STUDIES ON THE INTERSPECIFIC RELATIONSHIP BETWEEN GOBIID FISH AND SNAPPING SHRIMP II. LIFE HISTORY AND PAIR FORMATION OF SNAPPING SHRIMP *ALPHEUS BELLULUS*[1]

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With Text-figures 1–11 and Tables 1–5

Abstract

The snapping shrimp *Alpheus bellulus* and the gobiid fish *Amblyeleotris japonica* live together in the burrow dug by the shrimp and a tactile alarm communication is developed between them. The association is established at the juvenile stage soon after settlement and maintained throughout their lives. The members of the association are sometimes changed by the movement of the fish between burrows. Pair formation of the shrimp begins at the juvenile stage and the adults usually occur in pairs. Resin casts of burrows and the data on the daily positional change of the entrance of one burrow indicate that burrows are extensive enough to come close to the adjacent burrows within the sediment, suggesting that a solitary shrimp has a chance to acquire a mate through the connection of its burrow with the adjacent burrow. The early pair formation and the stable pair bond of this species are attributed to the difficulty in obtaining a mate owing to the discreteness of the habitat.

Introduction

The association between the alpheid shrimp and the gobiid fish is widely known for various combinations of the species in the tropical and subtropical waters (Luther, 1958; Klausewitz, 1960, 1969, 1974 a, b; Palmer, 1963; Magnus, 1967; Harada, 1969, 1972; Karplus et al., 1972 a, b, 1974; Yanagisawa, 1976, 1978; Polunin and Lubbock, 1977). These two animals live together in the burrow dug by the shrimp and a tactile alarm communication is developed between them. Antennal contact is maintained between them while the shrimp is outside the burrow. The quivering motion of the caudal part of the goby is transmitted to the shrimp through its antenna as an alarm signal and elicits the retreat of the shrimp into the burrow. This alarm signal is given selectively in response to the approach of certain species of the fish to the burrow. Recently, the communication system was quantitatively analyzed in the field (Preston, 1978; Karplus, 1979; Karplus et al., 1979).

The shrimp *Alpheus bellulus* is one of the representative alpheid shrimps on the southern coasts of Japan. This shrimp takes up the association with several species of the gobiid fish, predominantly with *Amblyeleotris japonica*, but never occurs on the sea bottom where none of the partner fishes is distributed. The association is

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maintained from the first stage of their benthic lives (Yanagisawa, 1976). The shrimp is entirely dependent on the tactile communication with the fish when it emerges from and is outside the burrow, and the fish always utilizes the burrow as a shelter and nesting site. Such mutually obligate relationship must have a great influence on the life history of each animal. In order to elucidate the nature and extent of influence, investigations on the two animals from populational and developmental aspects are required. However, comparatively little is known of the life histories and behaviours of these animals, due in part to the difficulty of making observations on burrowing organisms.

In this study, the activity and life history of the shrimp *A. bellulus* associated with the goby *A. japonica* and the communication system between them are investigated and analyzed. The structure of their burrows is also investigated. The process of pair formation of the shrimp is of interest, since it is puzzling how an individual shrimp in the isolated burrow can acquire its mate. The social behaviour and mating system of the fish *A. japonica* was presented in the previous publication (Yanagisawa, 1982).

Methods

Study Area

Field work was carried out at Rinkai Beach in Tanabe Bay (33°41′N, 135° 20′E) on the west coast of Kii Peninsula and at Murote Beach in Uchiumi Bay (33° 00′N, 132°30′E) on the west coast of Shikoku Island. Sea surface temperatures at both coasts are between 25°C and 28°C in summer and fall down below 15°C in winter. Rinkai Beach is shallow for some distance from the shore and the submerged rocks are surrounded by the sandy floor. The shrimp *A. bellulus* is distributed on the sandy bottom packed with pebbles, coral debris and shell fragments, that borders the rocky reefs. A 9 m × 9 m quadrat was set on the sandy bottom at 4 m depth for repeated observations. Murote Beach is a cove about 300 m long and steep cliffs stretch on the north and south sides. Two species of the shrimp, *A. bellulus* and *A. rapacida*, occur on the sandy bottom that fringes rocks extending from the cliffs. A 15 m × 40 m quadrat divided into 5 m × 5 m sub-quadrats was set over the bottom, the depths ranging from 5 m to 8 m. The sediment at the shallower part of the quadrat is composed of coasre sand (1.1 mm to 6.9 mm in median size) packed with pebbles, coral debris and shell fragments, while at the deeper part relatively fine sand is predominant (0.7 mm to 1.6 mm in median size).

Field Observation

At Rinkai Beach, positions of the opened entrances of burrows of the shrimp in the quadrat were recorded daily on the map from 5 August to 3 September 1978 to know the daily fluctuation in the number of the opened entrances and the daily displacement in the position of the entrance of each burrow. The approximate sizes of the fishes that occupied the burrow entrances were recorded, but the shrimp

size was not always recorded because it required an enormous amount of time to observe all of shrimps coming outside the burrows. Some of the fish were tagged for continued identified observation.

At Murote Beach, monthly observations were done in the 15 m × 40 m quadrat from September 1978 to August 1980 in order to obtain the information on the seasonal fluctuation in the number of associations and the growth pattern of the individuals. The smallest entrances were enumerated only in a narrow part of the quadrat (2.5 m × 40 m), which were apt to be overlooked in the whole quadrat census. In the census in July 1979, the species combination of the shrimp and the fish was ascertained for all burrows precisely.

The behaviours of the shrimp and the fish were recorded for about 20 hours at Rinkai Beach and for about 30 hours at Murote Beach. Watching by keeping motionless at a distance about 1.5 m from the burrow entrance did not seemingly disturb their normal behaviours.

To estimate the proportion of the shrimps in pairs to the whole population, shrimps coming outside the burrows were watched for up to 30 minutes per one burrow. Twelve series of this observation were made for the shrimps of various sizes. Sex descrimination of the shrimp in the field was made from the dimorphism in the large chela, being larger and broader in male than in female.

To analyze the stability of the pair bond, the positions of burrow entrances, from which a pair of shrimps were observed to come out, and the paired shrimps were recorded in and near the 5 m × 5 m sub-quadrat at Murote Beach at intervals of 2 to 4 weeks during the period from May to October in 1979. In July and August, some additional observations were made. For the identification of each shrimp, the characteristics such as the size, coloration and handedness (i.e., the side of the large chela) were adopted.

Subterranean structure of the burrow was examined by recovering the cast of polyester resin, mixed with 0.2 percent reactor and poured into the burrow.

