later by the resident. A fish that was a floater on one day was sometimes observed being a resident on another day. On the other hand, some resident fish became floaters after they had been expelled from their burrows by the dominant fish. A floater may be a more or less temporal condition and may result from social interactions among conspecifics.

Pairing behaviour. The bond between two paired fish was often loose, especially early in the reproductive season. One fish of a loose pair often visited the adjacent burrow which was occupied by the other and returned to its original burrow after a short stay there. In such a case, it was occasionally observed that the resident, when it was a female, nudged the belly of the visitor with the snout while the latter was staying near the entrance of the burrow. Soon after the visitor received the action, it always departed. This action may be a signal by which a resident mildly refuses to form a pair.

Males were more active in pair formation, and severe fightings were observed between males. Of four cases of circling observed at Murote Beach, three were obviously concerned with the acquisition of a mate by two males. The most outstanding fighting was observed on 30 July 1979 between the tagged male M4 and an untagged male X of similar body size. Until that day, the male M4 had paired with the female F2 for 10 days and they had occupied two adjacent burrows, and the male X had utilized a burrow 1 m apart from those of the pair. The two males were found engaged in circling on the substrate near one of the burrows

Table 4. Size-frequency of residents of burrows and floaters in *Amblyeleotris japonica* at Murote Beach in summer.

Standard length (mm)	30–	40–	50–	60–	70–	80–	Total
Resident	1.5	2.4	10.3	23.6	59.5	2.7	100 (N=1282)
Floater	17.4	18.9	27.5	20.3	15.9	0.0	100 (N= 69)

of M4, and the circling intermittently lasted for 30 minutes. While the males were fighting, female F2 stayed on the sand floor or on a small stone near the males and then moved to the burrow of X. Male X stopped fighting soon after the female went to its burrow, and it went there, too. On the next day, X and F2 were observed paired and inhabiting the burrow of X, whereas M4 was a floater and kept motionless on the substrate near its original burrow with its heavily broken dorsal fins folded. Its burrows were occupied by another male.

Males occasionally performed one peculiar action, "soaring". Holding their bodies perpendicular to the bottom, they rose up 10 to 40cm in the water, and remained motionless there for 5 to 30 seconds with the unpaired fins expanded (Fig. 5f). Brown bands on the body almost faded out just before and during this action. The pale body apparently reduced its conspicuousness in the water. It was exhibited by males that were paired or going to form pairs and mainly on the occasions when they were separated from their mates or were just after aggressive encounters with rivals. After soaring, the males often moved to the burrows of their mates or rivals. It is very probable that by soaring the males reconnoitre the surroundings, especially the positions and behaviour of their mates and rivals. I have never seen females performing this action.

In an established pair, no aggressive behaviour was seen between the mates. A display similar to mutual lateral display was frequently observed near the entrance of their burrow when either of them returned to the burrow after a prolonged absence. They approached each other and erected their fins, opening their mouths, but this behaviour ceased after three seconds or so and thereafter they remained close together. It may be regarded as a ritualized greeting display rather than an aggressive behaviour.

Some behavioural differences were observed between male and female of a pair (Table 5). Males stayed within the burrow longer than females. Males wandered on the substrate apart from the entrance for a considerably longer time than females. In the burrow with a depression extending from the entrance on the bottom surface which was formed by shrimps, females stayed at the distal part of the depression five times as long as males did. This means that female fish provide facility more often for the activity of shrimps outside the burrow than male fish do, since shrimps emerge from the burrow only while fish stay in the proximity of the entrance or the depression. Feeding behaviour of females occurred in higher frequency than that of males. In experimental situations of slow approach of a diver to a pair of fish staying at the entrance, intended to determine which mate was more sensitive to danger, males retreated first into the burrow in most trials and females reemerged first from the burrow without exception (Table 5). Males stayed within the burrow three times as long as females per each retreat.

Change of occupied burrows. At Rinkai Beach, twenty-four individuals were tagged in and near the 9 m×9 m quadrat in August 1978, which represented about a half of the whole population there. The daily records of the positions of the entrances of the burrows they occupied during the period from the day when they were tagged to 3 September 1978 are shown in Fig. 6. The positional change of the burrow entrance of tagged fish between successive days was simply due to the change in the position of the entrance of the burrow itself in 184 cases, and only in 15 cases it was caused by the movement of the fish between different burrows. In the latter cases, the movements of the fish M4 and F8 were done respectively between burrows 5 m and 10 m apart from each other, but other movements were between adjacent burrows. Five cases were obviously concerned with pair formation. Fourteen tagged fish stayed in their particular burrows throughout the observation period.

