SIPHONARIA (PULMONATE LIMPET) SURVEY OF JAPAN I. OBSERVATIONS ON THE BEHAVIOR OF SIPHONARIA JAPONICA DURING BREEDING SEASON[1]

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With Text-figures 1–9 and Tables 1–2

Introduction

Siphonaria japonica (Donovan) is well known as a pulmonate limpet which exhibits homing behavior. It is common in Japanese intertidal regions. Although homing behavior has been observed not only in pulmonate limpets belonging to the siphonaridae but also in many species of prosobranchiate limpets belonging to the Acmaeidae and Patellidae, the mechanism involved has been a matter of controversy and does not yet seem to have been given a conclusive explanation although many experimental examinations have been conducted (Ohgushi, 1955; Cook *et al.*, 1969; Cook, 1969, 1971). It is also important to know the time of movement in each species of limpet under natural conditions. In order to describe this precisely and completely, 24-hours continuous observation including both day and night periods is necessary. Furthermore, because *Siphonaria* is hermaphroditic as are other pulmonate molluscs, *S. japonica* also exhibits mating behavior during its breeding season. There have been, however, few observations of mating except for those of Abe (1940).

The present authors investigated the behavior of *S. japonica* during its breeding season from the viewpoints discussed above. They observed in detail the timing of movement, shifts of activities with special reference to different lunar phases (different tidal amplitudes), mating behavior, and homing behavior. All data were collected in the field.

Material and Methods

The study was conducted on the rocky intertidal shore of Matsugahana neighboring the Mukaishima Marine Biological Station, Mukaishima Island, northwest of Bingonada, Seto Inland Sea of Japan. Because preliminary observations were made many times since 1977, the authors had a general understanding of the breeding

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season and behavioral pattern of *S. japonica* in this area. Four periods of 24-hours continuous observations were made from April 29 to May 22, 1978, covering different phases of the moon (different tidal amplitudes): Waning half moon; new moon; waxing half moon; and full moon. The seawater temperature ranged from about 14°C to 19°C. Breeding activity was very high in this period of the study. Individuals occupying a relatively large boulder (height about 175 cm, girth about 560 cm) were the focus of this study (Fig. 1). Their vertical distribution was from 162 cm to 243 cm above the datum line (D.L., i.e. 25 cm below M.L.W.S. and 20 cm above E.L.W.S. in this area). Observed number of *S. japonica* and tidal amplitudes at each period of observation are listed in Table 1. At this site, the annual range of the tide is about 4 m and the mean water level is about 2 m. Therefore, the distribution of the observed population centered around the mid-tide level.

For observations at night the use of an underwater light did not appear to affect normal behavior. Each individual limpet and each side of the home site were marked by tagging with embossed Daimo-Tapes of various colors so that the relationship between limpets and their corresponding home sites might be known during

Fig. 1. Large boulder inhabited by *S. japonica*.

Table 1. Tidal data and sample sizes of *Siphonaria japonica*

Dates	Mean tidal amplitudes (cm)		Observed limpets (N)
Apr. 29–30	182±47	neap tide	14
May 7	267±33	spring tide	11—12
May 14–15	156±34	neap tide	17—18
May 22	294±33	spring tide	12—13

limpet excursions.   This operation was done on April 20.

The following data were collected: The number of active animals; the distance moved; the duration of active movement; and details of mating behavior.   The distance is not derived from an actual path but expressed as the radius from home scar to the furthest point at a given tide.   The moving duration is defined as the time in minutes spent off the sar; however, short pauses of movement out of the scar are not included.   As much data on mating behavior were collected as of possible. For example, behavior prior to coming across the partner, mode of copulation, duration of copulation, percentage of copulating individuals per total number observed during a given tide, and so on.   Tracks were also recorded as carefully as possible, particularly those of pre-copulatory and homing individuals.   Although the shell sizes observed in this study were 7–20 mm in shell length, a significant relationship between shell size and moving duration or distance could not be found.   The sea was calm and the weather was fine throughout all periods of observation.   The water of the Seto Inland Sea is generally very calm, like a mirror, on most days.