Results

1. *Habitat of Shrimp and Associated Fish*

The burrows of the shrimp *A. bellulus* occurred nearly all over the area of the quadrat at Murote Beach (Fig. 1). They were abundant on the bottom at the southern half of the quadrat where the sediment was composed of coarse sand packed with pebbles, coral debris and shell fragments, and relatively few at the northern half where the sediment was primarily composed of fine sand. The density of burrows was 0.39 per square metre at the southern half of the quadrat. This shrimp was associated with the fishes *Amblyeleotris japonica*, *Tomiyamichthys oni* and *Stonogobiops* sp. (Table 1). The associations with *A. japonica* were most numerous. The associations with *T. oni* and *Stonogobiops* sp. occurred mainly on the bottom where the sediment was composed of fine sand. A small number of burrows dug by another shrimp *Alpheus rapacida* were also found (Fig. 1), and it was associated with the fishes
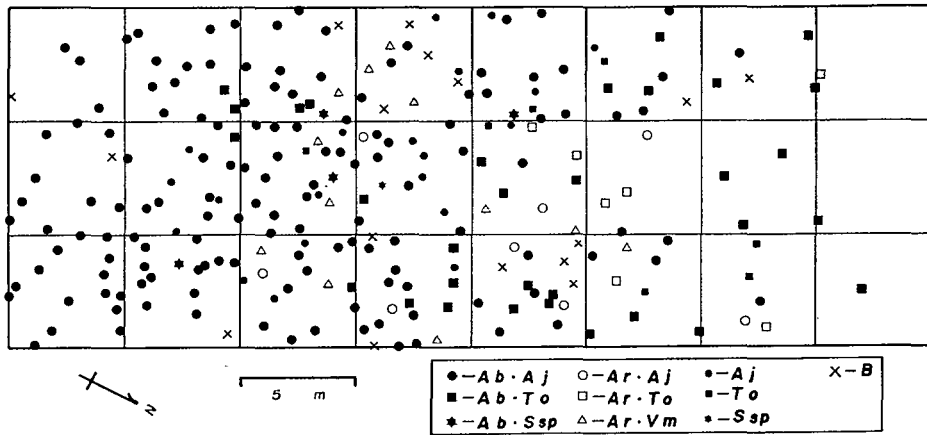
Fig. 1.   Distribution of associations between snapping shrimps and gobiid fishes in a quadrat at Murote Beach on 26 July 1979. Ab-*Alpheus bellulus*; Ar-*Alpheus rapacida*; Aj-*Amblyeleotris japonica*; To-*Tomiyamichthys oni*; Vm-*Vanderhorstia mertensi*; Ssp-*Stonogobiops* sp.; B-burrow.

Table 1.   Observed combinations of species of the snapping shrimp and the gobiid fish in association in a 15 m × 40 m quadrat at Murote Beach.

Shrimp \ Fish	Amblyeleotris japonica	Tomiyamichthys oni	Stonogobiops sp.	Vanderhorstia mertensi	Total
Alpheus bellulus	139	32	4	0	175
Alpheus rapacida	8	7	0	12	27

A. japonica, T. oni and *Vanderhorstia mertensi* (Table 1).

In the quadrat at Rinkai Beach where the composition of the sediment was very similar to that at the south part of the quadrat at Murote Beach, only the associations between *A. bellulus* and *A. japonica* were found.

2.   *Activity of Shrimp*

The activities of the shrimp *A. bellulus* and the fish *A. japonica* outside the burrows are restricted to the daytime.   During the observation at night, neither shrimps nor fish have ever been observed on the bottom surface.   The entrances of the majority of the burrows are tightly closed with the sediment carried up from the inside of the burrows by the shrimps.   Just after sunrise, fish appear first from each burrow, breaking through the sediment plugging the entrance, and then shrimps emerge from the burrow and expand the entrance.   Although the time of emergence from the burrows varies among the associations, most of the entrances are opened by the time about one hour after sunrise (Table 2).   Towards dusk, fish become inactive and both animals tend to remain longer in the burrow once they have retreated.   By sunset, all the shrimps and fish have entered the burrows.   The number of opened burrows in the daytime fluctuated greatly day by day (Fig. 2).   In bad conditions such as rough weather and a red tide, most of burrows remained closed

Table 2. Numbers of opened burrows observed in the area of 50 m² at different time in the early morning of 13 July 1978 at Murote Beach. The sunrise was 0508.

Time	0500	0520	0540	0600	0620	0640	0700	1100
Number of opened burrows	0	6	15	19	29	29	30	27

and their resident animals stayed inside the burrows all the day.

Each burrow is occupied by one or two individuals of the shrimp and one or two of the fish (Harada, 1969). When two shrimps are present, they are always heterosexual and the body sizes of the two are positively correlated (Fig. 3, r = 0.976, P<0.01). The body size of the female is slightly larger than that of the male in adult pairs.
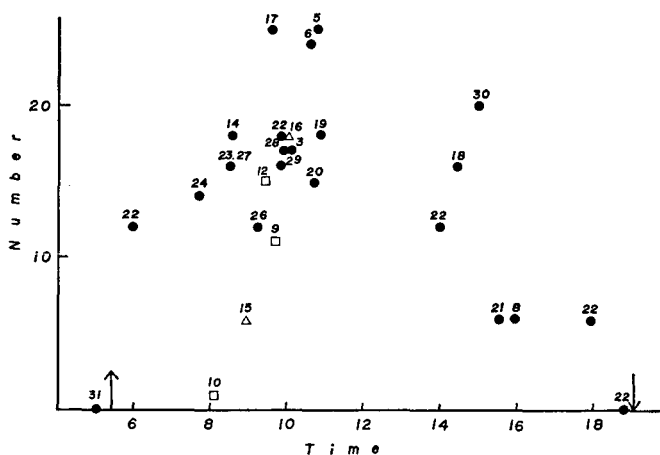

Fig. 2. The number of opened burrow entrances in a 9 m × 9 m quadrat at Rinkai Beach during the period from 5 August to 3 September 1978. Numbers indicate the dates. Arrows indicate the time of sunrise and sunset respectively. ●—calm weather; △—rough weather; □—red tide.

Around the entrance of a burrow, a funnel is formed, which usually has the size of 5 cm to 10 cm radius in adult's burrow. Many burrows have a shallow depression stretching from the funnel on the bottom surface. This depression is several centimetres wide and two or three centimetres deep and the maximum distance of its extension observed was about 80 cm. Both the funnel and the depression have been marked as the result of the shrimp's ladling sediment out.

Shrimps emerge from the burrow when the associated fish is staying in close vicinity of the entrance. On the occasion when the fish was away from the entrance or staying within the burrow, the shrimps remained within the burrow. Fish were found staying near the entrance for 68.6 percent of the observation period totalling 1560 minutes. While the fish were staying near the entrance, a male shrimp came out from the burrow 3.3 times and a female 2.8 times per 10 minutes on an average, and a male stayed outside the burrow for 175 seconds and a female for 100 seconds
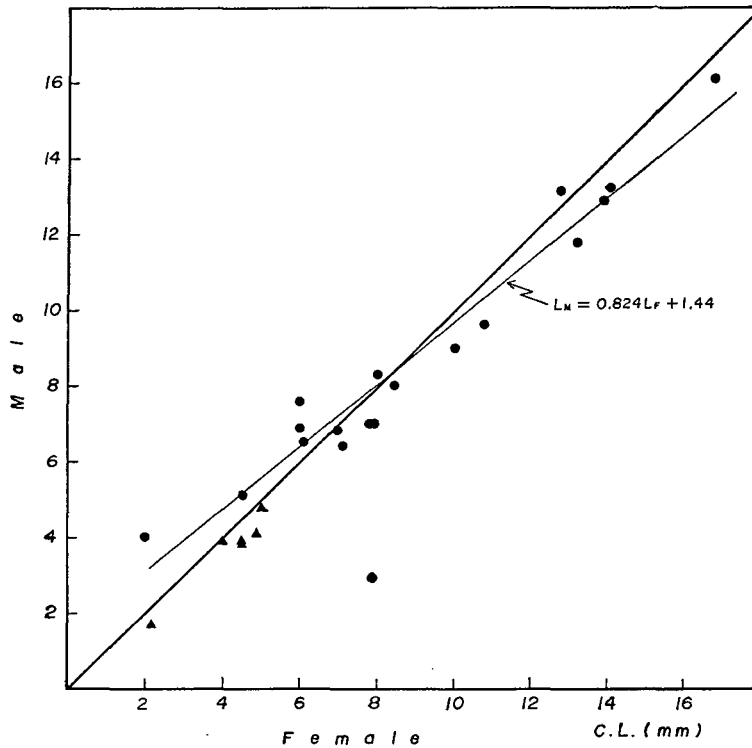
Fig. 3. Relationship between carapace lengths of a female and a male of
Alpheus bellulus in the same burrow. Triangles indicate pairs in which
descrimination of sex was impossible.

per 10 minutes on an average. The latter values are significantly different be-
tween sexes (P<0.05). Out of 164 emergences observed, shrimps came out, push-
ing sand in 101 cases, carrying a hard object such as a small stone and a shell frag-
ment in 12 cases, and without anything in 51 cases. Average duration of one emer-
gence was 49.8 seconds. Outside of the burrow, they scoop sediment loaded on
their flattened chelae out of the funnel and the depression, and pile up small stones
or shell fragments on the roof of the entrance seemingly to prevent the entrance
from collapsing. During these activities, they often show feeding behaviour on
the materials among the sediment.

