

An Essay on Inertial Navigation deduced in Return Habits of the Small Abalone *Sulculus aquatilis*

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Key words: abalone, inertial navigation, return

Abstract

The locomotion behaviour was monitored indoors to reveal the return habit of the small abalone *Sulculus aquatilis*. Before sunset, the animal was put centrally on a convex floor of 1 m ϕ and traced to obtain the locomotion track under red light in a dark room. Appearance frequencies were counted about three classified types of the locomotion tracks. The values were compared with those previously obtained on a flat floor to examine differences attributable to the alteration of a surface curvature.

For eight individuals, the repeating observations yielded 131, 31 and 82 appearance frequencies of the locomotion types as moving, return, and stationary, respectively. The effect of the convex substratum was indistinct because the above values approximately equaled the previous results. The return habit showed commonly a smooth trip of a looped track that was similarly observed on a flat substratum in the previous study. From geometrical consideration of looped tracks on a plane, a kind of inertial navigation was deduced to drive the return habit of abalone.

Hitherto, homing of marine animals has been mainly noticed in intertidal gastropods. Especially limpets and chitons are famous due to its widespread phenomenon. Their habitats are rocky shores. From the observation of homing animals on the rocky substratum, the descriptions show timing, distance, direction, and speed of a creeping behaviour of the animal that has culminated in a return to the original home.

They take a tidal trip and return home before the ebb tide, often showing a returning track close to an outgoing track scarcely overlapping. In limpets, homing occurs within a radius of 0.2 m from the home and most trips are expressed as an elongated or narrow loop in a plane figure¹⁻⁴⁾.

One of other species that show homing is abalone in the marine gastropod. Since the habit of abalone is nocturnal below the tidal zone, homing has not been commonly noticeable. A long time ago, Crofts (1929) referred to homing of abalone as to be an exceptional phenomenon in the ormer *Haliotis tuberculata*⁵⁾.

After that, field and laboratory investigations of abalone

sometimes recognized homing in such species as the Japanese abalone *Nordotis discus*, the ezo abalone *N. discus hannai*, the Siebold's abalone *N. gigantea* and the giant abalone *N. madaka*⁶⁻⁹⁾.

Especially in the ezo abalone and the Siebold's abalone, the locomotion behaviour has been first classified into moving, staying and homing types by fieldwork at rocky shores of the fishery grounds. In the ezo abalone, one animal among six individuals homed after a trip of 2.5 m length⁷⁾. Another fieldwork detected a homing trip of 2.5 m distance among 14 animals in the giant abalone⁹⁾.

The small abalone *Sulculus aquatilis* is also benthic and inhabits littoral rocks below the tidal zone. It goes out of the shelter in a cave or cleft after sunset and creeps on the rocky substratum. The animal shows a clear rhythm of the night activity similar to other abalone. The scar is faint and easily removable by washing¹⁰⁾ though intensive adhesion of slime has been confirmed at the home site. It is known in the ormer the locomotion trail has no scar in like manner with limpets

on the substratum⁵⁾.

The indoor and outdoor observations throughout nights revealed that more than 20% of the experimental abalone surely returned to a substitute shelter before sunrise in large tanks¹¹⁾. For this small abalone, the critical distance of homing was on average approximately 0.5 m from a home. In this connection, a homing ability of as many as 25% of individuals has been shown in the limpet *Acmaea digitalis*¹²⁾ or in some instances no precise return to a home has been reported¹³⁾.

How can abalone find its way to the starting spot? In response to this question, orientation attributable to dead reckoning was already proposed in the small abalone by the present author¹⁰⁾. Further behavioural observations seemed necessary to corroborate this subject.

Then, using a convex substratum, appearance frequencies of the locomotion types as well as return tracks were documented and compared to those already obtained in the previous study that has been conducted on a flat substratum^{11,14)}. Under the necessity of monitoring in detail, an indoor experiment was adopted and the observation was focused on a trip or return behaviour especially around the starting location.

Materials and Methods

Materials

Material animals were sub-adults or adults of the small abalone, or the tokobushi abalone named locally 'nagame'. Their number and shell size were 15 and 53.3 ± 2.7 mm. They were obtained from a live fish retailer named Iwatsubo in Nishino-Omote City, Tanegashima Island, Kagoshima Prefecture, where the fishery of this species has been well established.