Results

Time of Movement

Percentages of active individuals are shown in Fig. 2a and 2b, and were recorded on April 29–30 (the first period of observation) and May 7 (the second), respectively.   S. *japonica* did not always move during complete submergence.   Just before and after they were exposed to air on ebb tide they began to move.   Although the time when movement started differed more or less according to the height of each home site, 100 % of the observed population moved.   The low percentage recorded during the period on May 7 was due to the very short duration of movement exhibited by each individual; animals which had started earlier came back to their home sites before others began to move.

The stars in Fig. 2 delimit times when more than 50 % of all individuals were active.   Shifts in the time of movement as derived from Fig. 2 and similar figures for the third (May 14–15) and fourth (May 22) periods of observation simply follow shifts in the tide (Fig. 3).

Almost all individuals returned to their own home sites during emersion before the rock surface completely dried, and thereafter did not move again even when they began to be covered by water on flood tide.   Only a few individuals that failed to home during emersion moved on the flood tide.   Therefore, two periods of active movement, once during ebb and once during flood, were not generally observed throughout the present study.

Moving Duration and Distance

The mean moving duration and distance are summarized in Table 2 to show differences associated with day or night and with various lunar phases (tidal amplitudes, see Table 1).
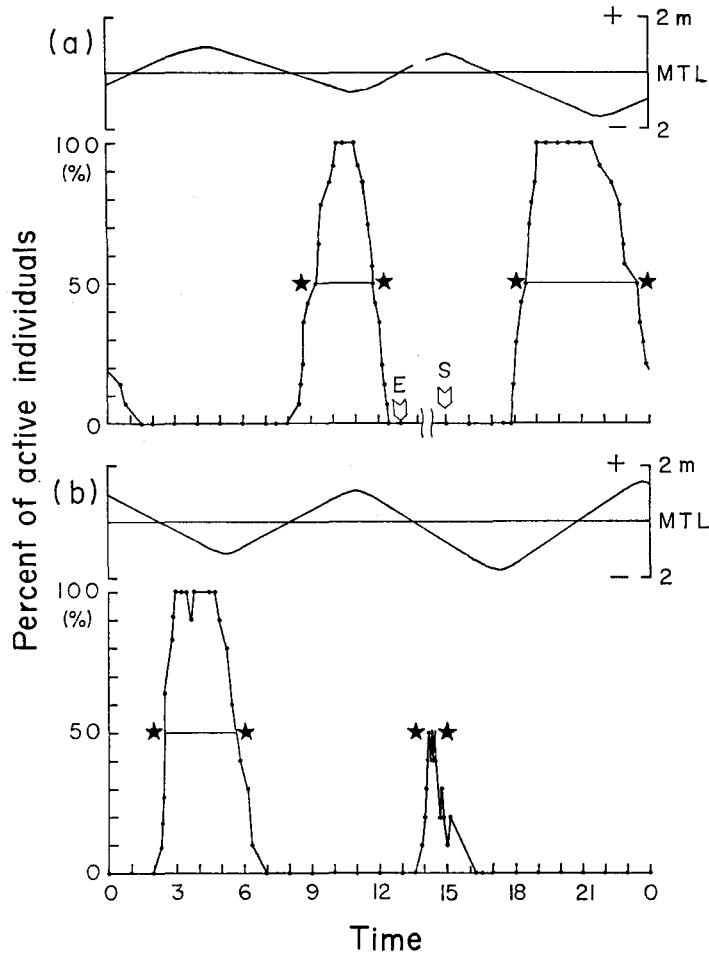
Fig. 2.   Percentage of active limpets in relation to phases of the tide.
(a): April 29–30, S and E indicate times of start and end of
observation, respectively.   (b): May 7.

Throughout all periods of observation, moving durations were always longer at night than during daytime.   On the other hand, differences in distance moved could not necessarily be seen between periods of observation.   But if days are divided into morning (the first and the third periods of observation) and afternoon (the second and the fourth periods of observation), then distances covered were also seen to be greater at night than during the afternoon.