3. Communication between Shrimp and Fish

The shrimp outside the burrow almost always maintains antennal contact
with the fish. The retreat of the shrimp into the burrow was elicited not only by
the tail quivering motion of the fish but also by any rapid and sudden movements
of the fish. The tail quivering motion was observed to occur on relatively rare
occasions in the natural condition. It was observed 47 times during the total ob-
servation period of 940 minutes. This signal was given only when the antennal
contact of the shrimp with the fish was maintained. It occurred with the approach

of the foraging fishes such as *Pagrus major*, *Therapon jarbua* and *Mugil cephalus* in 17 cases, and in the other cases by uncertain reasons, probably due to the existence of the observer. The retreat of the shrimp into the burrow was followed after this signalling in 12 cases. In other cases, it exhibited no behavioural change against the signalling or stopped for a moment as if it hesitated to go ahead.

In addition to this alarm signal, another kind of tactile communication was observed. When a shrimp emerged from the burrow, a fish sometimes responded to the antennal contact of the shrimp by soft undulation of the caudal part. A bout of the undulation continued for 1 to 3 seconds in a rhythm of approximately 1 to 2 cycles per second, which is much slower and has a greater amplitude than a tail quivering motion. The undulation was usually followed by the full emergence of the shrimp from the burrow. In the observations covering 520 minutes, this signal occurred 74 times. The shrimp came out of the burrow in 54 cases soon after the signal was emitted. In the other 20 cases, the signal was not followed by the emergence of the shrimp. The fish exhibited this signal motion only rarely when the shrimps were repeatedly engaged in coming out and in the burrow. On the contrary, it readily occurred after a long stay of the shrimps in the burrow (Table 3). Although it is not essential for shrimps to accept the signal before emergence from the burrows, this signal seems to have a function to elicit the emergence

Table 3. Occurrence of tail undulation of the gobiid fish in response to antennal contact of the snapping shrimp emerging from the burrow after staying in the burrow for various time.

The length of shrimp's stay in burrow before emergence (sec)	−10	−40	−90	−160	−250	250−	Total
Number of emergence observed	63	92	36	12	8	10	221
Occurrence of tail undulation	5	24	9	5	3	4	50
Frequency (%)	8	26	25	42	38	40	23

of shrimps, especially in the cases after a long stay in the burrows. For the shrimp, this signal may mean a kind of guarantee of the safety outside the burrows. This tactile signal is also reported in the association between *Alpheus djiboutensis* and *Cryptocentrus cryptocentrus* (Karplus et al., 1972 a).

Another behaviour of the fish also seemed to provide facilities for the activity of the shrimp outside the burrow. When a shrimp dared to leave any distance beyond the range of antennal contact with a fish, the fish moved forwards side by side, maintaining contact with the shrimp. This behaviour was frequently exhibited by the fish living in a burrow with a long depression in which the shrimps were repeatedly moving between the entrance and the distal part of the depression. This behaviour is also known in the gobiid fish in the Seychelles (Polunin and Lubbock, 1977).

The members of the partners in one burrow sometimes changed due to the movement of the fish between burrows. No apparent changes in the response of

the shrimps to the new partner have been noticed and tactile communication oper-
ated normally between them. The communication system is probably not based
on the individual recognition between the two animals.

There are often observed fish that do not occupy any burrows and are wander-
ing on the bottom surface. The number of such individuals amounted to 2 to 5
percent of the population (Yanagisawa, 1982). The burrows which seemed not
to be inhabited by fish are also occasionally found, although it is difficult to know
what proportion of the shrimp population is not associated with fish, since the bur-
rows of such shrimps may mostly be closed. In these burrows, the antennae of
the shrimp were occasionally found extending from the inside of the burrow through
a gap of sediment. This posture of the shrimp usually lasted from 7 to 30 seconds.
This behaviour may be regarded as the one to wait for the approach of fish to make
a new partnership. Fish wandering on the sea floor were sometimes observed to
occupy such vacant burrows and form a partnership with the shrimps.

4. *Burrow Structure*

Four burrows of the adult shrimp and four of the young shrimp were poured
with resin. In two cases of the adult's burrow, the burrows were filled up with
the resin of 4.2 and 12.5 litres respectively, but the full retrieval of the resin cast
was not possible. In the former burrow, a tunnel with a diameter of about 3 cm
was extending obliquely from the entrance to a point, about 70 cm deep and 100
cm distant horizontally, where it crept into underneath a big coral boulder. In
the latter burrow, a thick tunnel soon reached a flat coral remain of a diameter of
70 cm at a depth of 20 cm and branched through its crevices and along its side to
its underside. As the big coral boulders could not be removed by hand in both cases,
further recovery of resin casts from these points could not be done. The main part
of the burrows must lie under these boulders, since the amounts of the resin retrieved
were less than one fifth of the amounts poured in. In the other two cases of the
adult's burrow, the entrances collapsed before the resin filled up the space of the
burrows and the further pouring was impossible. No part of the poured resin was
retrieved by the excavation of the sediment in the area of about 50 cm radius and
60 to 70 cm deep around the entrances. This indicates that the burrows are spread-
ing out beyond the excavated area. These results show that the extent of the adult's
burrow is enormous both vertically and horizontally.