At the laboratory, the animals were kept in a cubic net cage (3 mm mesh size) after being marked with an individual number on the shell. This cage was accommodated in a glass aquarium of 60 L. The aquarium was provided with equipments composed of a temperature regulator and aeration-filtration tools. It was given a natural photoperiod in a dim room.

During the experimental period, the animals were fed on the dried brown seaweed *Laminaria japonica* at 22°C. Every two to three days, new pieces of the sectioned algae were supplied to them. At that time the old food and dead animal(s) were taken away. The experiment was conducted from July to October 2008.

Experimental design

The flat and smooth floor of a round tank used in the previous study¹⁴⁾ was remodeled for a convex substratum by pouring concrete. Then the plane surface of vinyl chloride was altered into a curved surface of a little grained concrete. Such convex surface was necessary as one simple model for the ethological analysis of abalone's return tracks. Its simplicity could avoid orientation attributable to an exocentric coding¹⁵⁾ and also yield the advantage of tracing an individual trip in detail.

As concerns this convex surface, a radius of the curvature was 2 m. In other words, a ratio of the central height to the radius of the round substratum was 0.127. This value was introduced to examine an effect of the curved surface on the return behaviour: if some kind of compass present in the abalone and affected by this uneven substratum, most of trip would fail and return tracks would come off the starting spot.

To trace the experimental animal in darkness, a red lamp was suspended centrally above the tank. Its light of over 600nm in wavelength showed less than 0.5 lx (510-03 photometer, Yokogawa, Tokyo) at a level of the tank. Generally for approximately 10 min but with a few exceptions overtime, locomotion of the animal was traced to obtain an individual track at a 1/10 reduction on squared paper under 0.75 W red light of a pencil-typed flashlight.

Before sunset, a water level of the experimental tank was adjusted to a height of 0.2 m and in still seawater the animal was put on the starting position of the central floor. In a case when the temperature of the seawater was different more than 2°C from that of the aquarium where the animals were stocked, then water in the tank was either heated or cooled using thermostat and equipments before enforcement of the experiment.

In any of the following cases, the experiment was ended in principle and the next observation of a different individual was started: 1) the animal passed across the starting site, 2) the animal reached the tank wall and crept along the circumference over one time, and 3) the animal stayed at the starting site overtime.

The above treatments without consideration of a night rhythm were attributed to the following reason. The purpose of the present study was not to get data of the wild activity of the locomotive rhythm but to get data of the return track due to a competent property of the abalone as possible as many for the experimental period. Before starting the successive

experiment with other individual, the whole floor, especially around the starting site, was brushed.

The nocturnal observations were conducted without supply of food at one- to seven-day intervals. Every night the experiment was ceased before 23:00. Every time the experiment ended, after removing with a spatula from the substratum, the experimental animal was accommodated into the stock aquarium and rested until the next experiment on later days.

Similarly to the previous study¹⁴⁾, the locomotion track was classified into moving, return and stationary types. The return type involved any return to the starting site centrally placed or its surrounding area of 8 cm ϕ . The stationary type corresponded to the experimental animals that were immobile or moved limitedly within the above central area of 8 cm ϕ .

To examine the effect of the curved substratum on the locomotion behaviour, the frequency and distribution of each appearance of the above classified types as well as tracing data especially of the return track were compared with those obtained on the flat substratum in the previous study¹⁴⁾.

For the statistical analysis of the individuality of locomotion patterns, the values of the appearance frequencies of the above types were applied to the chi-square test for independence using a multiple contingency table.

Results

During four months of the experimental period, seven animals were dead due to unknown reason(s): the feeding activity was not vigorous during the stock period. This activity was generally similar to that in the previous study¹⁴⁾.

As a result, 244 observations were obtained from locomotion behaviours of the eight remained animals. The survival percentage of 53 (8/15, survival indiv. per total indiv.) was approximately equal to both values of 67 (6/9) and 70 (7/10) in the previous study¹⁴⁾.

Appearance frequencies of the locomotion types are shown in Table 1. In this table, the previous values on a flat substratum are also added. One hundred and thirty-one of the moving type, 31 of the return type and 82 of the stationary type were counted on the values of the convex substratum.