Duration and distance of movement during daytime were always greater at half moons (neap tides) than at new moon and full moon (spring tides).   At night, however, there were no significant differences.   These trends are apparent in Fig. 3. It can be said that *S. japonica* is mostly active at night and during neap tides.
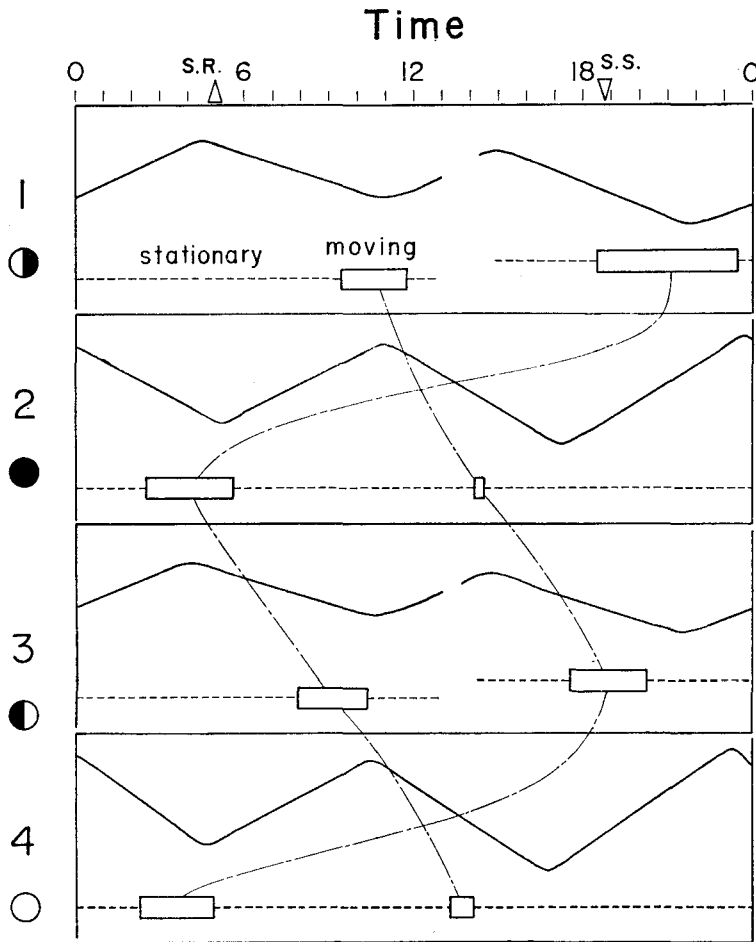
Time

Fig. 3. The time of movement in more than 50% of active individuals. Data were collected at four times of observation. S.R.: Sunrise, S.S.: Sunset.

Table 2. Comparison of mean moving duration and distance at different lunar phases. (mean±S.D.)

Phase of moon			Night	Day	
1	◑	Duration (min.)	298±64	163±44	
		Distance (cm)	36.1±22.4	28.6±11.5	morning
2	●	Duration (min.)	188±42	29±17	
		Distance (cm)	16.3±9.0	8.7±7.3	afternoon
3	◐	Duration (min.)	157±65	101±64	
		Distance (cm)	16.3±7.8	20.4±19.3	morning
4	○	Duration (min.)	158±61	41±13	
		Distance (cm)	13.5±7.1	11.5±4.9	afternoon

Observation of Mating Behavior

Seeking a Partner and Pre-copulatory Behavior

The directions of paths taken away from home scars seem to be random. Also random are the chances of encountering another individual because *S. japonica* distributes itself uniformly over the rock surface. In the case of individuals meeting head-on, copulation does not occur and the animals are seen to avoid each other (Fig. 4a).
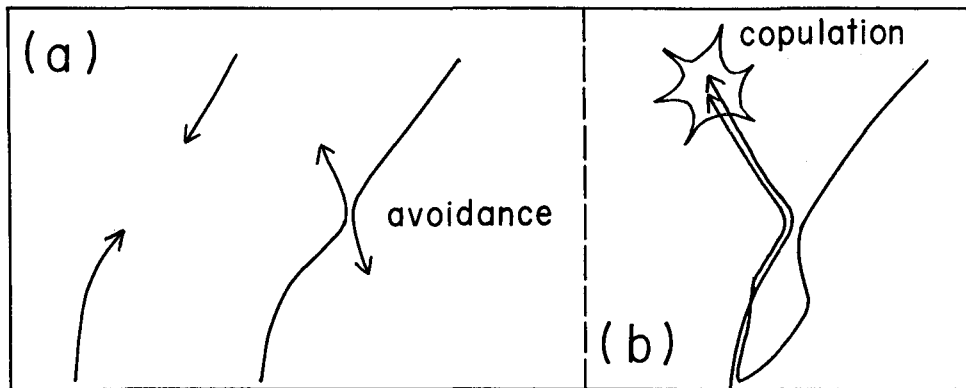