In four cases of the young shrimp's burrow, the resin casts were fully retrieved
(Fig. 4 A–D). The shrimps of those burrows were from 7 mm to 9 mm in carapace
length, seemingly at 2 to 4 months after settlement. The lengths of the burrows
are from 30 cm to 70 cm. The structure of the burrows appears to be determined
by the distribution of embedded hard objects. Each burrow has a chamber of
enlarged space at its deeper part, which is formed under a hard object such as a
coral boulder (Fig. 4 D) and a test of sand dollar (Fig. 4 C) or among the sediment
(Fig. 4 A and B). One or two offshoots of space ascending from the chamber are
usually present, some of which are attaining to the point just beneath the bottom
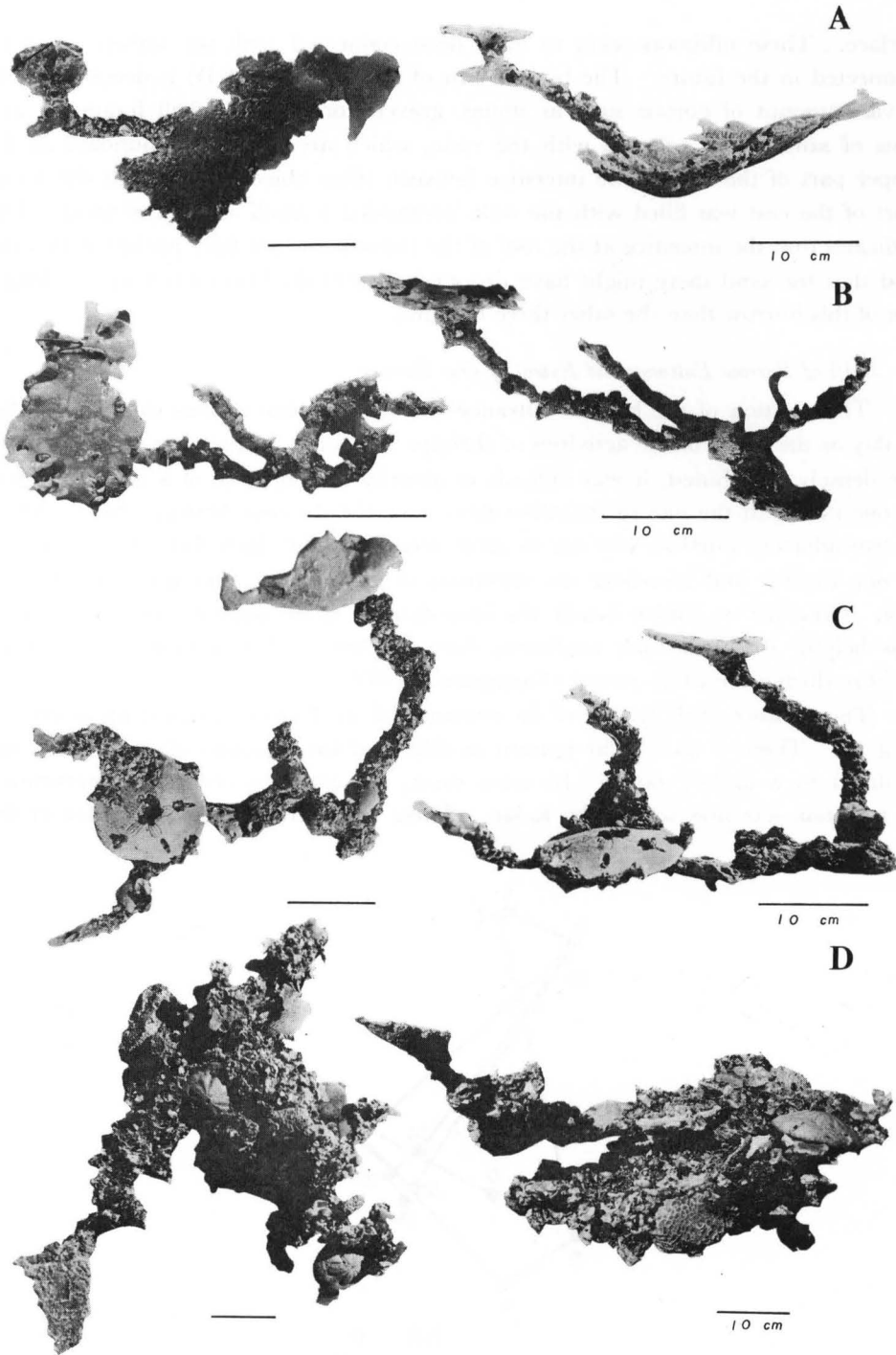
Fig. 4.   Burrows of young *Alpheus bellulus* moulded with resin in November 1979 at Murote Beach.
A-associated with one *Amblyeleotris japonica* (ca. 38 mm in standard length), 460 cc in resin
volume; B-one shrimp (ca. 7 mm in carapace length) with one *A. japonica* (ca. 24 mm), 390 cc;
C-two shrimps (ca. 9 mm and 8 mm) with one *Stonogobiops* sp. (ca. 30 mm), 990 cc; D-two
shrimps (ca. 9 mm and 8 mm) with one *A. japonica* (ca. 32 mm), 4000 cc.   Left is top view
and right is side view.

surface. These offshoots seem to have been connected with the surface or to be connected in the future. The biggest cast of the four (Fig. 4 D) is decorated with a vast amount of objects such as stones, gravel, coral debris, shell fragments and tests of sand dollar adhered with the resin, which are especially abundant at the upper part of the cast. The interstice between those objects adhered at the upper part of the cast was filled with the resin containing a small amount of sand. This indicates that the interstice at the roof of the tunnels was not fully packed with sand, and that the sand there might have dropped off into the burrow during the longer use of this burrow than the other three burrows.

5. Shift of Burrow Entrance and Extent of One Burrow

The position of the burrow entrance was moved over various extent from day to day as the result of the activities of shrimps and fish. In the area where burrows are densely distributed, it was difficult to identify the entrance of a certain burrow in one day with the one in the other day, since the distance between the entrances of two adjacent burrows was not so great relative to the daily shift of the entrance of one burrow and moreover the entrances of all burrows were not opened every day. However, at Rinkai Beach, the identification of the associated fish by tagging was helpful to avoid such confusion, because they seldom altered their partner shrimps during the study period (Yanagisawa, 1982).

The distance of daily shift of the entrance of one burrow attained up to 160 cm (Fig. 5). There is no regular pattern of shift, but the positions of one burrow are confined to a limited range. In some cases, the entrance occurred concentrated to a certain few sites within the range. These concentrations of occurrence of the
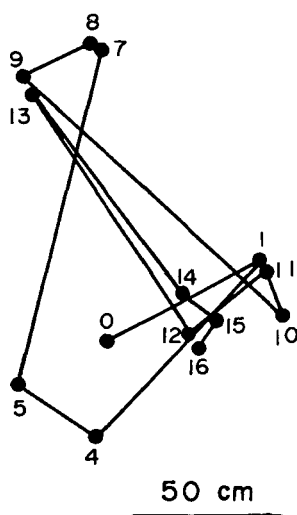

Fig. 5.   One example of daily shift in position of entrance of one burrow.   Numbers indicate the days after start of observation.

entrance may be related to the offshoots of the burrow. One concentration of the entrance was probably derived from the same offshoot and the number of the concentrations may be taken as an indirect indication of the number of the offshoots of the burrow.

Although the burrow structure could not be determined by the resin cast for adult's burrows fully, the area enclosing all the changing positions of the entrance of one burrow may approximately represent the horizontal extent of the burrow. Fig. 6 shows the cumulative positions of the entrances of adult's burrows in 27 censuses from 5 August to 3 September 1978 at Rinkai Beach. The range of entrances that belong to the same burrow was determined by using the positional information of the associated fish. In the burrows whose entrances were recorded more than 10 times, the area enclosing the displaced entrances usually has a horizontal extent of about a half to two square metres. In many cases, the area of one burrow is close to those of the adjacent ones, and in a few cases two areas partially overlap each other so that the boundary of them cannot be determined (Fig. 6). This result probably indicates that the offshoots of one burrow are stretching over within the substratum at least a half to two square metres horizontally and often reaching
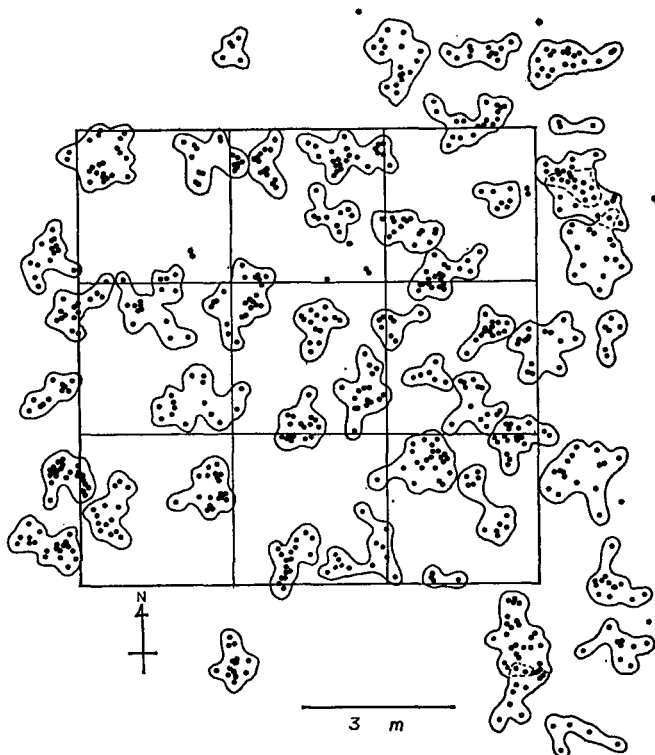
Fig. 6. Map of cumulative positions of burrow entrances in 27 surveys during the period from 5 August to 3 September 1978 at Rinkai Beach. A patch of entrances enclosed with a solid line is referred to one burrow. Broken lines indicate the overlap of two burrows.