At Murote Beach, 37 individuals were tagged in and near the 5 m×5 m quadrat in July and August 1979, representing about two thirds of the whole population there. Changes in the positions of their burrow entrances during the period from the day when they were tagged to 17 August 1979 are shown in Fig. 7. In the cases where one individual used more than one burrow within one census, the position of either burrow was recorded as the position of the individual. The positions of the burrow entrances where each fish was stationed were confined within the area of about 5 to 10 m^2. Since

Table 5. Differential behaviours between female and male in a pair.

	Female	Male	P
Total period on bottom more than 20 cm apart from entrance of burrow per 30 minutes (n=20)	2′30″	4′12″	>0.05*
Total period within burrow per 30 minutes (n=20)	2′03″	5′05″	<0.05*
Total period at distal part of depression per 30 minutes (n=10)	12′12″	2′10″	<0.01*
Aggressive behaviour against conspecifics per 30 minutes (n=20)	0.05	0.61	<0.05*
Frequency of feeding behaviour per 30 minutes (n=18)	28.9	16.3	<0.01*
Which withdraws into burrow first? (n=26)	5	21	<0.01
Which reemerges from burrow first? (n=28)	28	0	<0.001
Duration within burrow (n=25)	1′46″	4′08″	<0.01*

* Wilcoxon signed rank test

it was impossible to identify the entrance of a certain burrow on one day with that on the other days and therefore impossible to estimate the extent of one burrow, the number of burrows utilized by each fish during the study period could not be determined definitely. However, there is no doubt that most fish used more than one burrow, probably from two to as many as six burrows. For instance, it is estimated from the positional changes that the fish M14 moved among four adjacent burrows and the fish M10 among six burrows (Fig. 7). The ranges of the positions of the burrow entrances of particular tagged fish during the study period greatly overlapped one another, indicating that each burrow was occupied alternately by more than one fish.

It was ascertained in the fish M1 and F8, whose tags fortunately endured for a long time, that both had stayed in a few definite burrows throughout four months.

Change of social state. The social state of the fish was categorized into three conditions, i.e., paired resident, solitary resident and floater, and was observed daily for tagged fish at both beaches. The sequences of the social conditions at successive days surveyed are shown for each tagged fish in Tables 6 and 7. Some of the fish regarded as solitary may have been actually paired, since their social state was determined from short observations. At Murote Beach, the condition of paired residents was divided into two, that is, stably paired and transiently paired, although the discrimination between them is more or less arbitrary.

At Rinkai Beach, each fish did not appear on the substrate on many days, and therefore the complete sequence of the social condition of such individuals could not be obtained. About half of the tagged fish remained solitary throughout the study period. Pairs were formed between larger individuals and maintained for several days or so (Table 6).

At Murote Beach, males smaller than 70 mm and females smaller than 65 mm in standard length rarely paired (Table 7). Males that were large enough but slender, such as M1 and M11, rarely paired. Pairs often terminated in a few days, and the members of a pair sometimes changed. In a few cases, two fish that had once formed a pair paired again after a long period of separation. For instance, the male M5 and the female F13 that were observed paired from 25 to 27 July, paired again on 17 August. Some of pairs were maintained for a long time. For instance, the male M6 and the female F5 were in a pair on many days during the study period, and the pair of the male M4 and the female F2 continued for 10 days. Some of the fish formed pairs with more than one fish during