Fig. 4.   (a) Encounter and aviodance of limpets approaching head-on.   (b) Path-following resulting in copulation.
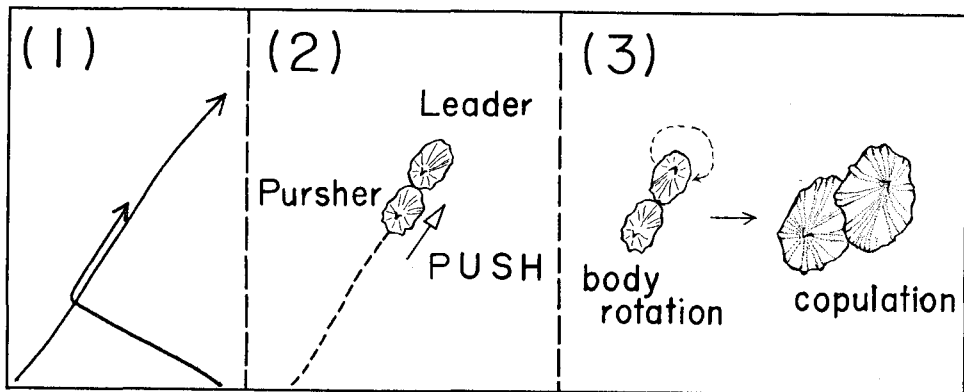

Fig. 5.   Pre-copulatory behavior.

Most copulations occurred as follows (Fig. 5): (1) When one individual across the pathway of another, the first began to follow. (2) The speed of movement of the "pursuer" increased; after the "pursuer" caught up with the "leader", the former pushed the shell of the latter from behind a number of times. (3) The pushed individual rotated clockwise 180° and lifted the front of its shell. Then, copulation began. The "pursuer" always inserted its body under that of the "leader". About one minute was required from the time of body rotation to the commencement of copulation.

Fig. 6 shows an actual example. X began to move at 08:34 on April 30 to the left, 45° downward, and changed its course at 09:05 when it reached the point marked by the arrow. Although no visible marks remained at that point of the rock surface, it was known from observations during the preceding night that the point lay at the intersection of previous outward and backward pathways of Y (dotted line). X followed the previous pathway of Y and arrived at the home site of Y. But Y was already absent from it. X then began to trace the outward trail of Y at a gradually accelerating pace until overtaking Y. Soon copulation began. When the individual passed in Fig. 4a met the pathway of another about three minutes later, it turned and followed. This time copulation ensued (Fig. 4b).
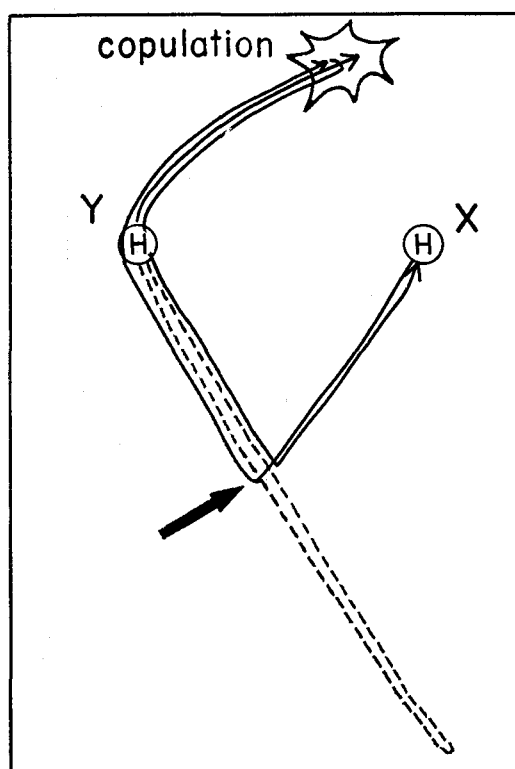

Fig. 6.   Paths followed in the case of an actual copulation.
See text for explanation.   H: Home sites.