Among the animals in Table 1, the individual No. 7 showed the most frequent return. On the contrary, the individual No. 46 did not show any returns. The individual No. 6 showed almost stationary. The individual No.19 moved the most frequently.

Table 1. Appearance frequencies of the locomotion types of the small abalone on the flat (cited from the previous study) and convex substrata

Specimen No.	L o c o m o t i o n t y p e s		
	Moving	Return	Stationary
On the flat substratum			
3	17	4	11
4	12	4	16
5	25	5	2
6	3	5	24
7	16	14	2
8	19	3	10
12	27	2	6
14	26	2	7
15	23	10	2
16	17	7	11
17	17	10	8
18	27	2	6
19	32	3	0
On the convex substratum			
36	17	7	11
39	19	4	12
40	14	1	8
41	19	6	10
44	11	5	19
46	17	0	3
48	22	6	7
49	12	2	12

By comparison with the previous result, the appearance frequency to the total on each locomotion type seemed generally equal: 0.60 and 0.54 for the moving, 0.16 and 0.13 for the return, and 0.24 and 0.34 for the stationary. Thus the effect of the curved substratum was not evidently recognized in the respective values of the appearance frequency.

The statistical treatment revealed that present data were insufficient for the chi-square analysis because of the excess presence of small numerals in most of the expected values.

The appearance distribution of the locomotion types during the experimental period is shown in Fig. 1. In this figure, another appearance pattern obtained from the previous study on the flat substratum is added. The return type in the present study contained another type of a return behaviour that did not go away but turned outside the starting area, though such a turning back also occurred a few in the previous study.

In the present study some individuals showed a decrease in the appearance frequency of the moving type, though this phenomenon was detected similarly in previous individuals. Unnoticed injury of the sole due to repeating removals from the not smooth but grained substratum may have restrained

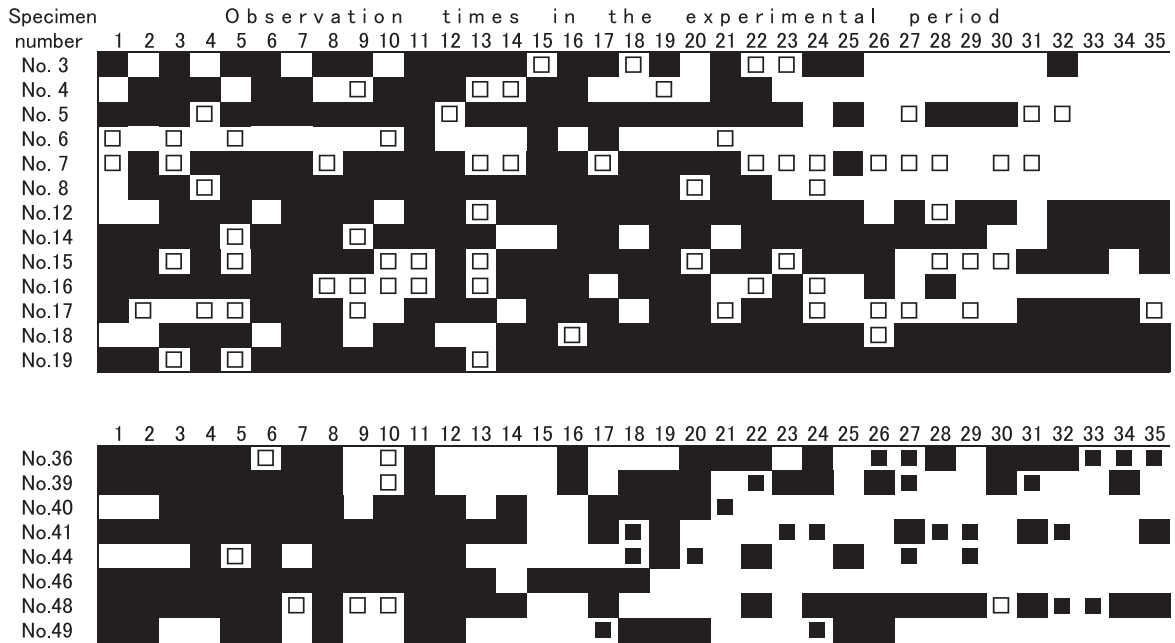


Fig. 1. Appearance distributions of the locomotion types during respective periods of the experiments. Upper, on the flat substratum, cited from the previous study¹⁴⁾; lower, on the convex substratum in the present study. Dark box, turn back type; dark space, moving type; frame box, return type; light space, stationary type.

the animal activity.