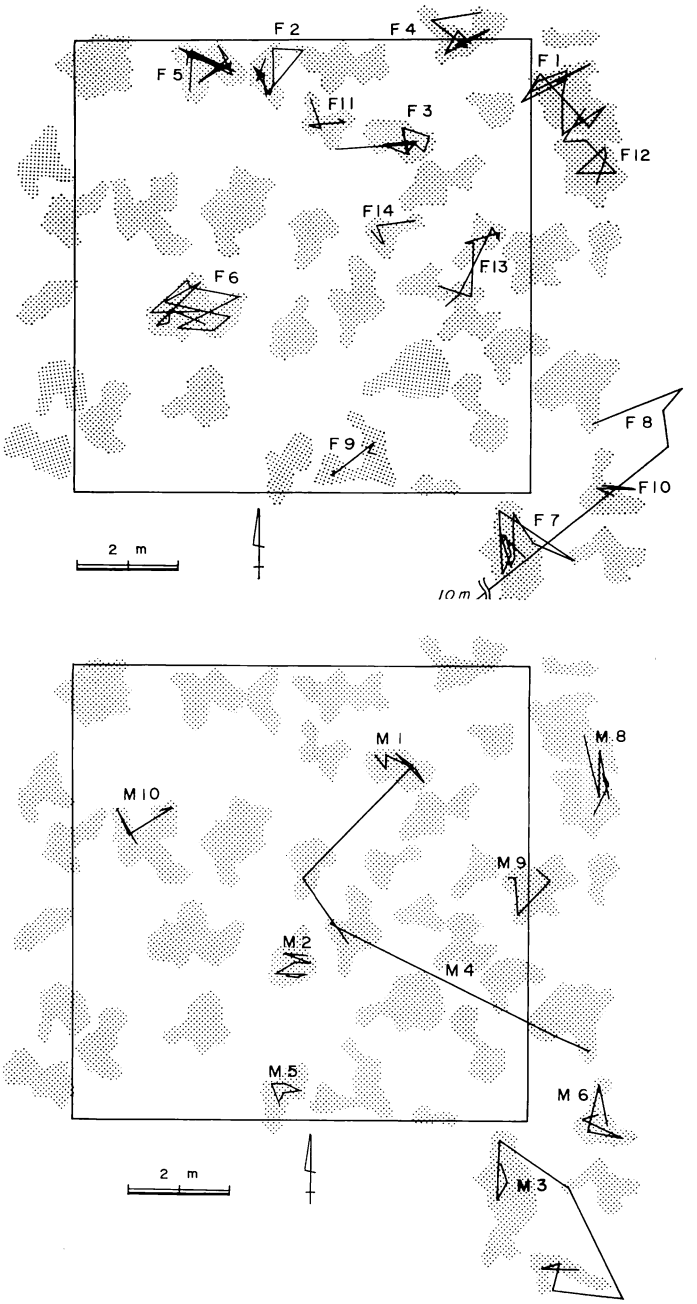

Fig. 6. Daily changes in the position of tagged individuals at Rinkai Beach during the period from the day when they were tagged to 3 September 1978. Females and males are shown on separate maps. Positions of each individual in two successive days are linked with a line. Each dotted area represents the horizontal extent of one burrow inferred from daily shifts in the position of burrow entrance.