Besides for individuals which meet head-on as described above, copulation also does not occur when the shell lengths of prospective partners are considerably different (e.g., one is 7 mm and the other 20 mm in shell length). In one instance, the larger one pushed the smaller one which turned its body but could not copulate. Copulating pairs would not respond to other individuals which arrived later even if their shells were pused. When one individual reached a small acmaeid limpet, *Chiazacmea pygmaea,* and pushed its shell by mistake, the latter did not respond at all.

Duration of Copulation

The mean ($\pm$S.D.) duration of copulation was 41 ± 15 minutes (n=37). The maximum and minimum times were 81 minutes and 13 minutes, respectively.

Proportion of Individuals Copulating

Percentages of copulating limpets out of the total number present at each period of observation are given in Fig. 7. More than 60 % copulated during all periods and there were no clear correlations with lunar phase or tidal amplitude. Therefore, it can be said that there is no clear periodicity of copulation in *S. japonica*.
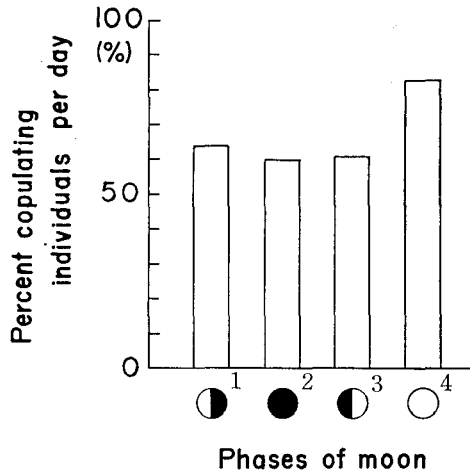

Fig. 7. Percentages of copulating limpets at each period of observation.
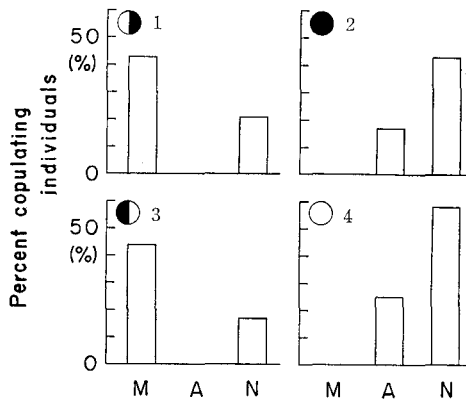

Fig. 8. Percentages of copulating limpets at different times of the day.
M: Morning,   A: Afternoon,   N: Night.

As for the times at which copulations occurred (Fig. 8), copulatign individuals were few at about 14:00, at which time moving duration was also shortest (cf. Table 2). But when comparing the data from sunset to midnight with that of morning (about 10:00), it is apparent that larger numbers copulated at morning than at night.

As stated above, proportion of individuals copulating is high at morning when it low at night, when it low during the afternoon it is high at night. This may explain that there is no clear periodicity of copulation with lunar phase or tidal amplidude.

Frequency of Copulation

Each individual usually copulated only once during any single period of activity. Sometimes, however, more than two copulations were observed. For example, the same partners were seen to copulate three times at 40–50 minute intervals. On another occasion, one individual copulated for 46 minutes, and 64 minutes later copulated again with a different partner for 42 minutes.