Second, the animal tripped not so frequently as the previous case on the flat substratum. Instead of a long trip, a turning back occurred especially during the later half of the experimental period.

After being put on the starting spot, the abalone stayed there for a short or long while, being immobile or often changing the frontal direction. Then except those classified into the stationary type, animals moved away but some of them successively returned. The rate of locomotion movements was approximately stable and commonly less than 0.5 m/min.

Four different tracks of the return type are shown together with one track of the moving type in Fig. 2. Three of them correspond to simple and smooth trips respectively (Rn₁₋₃). This type of the looped track was often observed in the previous study but a few in the present study. Another track of the return type corresponds to a turning back (Tb).

Other track of the return type showed a long trip or journey with a going track curving away. Before reaching the periphery, it turned and took a return route that passed by the starting site where any landmark was absent. If a substitute shelter had been present, the experimental animal would have stopped there.

In some cases, the experimental animal went to the periphery. It took a return route after creeping a certain

distance along the peripheral margin. It then passed across the starting site. Similar tracks sampled from the previous data are added in Appendix I, for reference. If the locomotion area had been prepared more widely, such a journey might have shown a looped track on a large scale.

The remaining track in Fig. 2 corresponds to a case of a

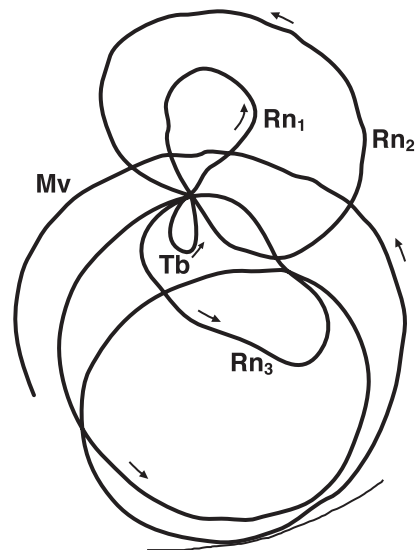


Fig. 2. Locomotion tracks belonging to the return and moving types. The return type involves three trips (Rn₁, Rn₂ and Rn₃) and one turn (Tb). The moving type corresponds to the track of Mv. Scale bar, approximately 10 cm; fine line, margin of the round tank.

failure in return and therefore classified into the moving type (Mv). Both in the present and previous study, the moving type contained a small number of such a failed return whose track passed apart from the starting site.

Thus compared to the previous result on the even surface, the indistinct change of the appearance frequency in the moving type could not afford a proof of the effect of the convex substratum. As for the moving and return types, reciprocal increase and decrease in respective frequencies would prove the curvature effect of the substratum on condition that an evident increase in the failed return occurred.

However, a positive interpretation is probable in addition. Namely the gradient compensation for curved circumstances on the substratum could be principally executed through the driving system of the abalone.

Major track of the moving type was simple: the experimental animal moved away and often curved on route. In every case it was difficult to forecast which side the animal would choose as a locomotion course. After reaching the periphery, it crept along the circumference as shown in the previous study (*cf.* Appendix II).

If observed in a large tank, most individuals of the moving type would have gone away like other species as the Japanese abalone and Siebold's abalone¹¹⁾. Other tracks of the moving type were complicated. They coiled between the starting site and periphery, or encircled the starting site apart from it (*cf.* Appendix II).

Discussion

Return tracks

Common trips showed the track of a loop except a trip such as a turn near the starting area. Concerning this turning habit, the frequent occurrence may have related to the unsmooth but a little grained surface of the substratum. In this connection, tracks of the loop have appeared thus far in trips of abalone on the even and smooth surfaced substratum made of glass-fiber¹⁰⁾, concrete-mortar¹¹⁾ or vinyl chloride¹⁴⁾.