close to the adjacent burrows.

6. Life History of Shrimp

Ovigerous female shrimps appeared first in early July. The proportion of ovigerous females attained to the maximum during the period from the middle of July to the middle of August. The minimum size of an ovigerous shrimp collected was 12.2 mm in carapace length (32.7 mm in body length) (Fig. 7). Newly
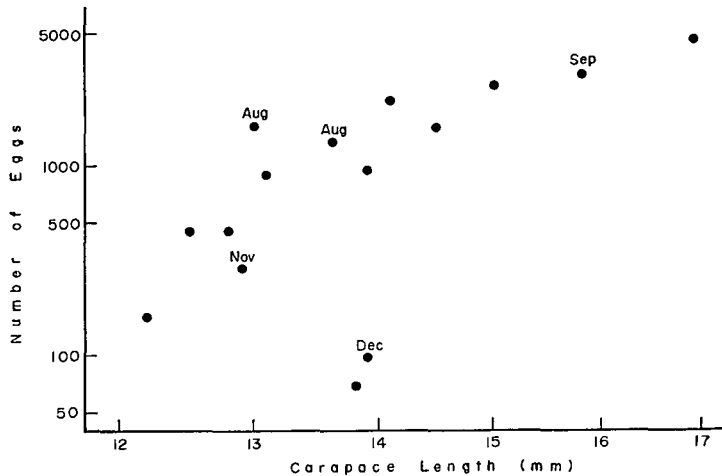
Fig. 7. Relationship between the size of female *Alpheus bellulus* and the number of the eggs brooded. All the specimens for which the month of collection is not specified were caught in July.

deposited eggs are spherical in shape and have diameters ranging from 0.59 mm to 0.62 mm. The number of eggs carried by a female varied with the size of the female, increasing nearly exponentially to the increase in female size. The maximum number of eggs in one brood was 4484. An ovigerous individual was exceptionally caught in December, and the number of eggs carried was very small (Fig. 7). The breeding seasons of this shrimp and the associated fish *A. japonica* greatly overlap each other. Gravid females of the fish appeared from late June to the middle of August.

The associations of the small juveniles of the two animals occurred in late summer and early autumn. They inhabited the bottom where adult associations were already settled, as well as its peripheral areas where no adult associations were seen (Table 4). A tactile alarm signal had already been developed between them. They are as alert as adults are and withdraw into the burrow whenever a diver comes close to them. The smallest juvenile shrimp collected was 1.7 mm in carapace length and had transparent body with a tint of red at the anterior-most part of the carapace and the posterior end of the telson. The smallest fish collected was 8.7 mm in standard length.

Table 4. Numbers of adult associations and juvenile associations between the shrimp *Alpheus bellulus* and the fishes in each 2.5 m × 5 m area of a 2.5 m × 40 m quadrat at Murote Beach in the season when juveniles settled. Number of adult associations is followed by that of juvenile associations.

Quadrate Date	← shallower					deeper →			Total
	1	2	3	4	5	6	7	8	
1 Oct. 1978	6:9	9:14	4:16	3:15	1:19	0:18	0:15	0:7	23:113
14 Sep. 1979	5:13	6:19	8:7	5:20	4:13	2:10	0:7	0:0	30:89

To collect juveniles successfully is not so difficult as in collecting adult individuals, because their burrows are not so deep and complicated as the adult's. A full excavation of a burrow is possible with a trowel and the two animals can easily be detected from the sediment turned up. A juvenile shrimp and a juvenile fish in the same burrow were caught together on 34 occasions by this method. There is a positive correlation between the size of the juvenile shrimp and that of the juvenile fish (Fig. 8; r=0.791, P<0.01, when calculated for shrimps smaller than 5.5 mm in carapace length and fish smaller than 25 mm in standard length). A small number of the juvenile fish that had no partner and were staying or wandering on the surface were also observed. As for the shrimp, it is difficult to know whether the juveniles not associated with the fish are actually present or not, because the
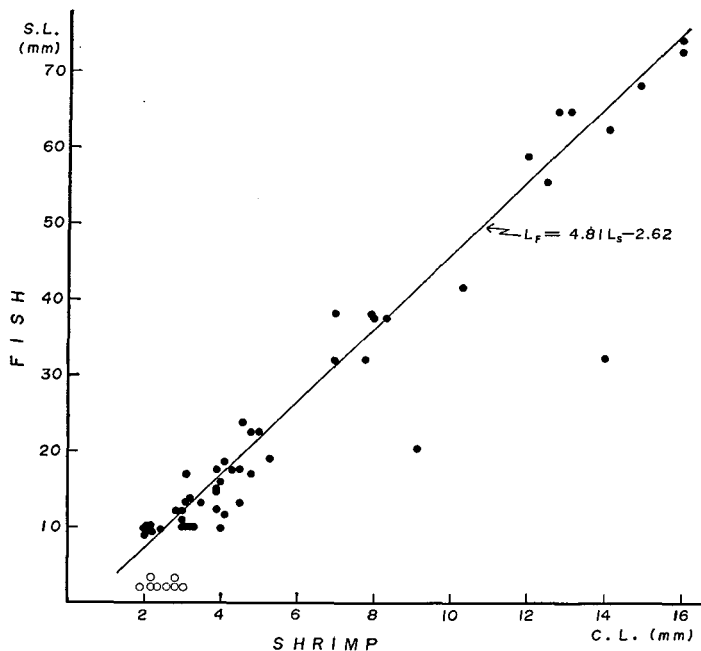

Fig. 8. Relationship between the sizes of *Alpheus bellulus* and *Amblyeleotris japonica* in the same burrow. Size of shrimp is represented in carapace length and that of fish in standard length. Open circles indicate shrimps that were not associated with fish.

shrimps not associated with the fish, if present, might be easily overlooked due to their scarce emergence from the burrows. Nevertheless, juvenile shrimps alone were caught from some burrows among a number of trials of a full excavation of burrow (Fig. 8), suggesting that their burrows had not been occupied by fish.