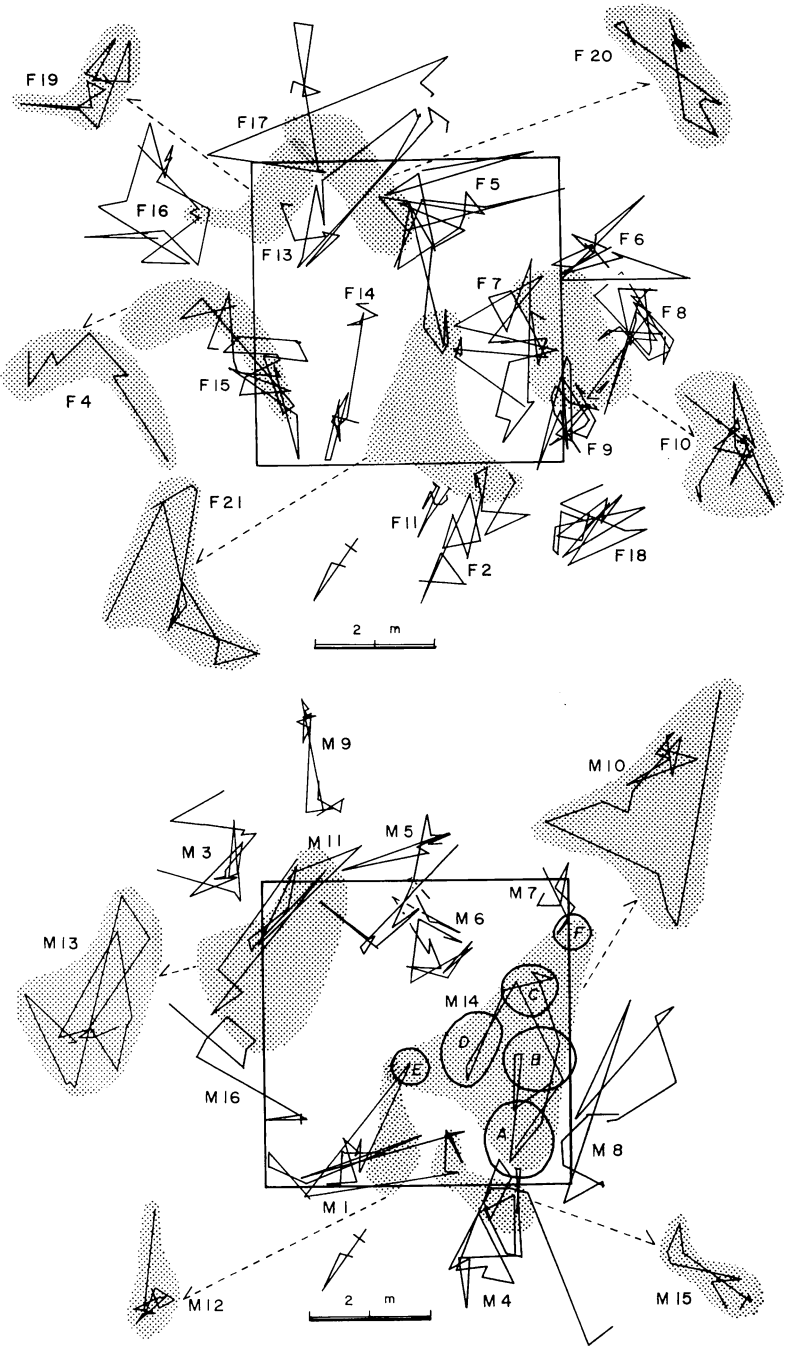

Fig. 7. Daily changes in the position of tagged individuals at Murote Beach during the period from the day when they were tagged to 17 August 1979. Females and males are shown on separate maps. Positions of each individual in two successive days are linked with a line. Since the movement areas of individuals overlapped one another, the movements of nine individuals (F4, F10, F19, F20, F21, M10, M12, M13 and M15) are shown within dotted areas in the margin and their actual places in the map are represented by dotted areas. Areas A to F encircled by a line are the positions of burrows referred to in Fig. 8.

Table 6. Daily observation on social conditions of tagged individuals at Rinkai Beach.

Individual number	Standard length (mm)	August, 1978																								September
		5	6	8	9	10	12	13	14	15	16	17	18	19	20	21	22	23	24	26	27	28	29	30	31	3
F 1	70	o	o		o				o			o		o				o		o	o	o	o	o	o	o
F 2	55	o	o				o				o	o		o	o		o				o	o	o			
F 3	65		o	P			o		P			P						P	P	P	P			o		
				x					x			x						1	1	1	1					
F 4	70		o					o	o	o			P	P			P	o								
													x	x			x									
F 5	64		o					o		o	o	o	o	o	o	o	o		o	o		o	o	o		o
F 6	76		P					P	P	P	o	P	P	P	o		o			o	P	P	P	P		
			x					x	x	x		x	x	x							x	x	x	x		
F 7	77							P	P				P	P	P		o	o	o	o	o		o		o	o
								3	3				3	3	3											
F 8	65							P							P	P	P							P	P	
								4							x	x	x							x	x	
F 9	69							P	P		P	P	o													
								x	x		x	x														
F 10	66								P								f		f			o				
									6																	
F 11	65										o	o		o	o		o	o								
F 12	72										P			o	o		o	o						P	P	P
											8													8	8	8
F 13	64											o	o				o	o	o	o	o	o	o	o	o	o
F 14	68													o						o		o		o		
M 1	74	o					o								o			P	P	P	P	o	o			o
																		3	3	3	3					
M 2	68		o					o	o			o					o					o	o	o	o	o
M 3	80							P	P				P	P	P			P					P	P	P	P
								7	7				7	7	7			x					x	x	x	x
M 4	73							P	o				o													
								8																		
M 5	69							o	o	o	o						o	o								
M 6	68								P						o		o	o			o			o	o	o
									10																	
M 7	75								o									o								
M 8	81										P										o	o	o	P	P	P
											12													12	12	12
M 9	64											o		o	o		o				o	o				o
M 10	71												o	o	o					o				o	o	

F, female; M, male; o, solitary resident; P, paired resident; f, floating. Each fish was tagged on the first day in the record. A blank column shows that the fish was not observed on the substrate. A figure below P means the individual number of its mate, x meaning that its mate is untagged.

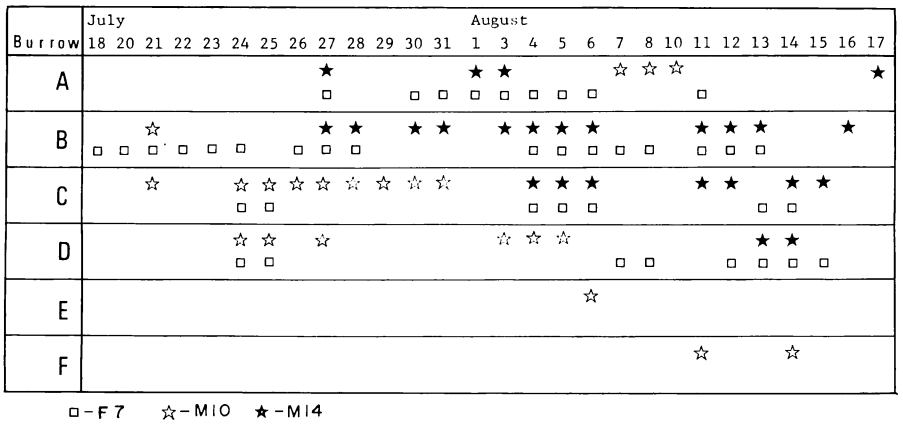

Fig. 8. Occupation of burrows by one female F7 and two opponent males M10 and M14. Positionsof burrows are shown in Fig. 7. For details see text.

the study period. The male M13 paired with two females at a time on 31 July and 1 August, although each pair was not stably established.