As concerns the track of trips, it is proper that the locus would change due to environmental situations of the experimental animal even on the similar substratum and also due to the length of a tracing^{10,11)}. Overnight observations of the small abalone in a tank of 2 m ϕ revealed the locomotion types around the substitute shelter; rounds at the central and peripheral areas and recurrent trips whose loci looked petals¹⁰⁾. A circular locus of the peripheral round resulted

from a transfiguration of the moving type due to the limited movements in the tank.

The nighttime observation of individual locomotion for 8 h on a tank floor of 10 m x 15 m, the animal showed a change of the locomotion type from recurrent returns to moving away¹¹⁾. In the case of the Japanese abalone, the experimental animal went and returned between the substitute shelter and forage. Both were set 2 m apart each other on the central area of a rectangular tank. Then the trip showed an elongated loop⁶⁾.

In the Siebold's abalone, the creeping animal showed a track of short and slender loop. It was about a length of 0.5 m between the forage and the starting spot in a tank⁶⁾. In the ezo abalone, the experimental animal crept an extremely long distance on the floor and wall as well of a rectangular tank, 2.5 m x 3.5 m. After two anticlockwise rounds, it returned to the starting spot at the corner of the tank floor⁸⁾.

In wild life of the abalone, however, a trip such as trailing the loop mentioned above would not appear. That is because differing from the experimental plane a rocky substratum as the animal habitat should not be smooth and even but topographically complicated⁶⁾, though execution of the return itself would become easy due to the presence of many useful landmarks.

Furthermore, in natural surroundings many kinds of environmental variables should interfere in the course of abalone's trip. In some cases a return course may be easily altered into a removing course by a temptation related to foraging or mating.

In the field, nevertheless, the competent ability would enable the animal to take a trip through a large transfiguration of the looped track into, for instance, an elongated or in some cases distorted track, as the case may be⁷⁾.

For other species of the gastropod, homing tracks of the common limpet *Patella vulgata* showed loops similar to the abalone in aquaria¹⁷⁾ but elongated or slender loops on even rock and concrete jetty^{2,3)}.

In limpets, how these animals find their way home or find their home seems not yet to be concluded. Some kind of kinesthesia or muscular memory has been proposed in the common limpet *P. vulgata*¹⁸⁾. Limpets did not determine their orientation on the homing spots by the trial and error method, and the homing power was independent of a geotropism in the tortoiseshell limpet *Acmaea scabra*¹⁹⁾.

Limpets failed in homing when placed in areas where they had not been previously seen, and a series of displacement

experiments eliminated dead reckoning as a homing mechanism in the pulmonate limpet *Siphonaria normalis*²⁰⁾.

Homing was unaffected by dislodgement and replacement, though their arrival at home was delayed. Information available for homing was restricted to the rock and the past movements of the limpets in *P. aspersa*, *P. depressa* and *P. vulgata*²⁾.

Most of the study denies the following theories as the celestial navigation, the kinesthetic memory, the topographic memory and simple chemical trail following as homing cues. Trail-following has been also negated in the crevice-dwelling limpet *Helicon pectunculus*²¹⁾, though there was a proposition as its basic orientation mechanism for homing in the Japanese limpet *Siphonaria japonica*¹⁾ and the Mediterranean limpet *P. rustica*⁴⁾.

Trip on a compass

For orientation of the trip in the small abalone, the trial and error method and trail-following method have been both negated in the study to date by the present author: the trip lacks in a winding character and possesses a returning track not overlapping with an outgoing track.

In darkness and without any incentive, approximately 15% of the experimental animals exactly returned while drawing a looped track. This fact deduces that the trip of abalone has been achieved by a kind of inertial navigation, or inertial movements on some compass.

Inertial guidance systems for navigation are thought to be entirely self-contained and require no input of external information for the purpose of navigation: the systems thus operate without perceiving any clues concerning local landmarks or celestial bodies²²⁾.

As concerns the trip of abalone, inertial navigation seems to be interlocked with a clockwork compass in principle. The theory is as follows. The preset value of the compass course is fixed on 360° at the start. The clockwork compass drives the animal with encoding successively the time change of tangent angles along a route.

Next the monitoring component works to deduct these input angles from the preset 360° and facilitate the reserved angle of the compass to approach 0° during a trip. The compass always keeps a register of the reducing angle until a goal. In aid of an outside cue, namely the original home, the strike of a balance is executed at the goal while the angle of the compass should be adjusted to 0°.