Homing Pathway (Pathway of Return Journey)

X in Fig. 6 homed along a path completely overlapping its own outward path, a distance of some 44 cm, in spite of the fact that only 7 cm separated its home scar from the site of copulation. Conversely, homing behavior which did not follow the outward trail and made loop-like excursions as also observed as shown in Fig. 9. Both types of homing occurred with about equal frequency.
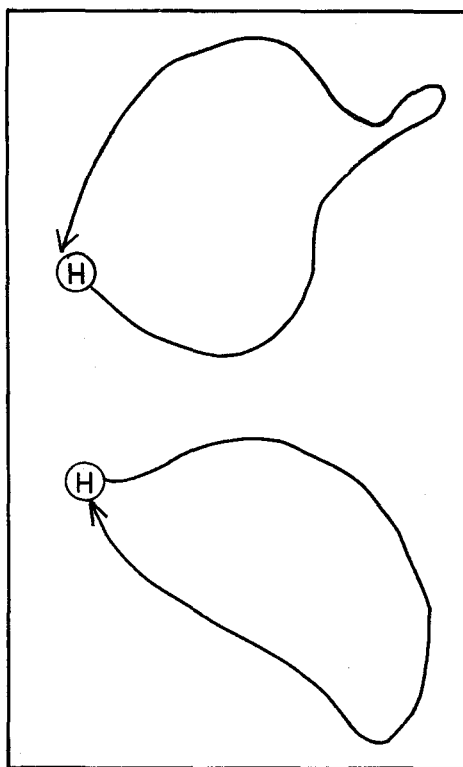

Fig. 9.   Examples of loop-like excursions.

Discussion

The behavior of *Siphonaria japonica* has previously been investigated by Abe

(1940) and Ohgushi (1954). In those works, however, observations were not made during night. Therefore, the complete daily rhythm of activity has not yet been brought to light. The present study revealed that *S. japonica* moves more actively during night than daytime. This result is the same as reported for *Siphonaria atra* (Abe, 1935).

It was also found from several observations during different tidal conditions that the activity of *S. japonica* is greater at neap tides than at spring tides (Table 2). Similar trends were reported in *Siphonaria normalis* and *S. alternata* by Cook and Cook (1978), who explained this phenomenon by the direct effects of different tidal amplitudes such as different rates of drainage at low tide. Although they reported that no effect of tidal amplitude was evident at the most benign site, our observations were also made at a very calm site. Therefore, we consider changes of activity in *S. japonica* at different tides to be due chiefly to the time lag of movement during day: Ebb conditions (active times for *S. japonica*) during daytime always coincide with midday during spring tides at this site (Fig. 2b and Fig. 3). Activity under these conditions was minimal, probably attributable to dessication effects caused by the strong, direct sunshine. Conversely, daytime ebb conditions at neap tide do not always occur at midday but also in the morning or evening, and activity was high under these circumstances (Fig. 2a and Fig. 3). Because nighttime activities did not fluctuate with different tidal conditions (Table 2), the differences among daytime activities seemed to determine the changes of total daily activity during each period of observation.

Abe (1940) found that the creeping of *S. japonica* began just before or after the time when it was exposed to air during ebb, and continued for about two hours, and did not usually occur in the water. On the other hand, Ohgushi (1954) stated that two periods of movement were apparent, the first just before *S. japonica* is exposed to air and the second immediately after being submerged in the water (the animal is stationary at its home site between times of activity). In the present study, movement was observed at ebb only once which seems to corroborate Abe's report. During summer, the same pattern of activity was observed (Hirano, unpubl.). Similar results have been reported for other siphonariid limpets as well. *S. pectinata* moves on ebb tides only (Thomas, 1973). *S. normalis* and *S. alternata* move on ebb and flood (Cook, 1969, 1971). The different results which are obtained from the same species (*S. japonica*), however, seem to be a function of different environmental conditions at the various sites. At the present study site, fully wet conditions continue for some time after the air-water interface passes by the animals on ebb tide; this condition is mostly conducive to the movement of *S. japonica*. On the other hand, the water is so still that splash is very slight on flood tide and there is only a brief intermediate period between complete emersion and complete immersion. This is unsuitable for active movement in *S. japonica*. Recently, Cook and Cook (1978) found that "limpets (*S. normalis* and *S. alternata*) at rapidly draining sites tended to be more active on rising tides than on falling tides near the spring end of the tidal spectrum, while limpets at other sites either divided activity equally between ebb and flood

tides or were active on ebbing tides". Our observations do not belong to either type but show that there is always only one period of movement on ebb, which is not affected by tidal amplitudes.