The social state of the tagged fish often changed as a result of social interactions with adjacent fish, accompanying the movements of the fish between burrows. The most remarkable change of social state was exhibited by the male M10 that competed with M14 for the acquisition of F7 (Fig. 8). The male M10 remained paired with F7 and kept two burrows (burrows C and D in Fig. 7) under their control on 24 and 25 July. However, M14, appearing from somewhere, replaced M10 as a mate of F7 and occupied the burrows A and B on 27 July. After M14 and F7 established a stable partnership, M10 was frequently attacked by M14 and was forced to move from the burrow C to the burrow D or E. It moved to burrow A and became dominant there for a few days while M14 disappeared on the substrate (7 to 10 August), but was driven away to burrow F after M14 reappeared.

Mating. The belly of every adult female was more or less swollen throughout the reproductive season, but gravid females with remarkably swollen bellies were found among the pairs. Of such gravid females at Murote Beach, F5 on 22 July, F2 on 31 July, F9 and F18 on 1 August, F7 on 6 August and F8 and F21 on 8 August displayed normal abdomens and became solitary on the following day (Table 7). Each of them probably spawned on or around that day. Thereafter, they were solitary on the substrate at least for four days. On the other hand, the males that had paired with them were never found on the substrate for four to seven days after that presumed spawning day. The absence of M6 from 23 to 28 July, M8 from 3 to 7 August and from 9 or 10 to 12 August, M14 from 7 to 10 August and M15 from 9 or 10 to 14 August were such cases (Table 7). This sort of absence was also seen in M3 from 3 to 7 August after it had paired with an untagged gravid female. Probably, the males were staying within the burrows to care for and guard a clutch of eggs during that period. If so, the duration of incubation may be estimated to be between four and seven days. The female probably did not guard the eggs, since they were observed on the substrate after spawning.

All males and females that were presumed to have participated in spawning were the dominant ones, and they were presumed to have spawned only once in the study period. The male M8 was the exception and it spawned twice, once with F9 on 1 August and a second time with F8 on 8 August, and one additional spawning around on 24 July may have occurred, since it had stayed within the burrow from 24 to 29 July (Table 7).

Discussion

Activity and mating. The number of fish species on the sandy bottom is usually much smaller than that in the rocky or coral area.

Those species that can burrow by themselves or utilize burrows made by other animals may take the sandy bottom as an advantageous habitat. The gobiid fish *Amblyeleotris japonica* cannot provide themselves with sheltering burrows, and unless there are burrows dug by snapping shrimps, the sandy bottom is not an available habitat to them. For this species, to obtain partner shrimps and to protect them from attacks by predators are equivalent to the acquisition of living place and are requisite to its life.

As has been shown, the fish *A. japonica* spend more than 60% of the time in the area near the burrow entrance in daytime. Fish staying here have the advantage not only of safe shelter for themselves in the burrows when attacked, but also to provide a facility to the shrimps for sustaining the burrows. They need not move great distances from burrow entrances for food, since food items are generally plentiful on the sandy bottom and they can easily get enough food. However, they have to journey over the substrate to acquire their mate.

Fish did not move around freely over the substrate. Fish wandering on the substrate were often attacked by the adjacent resident fish, and rarely ventured more than some 3 m from their burrows. Changes in the occupation of burrows, if they occurred, were usually be-