For a case of simple trips as shown in Fig. 2, the outgoing track seems to have correlatively a tangent angle to the return track. In such a round trip on the plane, about a 360° consumption in some kind of compass should be geometrically required as the sum of tangent angles along the route.

Thus information about the angular change of pedal directions seems to be encoded. The requirement should be available to any trip that has a positive curve outwardly on an even substratum.

However, if the compass was not much on compensation for the gradient change en route on an uneven substratum, a complete achievement of the return to the starting spot should be difficult owing to the curvature effect.

Though this expectation has not been evidently met in the present study, it seems to have related and consisted with the low appearance frequency of the long trip. That is because it is probable that the convex substratum has alternated a return with a turn back that frequently occurred in the later half of the experimental period.

Since a recurrent trip did not occur successively next night in the same animal as shown in Fig. 1, individual trips are thought to occur without aid of the previous memory if it were present. That is the memory of abalone's trip seems analogous to a volatile memory in insect orientation. The volatile memory is reset to zero when the animal has returned home²³⁾.

One trip in the previous study exceptionally showed a singularly curling locus after arrival at the starting location (Fig. 3)(unpublished data, 2003). This behaviour was observed under red light on the even and smooth floor of an indoor tank concrete-mortared in a laboratory house of the Marine Station at Nagashima Island.

In this case, after all, the animal went away after curling more than 15 times the starting site around. First, the animal went out of the home block at 19:00, when the block was lifted. It took a large round clockwise about 40 cm apart from the starting site and returned at 19:05. It passed repeatedly across the corner or lateral of the starting site, whirling five times clockwise (Fig. 3a).

At the 6th round, it passed outside the starting site and then curled nine times clockwise while passing two times across the latter (Fig. 3b). After that, it went away, whirling nine times clockwise here and there (Fig. 3c).

From this observation and four tracks of the trips in Appendix I, the driving system of the abalone suggests to have fallen into runaway conditions. It seems necessary that