Although the collection of shrimps was not made quantitatively at regular intervals, the crude growth pattern of the shrimp can be deduced from the measurements of the specimens collected (Fig. 9). In monthly censuses at Murote Beach,
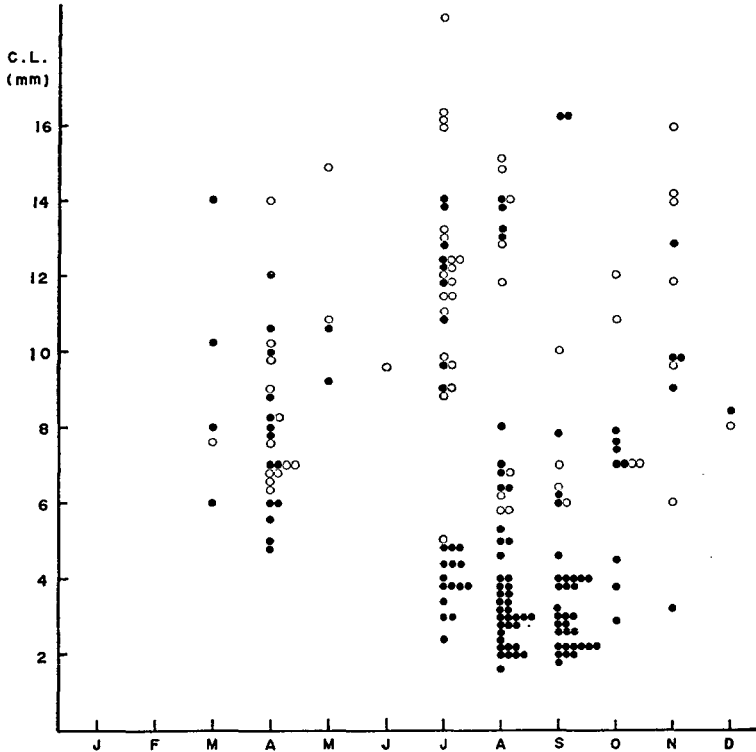

Fig. 9. Carapace lengths of *Alpheus bellulus* collected during the period from 1972 to 1979. ●–female or juvenile; ○–male.

the approximate sizes of the associated fishes were recorded for all the associations found within the narrow zone of the quadrat (2.5 m × 40 m) (Fig. 10). Associations of the shrimp *Alpheus rapacida* may also be included among them, but the number of them is negligible (Table 1). Since the size of the fish *A. japonica* and that of the shrimp in the same burrow have a strong positive correlation (Fig. 8; r=0.989, P<0.01, when calculated excluding two exceptional associations), monthly size distributions of the associated fishes may be taken as an approximate indication of the growth pattern of the shrimp.

The estimated growth patterns of the shrimp obtained from the two sources stated above nearly coincide with each other. Juvenile shrimps, that settled during the period from late July to early October, attain to 3 mm to 9 mm in carapace
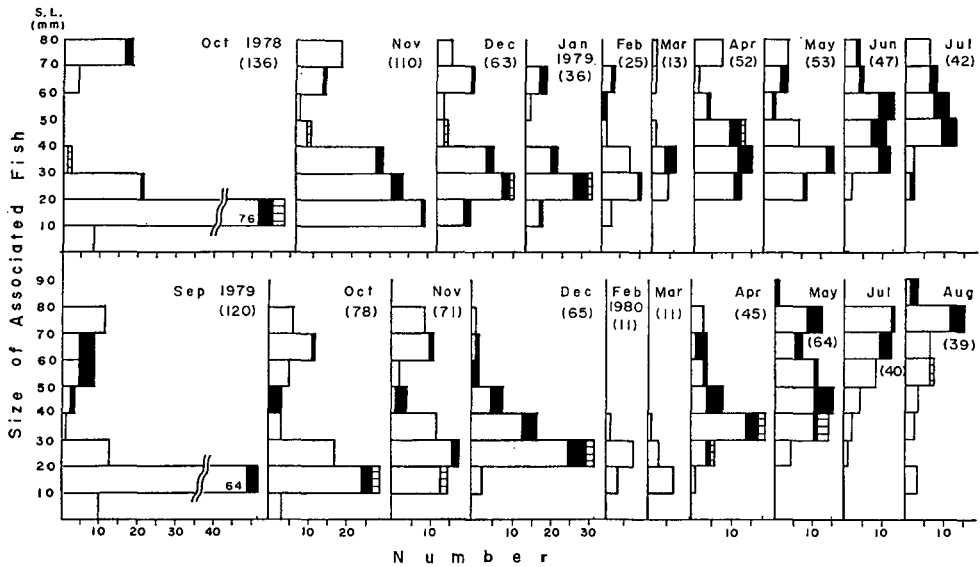
Fig. 10.   The number of associations in a 2.5 m × 40 m quadrat at Murote Beach and the size of the associated fish.   White-*Amblyeleotris japonica*; black-*Tomiyamichthys oni*; stripes-*Stonogobiops* sp.

length by December.   During the winter from January to March when the water temperatures decrease below 15°C, most of shrimps and fishes remain within the burrows and their growth rate may remain small.   Shrimps reach 5 mm to 12 mm in April and some of them exceed 13 mm by July.   This means that the shrimps come to maturity and participate in reproduction within one year after settlement, since the minimum size of ovigerous females observed was 12.2 mm in carapace length.   The life span of the shrimp could not be ascertained directly, but, judging from the largest size obtained and the growth pattern, adult population is probably composed of one year and two years groups.   Shrimps more than two years old, if any, may be very rare.

The number of associations observed in one census does not necessarily represent the whole number of the associations established there, since the number of closed burrows which could not be counted in the census may be considerably great, especially during the winter.   In the warmer season, however, the number of associations observed can be taken as a good approximation of the number of the whole associations.   The number of associations between the juveniles was about 5 times as many as that between the adult individuals in October 1978 and about 3 times in September 1979 (Fig. 10).   Among juvenile associations, the distance from one burrow entrance to the nearest one was 43 cm in 1978 and 75 cm in 1979 on an average in the typically densely populated area.   The decrease of associations between the young individuals seems to be condiserably great, especially during the first three months after settlement.   Their number reduced by about 60 percent during the period from October to December in 1978.   In 1979, the majority of

associations that had settled by September were swept by the attack of the typhoon and most of juveniles associations appeared in October were newly settled ones.

7. *Pair Formation and Stability of Pair Bond*

One burrow is occupied by either one or two shrimps, as mentioned earlier. In adult's burrows, more than 80 percent of them were ascertained to be occupied by two shrimps in the observations for 15 to 30 minutes per one burrow (Table 5).

Table 5. Numbers of burrows with one shrimp and two shrimps. Observations with a symbol (*) were carried out at Rinkai Beach, and the others at Murote Beach. Values when the duration of observation per one burrow is divided into each ten minutes are given in parentheses.