Table 7. Daily observations on social condi tions

Individual number	Standard length (mm)	July, 1979																
		12	13	14	15	16	17	18	20	21	22	23	24	25	26	27	28	29
F 2	74	o	o		o	o		o	o	P	P	P	P	P	P	o	P	P
										4	4	4	4	4	4		4	4
F 4	76				P	P	P	P	o	o	o	o	o	o				
					2	2	2	2										
F 5	73				o	P	P	P	P	P	P*	o	o	o	o	o		P
						6	6	7	6	6	6							6
F 6	67				P	o					o	o	o	o	o	o		
					x													
F 7	73				o		o	o	o	P	o	o	P	P	o	P	P	
										10			10	10		14	14	
F 8	74				P	o	o	P	o	o	o	o	o	o	o	o	o	o
					8			8										
F 9	74				o	o	o	o	o	o	o	o		o	o		o	o
F 10	59				o	o	o		o	o		o	o	o			o	
F 11	56				f	o	o	o	o		o					o	o	o
F 13	76					o	P			o	P	o	P	T	P	P		o
							5				x		x	5	5	5		
F 14	66					o	o	o		o		T					o	o
												x						
F 15	66					o	o	o	o	o		o	o	f		o	o	o
F 16	77					o	o	P	o	o	o	o	o	o	o	o	P	
								x									x	
F 17	71							P	o	P		o		o	o			o
								9		9								
F 18	73									P	P	o	o	o	o	o	o	o
										x	x							
F 19	63																	
F 20	75																	
F 21	68																o	

tween adjacent ones. Some fish were observed using a few definite burrows throughout several months. These results suggest that the fish is rather stationary. This means that the number of potential mates each fish can encounter is limited to a few, suggesting that the competition for acquisition of mates is severe among neighbouring consexuals.

As has been shown, the competition was much more severe among males than among females. Males were usually ready to form pairs and prolonged fighting was observed between males, whereas females were rather passive and sometimes refused to form a pair. The competitiveness and contentiousness of males in this species may be accounted for by the fact that only a small portion of females are gravid at one time while most adult males are seemingly sexually active throughout the breeding season, resulting in the fact that the ratio of fertilizable females to sexually active males in one area at any given time is biased towards males, like most animal species.

Pairs of adult fish appeared one and a half months before the females became gravid, but were often loose and broke up without spawning. Paired males were sometimes attacked and replaced by other males. All the males that were presumed to have successfully spawned were the larger ones that were socially dominant.

of tagged individuals at Murote Beach.

August, 1979																Standard Length (mm)	Individual Number
30	31	1	3	4	5	6	7	8	10	11	12	13	14	15	16	17	
P* 4	P* x		o	o	o												74	F 2
	o	o	P	o	f	o	P	P	o	o*	P*	o*		o	P	o	76	F 4
			6				6	6			6				6		73	F 5
	o	o	o	o	o	o	o		P* x		o			o	o	o	67	F 6
o	o	P* 14	P* 14	P* 14	P* 14	P* 14	o	o		P 14	P 14	P 14	P 14	o	o		73	F 7
	o	o	o	o	o	o	P* x	P* 8	o	o	o	o	o	o	o	o	74	F 8
o	P* 8	P* 8		o		o	o	o		o	o	o	P 8	P 8	P 8		74	F 9
o	o		o	o		o					o			o			59	F 10
	o					o			o	o			o				56	F 11
o	T 13	T 13	o	o	P 13	P 13	P 13	o	o	o		o				P 5	76	F 13
o	o	o	o	o		o	o	o		o	o		o		o	o	66	F 14
o	o	o	o	o	T x	o	o	o	o		o	o	o	o	o	o	66	F 15
o	P x	P x	o	P x	o	P x	P* x	P* x									77	F 16
T 13		o	o	f					o		o			o	o		71	F 17
o*	P* x	P* x	o		o	o	o	o	o	P x	P x				o	o	73	F 18
o		o	o	o	o	o	o	o	o	o	o	o	o	o		o	63	F 19
o	T 13	T 13		o	o	P 5	P 5	P 5	o	o	P 5				o	o	75	F 20
o	o	o	o	T 15	T 15	P* 15	P* 15	P* 15	o	o	o	o	o		o	o	68	F 21

Table 7.

Individual number	Standard length (mm)	July, 1979																
		12	13	14	15	16	17	18	20	21	22	23	24	25	26	27	28	29
M 1	77		o					P 1	o	o	o		o	o	o	o		o
M 3	77			f		o						o		o	o	P x	o	T x
M 4	76				o	o	o		o	P 2	P 2	P 2	P 2	P 2	P 2		P 2	P 2
M 5	78					P x	P 13	o		o	o	o		T 13	P 13	P 13		
M 6	76		o	o	o	P 5	P 5	o	P 5	P 5	P 5*							P 5
M 7	76				o	o	o	P 5		o	P x*	o						
M 8	80				P 8		o	P 8		o	o	o						
M 9	77							P 17		P 17	o		o				o	
M 10	76									P 7			P 7	P 7	o	o	o	o
M 11	77												o	o	o			o
M 12	59															o		o
M 13	76															o	o	T x
M 14	80															P 7	P 7	
M 15	78																	
M 16	77																	

F, female; M, male; o, solitary; P, stably paired resident; T, transiently paired resident. Each fish was
A figure below P or T means the individual number of its mate, x meaning that its mate is untagged. Female

However, most males spawned only once during the study period, suggesting that the degree of monopolization of spawning by one dominant male is not extreme. This may be attributed to the breeding habit of this species where one male breeds with only one female at a time and thereafter it takes several days to care for the clutch of eggs within the burrow.