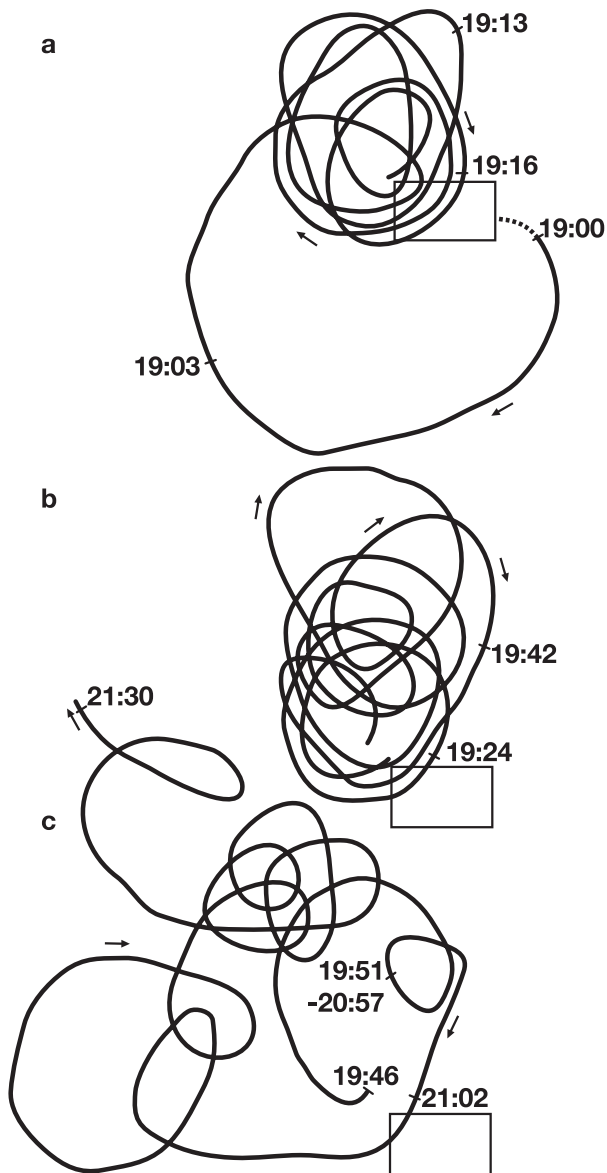


Fig. 3. Locomotion track observed between 18:50 and 21:30 on 2 October 2003. Transit times on the track are added. To avoid a presentation of excessive crossings, the track is divided into three parts as **a**, **b** and **c**. **a**, observation between 18:50 and 19:19; **b**, observation between 19:19 and 19:46; **c**, observation between 19:46 and 21:30. Dotted and solid curves, locomotion tracks before and after lifting the block (substitute home); Solid rectangle, contour of the inner margin of the block (substitute home), 15 cm x 9 cm.

the experimental animal perceives some landmark at the goal to finish the undertaking trip or inertial navigation. This perception of an object such as the shelter would become a cue that nullifies completely the preset course of the clockwork compass.

It is said an error in return occurs on the basis of an approximate updating or inaccuracy of the animal's

measuring system¹⁵⁾. In the abalone, the failure in return that has passed away from the starting spot is thought caused by misreading of the measuring system.

Furthermore, runaway movements mentioned above suggest the nervous control of return habits to be primitive in the abalone whose inertial navigation system lacks in the fail-safe component.

No reliability of the following occurrence of return night after night and the execution of variable locomotion as well seem attributable to voluntary activities of the individual abalone. Such intentional habits would not be antagonistic to a capacity of the abalone for inertial navigation deduced above.

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References

- 1) Abe, N. (1940). The homing, spawning and other habits of a limpet, *Siphonaria japonica* Donovan. *Sci. Rep. Tohoku Imp. Univ. Sendai.*, **15**: 59-95.
- 2) Cook, A., O. S. Bamford, J. D. B. Freeman and D. J. Teideman (1969). A study of the homing habit of the limpet. *Anim. Behav.*, **17**: 330-339.
- 3) Hartnoll, R. G. and J. G. Wright (1977). Forage movements and homing in the limpet *Patella vulgata* L. *Anim. Behav.*, **25**: 806-810.