	Date	Number of observations	Duration of observation per one burrow (min.)	Size range of shrimps (C.L. in mm)	Burrows with one shrimp	Burrows with two shrimps	Frequency of burrows with two shrimps (%)
Juvenile and Young	Aug. 1978*	15	15 or 20	2.5–5	15	0	0.0
	Sep. 1978	25 (25)	10 or 15 (10)	2.5–7	20 (20)	5 (5)	20.0 (20.0)
	Nov. 1978	22	10	4 –9	13	9	40.9
	Dec. 1978	20	10	5 –11	9	11	55.0
	Feb. 1979	16	10	5 –13	7	9	56.3
	Mar. 1979	12	10	7 –11	6	6	50.0
	Apr. 1979	21	10	6 –11	9	12	57.1
	Dec. 1979	15	10	5 –10	9	6	40.0
Adult	Aug. 1978*	14 (19)	15–30 (10)	13 –17	2 (3)	12 (16)	85.7 (84.2)
	May–Jun. 1979	15 (26)	20 (10)	10 –17	2 (8)	13 (18)	86.7 (69.7)
	Jul.–Aug. 1979	47 (105)	20 or 30 (10)	12 –17	7 (31)	40 (74)	85.1 (70.5)
	Dec. 1979	5 (10)	20 (10)	13 –17	0 (0)	5 (10)	100.0 (100.0)

This probably means that almost all of adult shrimps are in fact paired. On the contrary, in the majority of small juvenile's burrows only one individual was observed in the observations for 10 to 20 minutes per one burrow (Table 5), which suggests that small juveniles are mostly solitary, although a small number of paired juveniles were caught at the early stage after settlement, including a very small individual with the size of 1.7 mm in carapace length (Fig. 3). The frequency of burrows in which two shrimps were witnessed gradually increased with growth and it exceeded 50 percent in the first winter about 4 to 6 months after settlement. These results obviously indicate that the shrimps are solitary at the start of their benthic lives and form pair bonds one after another with growth, and the adults are mostly in pairs.

As a consequence of pair formation of the shrimp, the number of associations inevitably reduces, up to one-half, even if the mortality rate of the shrimp is negligible. The observed decrease of associations in the young stage (Fig. 10) is

naturally partly due to the pair formation of the shrimp. This is not the case with the fish that pairs generally only in the breeding season. The pair formation of the shrimp must result in the loss of the partner shrimp for some part of the fish population.

Since adult shrimps are usually in pairs in the separate burrows, it is suggested that each pair of adult shrimps is maintained for a long time without altering its members. Fig. 11 shows the cumulative positions of the burrow entrances at the
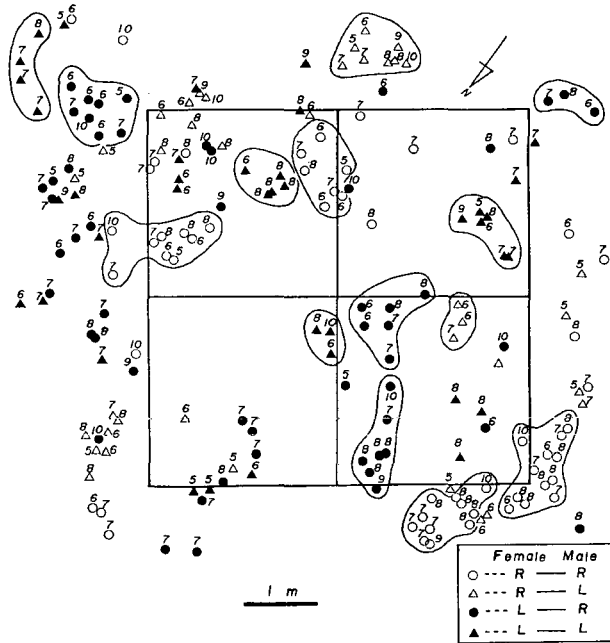

Fig. 11. Map of the entrances of the burrows from which a pair of adult *Alpheus bellulus* were observed to come out in and near a 5 m × 5 m quadrat at Murote Beach at repeated observations during the period from May to October 1979, and the combination of the side of large chela of male and female shrimps of the pair. Numbers indicate the month observed. A patch of entrances enclosed with a line indicate a stable association whose members did not change during observation period. R-large chela on the right side; L-large chela on the left side

repeated observations conducted during the period from May to October in 1979 in and near a fixed quadrat of 5 m × 5 m at Murote Beach, from which a pair of adult shrimps were observed to come out. The combination of the sides of large chela of male and female shrimps of the pair is also shown for each entrance plot. Although it was impossible to confirm the identity of every pair of shrimps at successive observations and to distinguish it from others, the characteristics of the shrimp such as the handedness, the size and the coloration could safely be taken as the indications of the pair in some pairs. Of these, at least 14 pairs were confirmed to have

been maintained without altering the members for 2 to 5 months (Fig. 11). The entrance of the burrow in which the same pair was observed at the different observations shifted only within a limited range of two square metres at most, indicating that each pair has been maintained in the same burrow. The difference of the handedness between the successive observations does not necessarily mean that the two individuals observed at different time are different, since the small chela becomes the large one on the occasion when the large chela has been amputated (Wilson, 1903). Some of the pairs showing different combinations of handedness at different time may be the same one. Nevertheless, the reliable alteration of the member was observed in a few cases.

Although these results have some uncertainty, it may be safely concluded that the pair bond of the adult shrimp is usually stable and some pairs are maintained more than several months. However, the replacement of the members of a pair may be not very rare incidents.

Discussion

Partnership between Shrimp and Fish

From the observation that the shrimp outside the burrow thoroughly depends on the tactile signals from the associated fish and the fish always utilizes the burrow provided by the shrimp as a sheltering and nesting site, it is suggested that each animal can not keep alive for a long time without maintaining the association with the other. This is supported by the fact that no individuals of the two animals have been found to live independently in the area where the partner animal is not distributed. Although a small number of fish that possess no burrow and shrimps whose burrows are not occupied by fish were witnessed, their occurrence was restricted to the bottom on which the associations are densely populated, suggesting that such individuals had been associated with the partners in the past and had been produced by the death of the partners or the social interactions among the adjacent individuals.

For both of them, to establish the association as early as possible after settlement must be essential to escape from predators. As has been stated, even the smallest juveniles of the two animals, seemingly immediately after settlement, occurred together in one burrow. From the observation that juvenile shrimps whose burrows have not been occupied yet by fish are present, it can be presumed that a post-larval shrimp starts to dig a small burrow for itself as soon as it settled on the bottom. Meanwhile, a fish at free-swimming stage or benthic stage that is exploring on the bottom will come up to such burrows. However, if the numbers of juveniles settled in one area are disproportionate between them, some members of the species in excess have to wait for a time to get a chance to encounter a partner. Although the synchronized breeding season of the two species may be favourable to avoid such disproportion, it is improbable that the numbers of juveniles settled

are equal between them in one area at any given time. The mortality of the two species at this stage must be considerably great.

The juvenile associations were several times as abundant as the adult associations, but they decreased greatly during the first several months after settlement. Some of this decrease is attributed to the pair formation of the shrimp. At the time soon after the juveniles have established the associations, one burrow is usually occupied by one shrimp and one fish (Table 5), and therefore the population size is nearly equal between the two species. The gradual increase of paired shrimps with growth will decrease the number of burrows and will bias the ratio between the population sizes of the shrimp and the fish towards 2:1. About a half of the fish population will be deprived of the burrows in this process. The intraspecific competition for the burrows must be intense among the individuals of the fish. Judging from the fact that fish without burrows amount to a few percent of the population, the individuals expelled from the burrows may have been made a victim of predators.

The pair formation of the fish in the breeding season or the death of the fish, on the other hand, will produce burrows in which a fish is absent. But the absence of the associated fish does not seem to bring the shrimps to a crisis unless the duration of the absence is extremely long. They are probably able to endure for a good while without emerging from the burrow, which is suggested from the observation that shrimps were mostly staying within the burrows throughout the cold water season. They may have an opportunity sooner or later to be visited to their burrows by other fish. Fish wandering on the sea floor must be important as a stock to supplement the vacant burrows. The existence of fish that use more than one burrow at a time (Yanagisawa, 1982) may also lighten the deficiency of fish partners.

In short, the partnership between the shrimp and the fish is the mutually obligate one in the sense that each individual of the two species can not keep alive for a long time without associated with the partner, but is not the one in which the disappearance of one partner in one association directly causes the death of the other partner. The ability of the fish to move between burrows and to keep alive for a time on the bottom and the ability of the shrimp to endure for a good while within the burrow provide a chance to re-establish the associations.