Although both this gobiid fish and its host shrimp, *Alpheus bellulus*, take the burrows as their habitat, they have quite different patterns of pair bonding. In the shrimp, some individuals form pairs even at the juvenile stage and adult individuals usually occur in pairs. The pair bonds are usually stable and some of them are maintained for several months (Yanagisawa, MS.). The difference in the pattern of pair bonding between the two animals may be attributed in part to differences in the way of obtaining a mate. A solitary fish can meet with individuals of the opposite sex by moving on the substrate from one burrow to another, while a solitary shrimp in the isolated burrow has a chance to encounter a mate only through the connection of its burrow with the adjacent burrow within the sediment (Yanagisawa, MS.). The number of potential mates accessible to each individual may be greater in the former animal than the latter. Individual fish probably gain little or no reproductive advantage by establishing pair bonds at an early stage of life, long before maturation. Rather, to share one burrow with another fish for a long time may be less advantageous to each fish than to have one

(continued)

August, 1979																	Individual number	Standard length (mm)
30	31	1	3	4	5	6	7	8	10	11	12	13	14	15	16	17		
o	o	o	o	f	o	o	o	o	o	o	o	o	o	o	o	o	77	M 1
o	P x	P x*						o	o	o	P x*	P x*	P x		o	o	77	M 3
P 2*	f	o	o	o		o	o	o	o	o	o	o	o	o	o	f	76	M 4
	o		o			P 20	P 20	P 20	o	o	P 20	o	o	o		P 13	78	M 5
o	o		P 5			o	P 5	P 5	o		P 5	o	o	o	P 5	o	76	M 6
	o	o															76	M 7
o	P 9*	P 9*						P 8*				o	P 9	P 9	P 9	o	80	M 8
P x	P x	P x	P x	P x	P x	P x	P x	o	o	o		o		o	o	o	77	M 9
o	o		o	o	o	o	o	o	o	o			o				76	M 10
o			o	o	o	o	o	o		o	f	o			o	o	77	M 11
o	o			o	o		o	o	o	o	o	o	o	o	o		59	M 12
T 17	T 20 T 13	T 20 T 13	o	o	P 13	P 13	P 13	o	o	o	o	o		o	o	o	76	M 13
o	o	P 7*	P 7*	P 7*	P 7*	P 7*				P 7	P 7	P 7	P 7	o	o	o	80	M 14
	o	o	o	T 21	T 21	P 21*	P 21*	P 21*						o	o	o	78	M 15
						o	o	o	o	o	o	o	o	o	o	o	77	M 16

tagged on the first day in the record. A blank column shows that the fish was not observed on the substrate. or mate of male with a swollen belly is indicated with a symbol (*).

burrow all to itself, since the space of the burrow is not wide.

Nevertheless, the pair bond in this gobiid fish, which is usually maintained for several days or more, is exceptionally stable among the species of Gobiidae (Breder and Rosen, 1966). In most of gobiid fishes, females and males live together only while they are engaged in courtship and spawning behaviours. Relatively stable pair bonds in this species may be attributed to the condition that its habitat is discontinuous and potential mates that one individual can encounter are not abundant owing to their restricted home range.

Variation in behaviour. I have an impression from observations on various coasts in Japan that there is great variability in this species in the number of individuals that stay on the substrate apart from their burrows. At some localities, the majority of fish attached themselves to the entrances of burrows and were alert and ready to withdraw into the burrows. At other localities, on the contrary, a number of fish moved freely away from their burrows and returned to their burrows rather sluggishly when a diver approached. This impression of difference was also ascertained in the two populations in this study. Fish at Rinkai Beach spent most of their time in close proximity to the entrances and the total length of their stay on the substrate was shorter, as compared with those at Murote Beach.

This variation seems to be related to the difference of predation pressure between the

localities: potential predators are relatively common at Rinkai Beach but rarer at Murote Beach. It is quite reasonable that fish under high predation pressure adhere to the burrow entrances to lower the probability of attack. The density of burrows may be also responsible for this variation: the density of burrows at Murote Beach was about three times as high as at Rinkai Beach. Even within the same locality, there was a tendency that fish in the densely populated area left their burrows more frequently than those in the sparsely populated area. Fish in areas where burrows are closely distributed may be able to shelter themselves more easily and safely in any of the burrows when attacked by predators.