Detailed observations on homing and mating pathways may suggest some important problems. Homing pathways which completely overlap the outward trails lead us to hypothesize that homing limpets retrace chemical trails that they have laid previously. This hypothesis has already been supported in experiments on *S. alternata* by Cook (1971). On the other hand, loop-like excursions not following outward trails were also observed in this study (Fig. 9). The same results were reported by Ohgushi (1955), and this pattern of homing behavior has been a matter of controversy among many students because it seems not to be accounted for by a simple chemical-trail theory. Incidentally, it was demonstrated in the present study that the pathways of other individuals may play a part in seeking a partner but that the sense of sight may not be useful (Figs. 4, 5 and 6). If these pathways are laid down on the rock surface like cobwebs, *S. japonica* can find partners very efficiently merely by following them. In fact, the pathway of one individual during the last night of observation was traced by another (Fig. 6). The authors suspect that loop-like excursions in *S. japonica* could also be explained by the trail-retracing hypothesis, because the limpet need not necessarily retrace the outward trail it has just made if a previous one is detectable.

Now, if the ideas outlined above have any merit — either way, it may safely be said from our observations that previous paths of *S. japonica* are used both in homing and in seeking partners — the next question should be: Does an individual *S. japonica* distinguish its own pathway from that of another? Cook and Cook (1975) found from their experiments both in the laboratory and in the field that homing *S. alternata* followed their own mucus trails toward the origins of these trails (i.e., toward their home scars). Certainly, this behavior seems to be suited for homing, although it has not yet been examined in *S. japonica*. But movement in the reverse direction has been observed in the case of individuals approaching copulatory partners, that is to say, a tracing movement outward from the home scar of the "leader". If these directional differences in pathway-following behavior are real, directionality might be determined by whether or not a path is one's own. Probably *S. japonica* could obtain such information from the path itself. Investigation of its chemical composition is required.

Although Abe (1940) pointed out that *S. japonica* mates primarily during the time of waxing half moon, it was shown in this study that more than 60 % of the population could be found copulating regardless of lunar phase (Fig. 7); therefore, a clear periodicity of mating does not seem to exist. Furthermore, as some individuals were sometimes observed to copulate repeatedly without regular intervals, the period of time between copulation and spawning is suspected to be quite flexible. This problem is going to be dealt with in the next paper. The number of copulating individuals was seen to change, however, with the time of day (Fig. 8). This is probably a function of whether or not the dampness at a given time is suitable for mating.

Summary

1) Behavior of the pulmonate limpet *Siphonaria japonica* (Donovan) was investigated during its breeding season from April to May, 1978. Observations were chiefly directed at the daily rythm and mating behavior in a field population under various tidal conditions.

2) *S. japonica* begin to move just before and after they are exposed to air on ebb tide. Although movements continue for some time, individuals which have homed during emersion do not again move when they are washed by the flood tide and they remain stationary at their home sites under complete submergence.

3) Shifts in the time of movement simply follow shifts in the tide. Higher activity occurs at night than in the daytime. While nighttime activity is almost the same regardless of tidal conditions, during the daytime it is greater on neap tide than on spring tide, and this is reflected in total daily activity. This seems to be caused by a time lag of movement during the day; at the present study site, spring tide always occurs at midday at which time activity is least.

4) Observations on mating behavior indicated that the pathways of other individuals may play a part in seeking for partners with which to copulate but that the sense of sight may not be useful.

5) More than 60 % of the population may be found copulating under all tidal conditions. There does not seem to be a clear periodicity to copulatory behavior. Sometimes, the same individual will copulate several times in one day.

6) Homing *S. japonica* do not necessarily follow their own outward trail which has just been laid; rather, loop-like excursions may occur. Both types of return trip were observed with similar frequency.

7) The hypothesis is offered that an individual *S. japonica* can distinguish its own pathway from that of another and that directionality may be distinguished as well.

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