Mating System of Shrimp

The pair formation of the shrimp *A. bellulus* begins at the juvenile stage (Fig. 3), the proportion of paired individuals gradually increases with growth and the great majority of the adults occur in pairs (Table 5). From this fact, it is suggested that a shrimp at any developmental stage is ready to establish a pair bond. However, we have no direct evidence to describe how a solitary shrimp gets a chance to meet with a mate. One thinkable way is that a solitary shrimp travels over the bottom surface until it encounters the burrow of a shrimp of the opposite sex. But this possibility is denied because the shrimp has never been witnessed to venture apart from its entrance enough to reach the adjacent entrances in daytime and at night

the entrances are all closed with sand. An alternative could be that shrimps meet with and obtain their mate within the sediment. Although the distance between two adjacent burrow entrances usually exceeds 50 cm, it was elucidated in this study that the extensions of one burrow are great enough to come close to the adjacent burrows. Under these conditions, one burrow meets with the adjacent burrows sooner or later if the shrimp enlarges the space of the burrow. A solitary shrimp can establish a pair bond when a resident of the conjoint burrow is a solitary one of the opposite sex.

If this underground pair formation is primary and usual way in this species, individuals that lost their mate may also have an opportunity to meet with and secure another mate through a connection between burrows. Often, a pair in which the sizes of the mates are disproportionate was observed. This may be taken as an indication that the re-establishment of pair bond is occurring. On digging the burrow, however, the shrimp actually has a chance to come across with other individuals of the same sex as well. In such case, they must be intolerable each other and get into fighting to expel the other, that may be one of the reasons for the lack of either or both of the chelae occasionally observed in the sea.

Anyone may be impressed by the restless work of shrimps both in the field and laboratory observations. Almost all their activities are seemingly devoted to the enlargement and maintenance of the burrow. It is not likely that they are very diligent only to maintain the minimum space of the burrow necessary to nestle a pair of the shrimps and the associated fish. The space seems to be too large to be used only for this purpose. The condition that the shrimp can obtain a mate only by means of the underground connection between adjacent burrows may in part explain the diligence of the shrimp and the necessity of extension of the burrow.

It is suggested above that an individual at any developmental stage is ready to establish a pair bond if a mate is available. A solitary shrimp that is isolated from the others within the burrow has no clues to know the abundance of the conspecifics around it and therefore can not predict the degree of the difficulty in having an opportunity to encounter the potential mates. Under these conditions, it is reasonable for the shrimp to form a pair with the individual of the opposite sex with which it meets at the first time and maintain the pair bond for a long time. Probably, this is the way actually adopted by this species.

In the shrimps other than *A. bellulus*, that live associated with the gobiid fishes, it is not known how they establish the pair bond and how they maintain it. The number of shrimps per one burrow has, however, been reported for several species. *Alpheus* sp. associated with *Cryptocentrus caeruleopunctatus* and *Vanderhorstia delagoae*, *A. purpurilenticularis* with *Cryptocentrus steinitzi* and *A. rapacida* with *Psilogobius mainlandi* all live in a heterosexual pair (Magnus, 1967; Preston, 1978; Karplus, 1979). The associations of these species, judging from the facts described, are all obiligatory. While, *A. rapax* associated with *P. mainlandi* "were observed three to a burrow, two females and one male, or in pairs consisting of two females or a male and a female" (Preston, 1978). The individuals of this species were found travelling on the surface

of the substratum not accompanied by gobies, on very hot days when the tide was low, indicating that their association with the gobiid fish was facultative. These observations suggest that the shrimps usually live in a pair in obligatory association and those in facultative associations do not necessarily live in a pair. In the species of the shrimp in facultative associations, shrimps can easily encounter the conspecifics in the adjacent burrows, travelling on the surface. The potential mate available for each individual is abundant, and therefore the establishment of stable pair bond may not greatly beneficial for each.

Of the alpheid shrimps not associated with the gobiid fishes, several species are also known to live in a pair, e.g., *Alpheus heterochaelis* living in burrows or beneath shells and rocks (Nolan and Salmon, 1970; Schein, 1975; Conover and Miller, 1978), *A. normanni* living beneath shells (Nolan and Salmon, 1970), *A. frontalis* inhabiting algal tubes (Fishelson, 1966), *A. lottini* associated with corals (Lassig, 1977) and *A. armatus* associated with a sea anemone (Knowlton, 1976, 1980). In *A. heterochaelis*, even the young less than 8 mm in carapace length were collected as a pair. In *A. armatus*, mates in a pair stay together for 6 to over 79 days. Besides the alpheid shrimps, many crustacean species are known to live in a long lasting pair (Patton, 1967, 1976; Bruce, 1976). The shrimp *Spongicola venusta* in the glass sponge, the crabs *Trapezia* spp. living on scleractinian corals and the banded shrimp *Stenopus hispidus* are well-known examples (Arndt, 1933; Johnson, 1969; Preston, 1973; Castro, 1978). In *Trapezia* spp., it is known that the individuals occasionally move between coral colonies and heterosexual pairs are formed early in life (Castro, 1978). In Pisces, the blind goby *Typhlogobius cariforniensis* living in the burrows constructed by the shrimp *Callianassa affinis* form permanent pairs early in life (Mac-Ginitie, 1939).

All the species that occur in pairs mentioned above live in the discrete habitat (home sites such as hosts, burrows and tubes), and each unit of the habitat is so small that only a few individuals can be accommodated in it and is isolated from the others by areas in which the animals suffer high mortality from predation. The species living in such habitat may be abundant in the shallow waters, especially in the tropical reefs where species diversity is maintained by specialized biotic relationship, e.g., symbiosis and parasitism (Lassig, 1977) and potential predators are abundant (Johannes, 1978). Under the circumstances where movement from one unit of the habitat to another is extremely hazardous, the animal will have little chance to obtain a mate, and therefore it is advantageous for them to maintain stable pair bonds. While, in the cases where the animals in one unit can migrate freely to others, it is expected that they establish temporary pairs like the animals living in the continuous habitat. Permanency of pair bond will depend on the degree to which a mate is hard to get, and hence on the degree to which movement between units of the habitat is difficult.

The degree to which a mate is hard to get is also considered to affect the timing of pair formation. If the movement between units is critically difficult and there is little chance to meet with the individuals in other units, a pair will be established

on settlement on the habitat or as early as possible. In the animals that have no clues to know the abundance of the potential mates like the shrimp *A. bellulus*, an individual may establish a pair bond with the individual of the opposite sex with which it meets at the first time, even if the actual potential mates are not very rare.

The advantage and disadvantage of keeping a pair in a restricted space of one unit must be taken into consideration as one of the factors which affect the stability of pair bond and the timing of pair formation. In the cases where the presence of two individuals in one unit deteriorates the condition of the unit too much, the individuals will keep a solitary life in spite of reproductive disadvantage. For instance, in the pinnotherid living solitarily in the mussel it is believed that the presence of two individuals in one host is too much of a drain on the host (Pearse, 1962; Patton, 1967). By contrast, in the cases where the animals make a burrow by themselves and great efforts are required to sustain the burrow, the presence of two individuals in one burrow may be as well advantageous for the enlargement and maintenance of the burrow as for the reproduction. In those animals, it is likely that pairs are formed from the earlier stage and maintained more stably. One of the reasons for the early pair formation in *A. bellulus* may be attributed to this condition.

Acknowledgements

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