Differences were also noticed in other behaviours and social interactions between the two populations. At Rinkai Beach, each fish usually used one burrow at a time and stayed in one particular burrow over some weeks. At Murote Beach, one to two burrows were used by one solitary fish and one to three burrows by one pair at a time, and each fish moved among two to six burrows within a month. In the former population, aggressive encounters between individuals were much rater and the proportion of floaters to the whole population was smaller than in the latter population. These differences may also be explained by the above two ecological parameters, i.e., predation pressure and the density of burrows. In areas where leaving a burrow is hazardous for a fish owing to the high predation pressure and the low density of burrows, it may be profitable for the fish to adhere to one definite burrow both in short term and long term. Consequently, the frequency of encounters among the individuals will be kept low. Floaters will not be allowed to survive for a long time due to high predation pressure.

These two ecological parameters may also have an influence on the pattern of pair bonding. As has been discussed in another paper (Yanagisawa, MS.), for the animals living in the discrete habitat each unit of which is so small that only a few individuals can be accommodated in it, the timing of pair formation and the stability of the pair bond depend on the degree to which a mate is hard to obtain and hence to which movement between units of the habitat is difficult. In the two populations studied, no essential differences were perceived both in the timing of pair formation and the stability of the pair bond, as mentioned above. Presumably, the difference in difficulty of movement between burrows is not critical enough to bring about an obvious variation in the pattern of pair bonding between them. However, a somewhat different pattern was perceived in another population. At Motogoe Beach near Murote Beach, out of 10 burrows which were isolated from one another by more than 4 m distance, three burrows were occupied by established pairs of fish in the middle of April when no pairs were found at Murote Beach, suggesting that pairs are established earlier in sparsely distributed populations.

As has been described, the gobiid fishes *Tomiyamichthys oni* and *Stonogobiops* sp. that are sparsely populated at Murote Beach presented a remarkable difference in the pattern of pair bonding from the fish *A. japonica*. Pairs in those two species were found nearly all the year round (Table 1) and some pairs were established by small individuals long before maturation. The difference of those species from *A. japonica* may be related to the difference of population density and therefore to the difference in the availability of mates, but cannot be attributed only to these factors. In *A. japonica*, neither pairs in the winter nor those between small individuals long before maturation have been found in any localities. The feature of pair bonding may be to some extent a species-specific characteristic.

Recently, the variation in behaviour and social organization of various fish species has been related to the ecological parameters that are different from one locality to another (Keenleyside, 1979; Fricke, 1980: Moyer, 1980). In the coral-dwelling damselfish *Dascyllus marginatus*, the variation in mating system is attributed to one ecological parameter: the number of available hiding places in the coral (Fricke, 1980). In the anemonefish *Amphiprion clarkii*, the population in warm temperate waters shows many differences in behaviour and social interaction when compared to populations in the tropics, and such differences are attributed to differences in water temperatures, predation pressure and the size of host anemones (Moyer, 1980). These fish live in a discrete habitat, each

unit of which has only a small space, similar to the gobiid fish *A. japonica*. For fishes living in such habitats, the size of one unit of the habitat and the difficulty in movement between units must be critical factors in regulating the behaviour of individuals and determining the social organization. These ecological parameters may be changeable enough from place to place to bring about perceivable variation in behaviour and social organization.

Acknowledgements

I wish to express my sincere thanks to Prof. Eiji Harada for his invaluable advice and critical reading of the manuscript. Prof. Tatsumi Uematsu and Mr. Tetsuo Kuwamura have kindly informed me of literature, for which I am indebted. I express my thanks to Prof. Takeo Itô and Dr. Nobuhiko Mizuno for their helpful suggestions, and to Messrs. Yasuo Niimura, Hideo Suga and Shigeyuki Yamato for their willing assistance in the field.

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ダテハゼの社会行動と配偶形態*

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ダテハゼはニシキテッポウエビが掘った巣穴をかくれがとして利用している．ハゼは日中巣穴の入口付近を中心に活動しているが，繁殖期には地表上を移動して隣接個体とペアを形成する．ペアは通常2～3日以上維持されるが，産卵に至らないで別れるものも多い．配偶者獲得をめぐる競争は雄間で烈しく，授精に成功したと推測される雄は社会的に優位な大型個体であった．巣穴を離れている時間，攻撃的出会いの頻度，巣穴を所有しない個体の割合については，調査個体群間に差異が認められた．この差異は，生息地の捕食圧と巣穴密度に関連づけて理解できることを示唆した．

*同居関係を結ぶハゼ類とテッポウエビ類の種間関係について III.

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