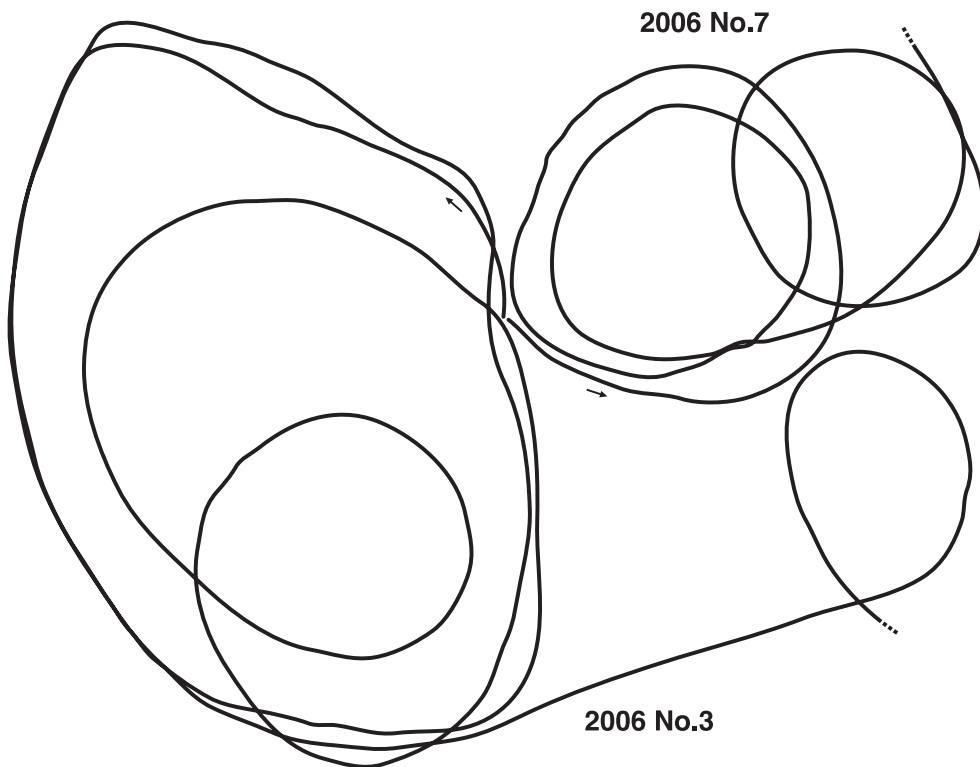
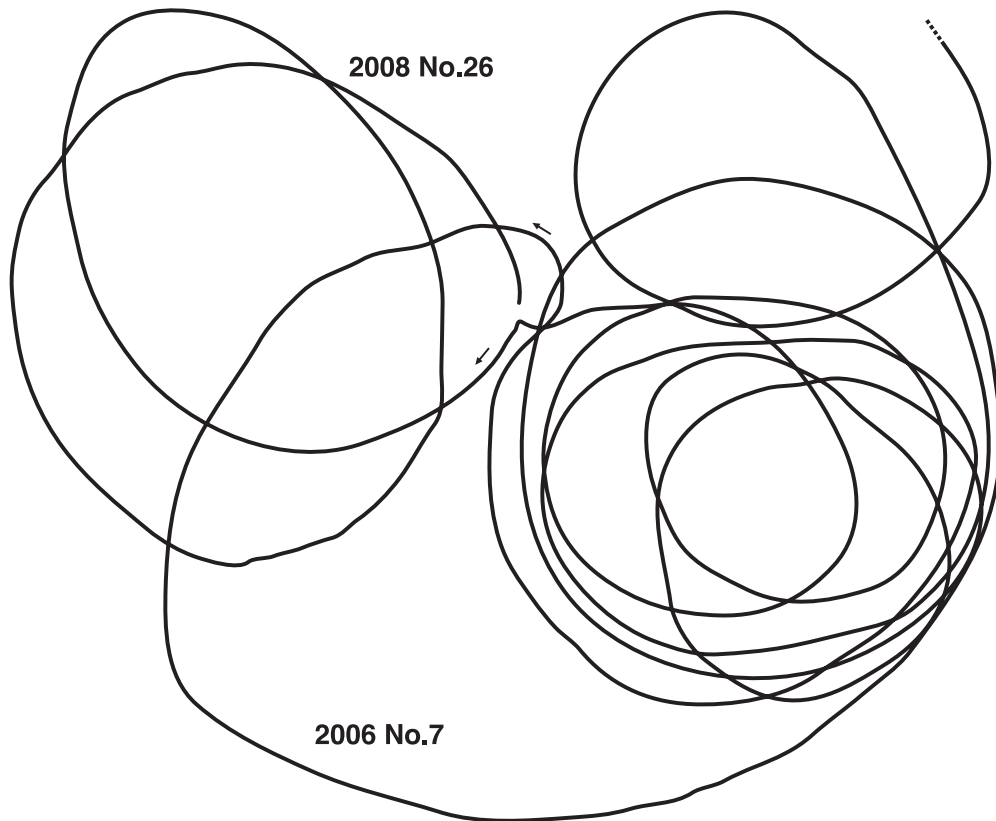
- 4) Santina, P. D. (1994). Homing pattern, activity area and trail following of the high shore Mediterranean limpets *Patella rustica* L. (Mollusca Gastropoda). *Ethol. Ecol. Evol.*, **6**: 65-73.
- 5) Crofts, D. R. (1929). *Haliotis*, Proc. Liverpool Biol. Soc., Liverpool. pp.174.
- 6) Uno, Y. (1967). Abalone, in "Fish Culture" (ed. by Kawamoto, K.), Koseisha-Koseikaku, Tokyo, pp. 648-656 (in Japanese).
- 7) Momma, H. and R. Sato (1969). The locomotion behavior of the disc abalone, *Haliotis discus hannai* Ino, and the Siebold's abalone, *Haliotis sieboldi* Reeve, in the fishing grounds. *Tohoku J. Agric. Res.*, **20**: 150-157.
- 8) Momma, H. and R. Sato (1970). The locomotion behavior of the disc abalone, *Haliotis discus hannai* Ino, in a tank. *Tohoku J. Agric. Res.*, **21**: 20-25.
- 9) Okamoto, M. (1991). Behaviour of giant abalone *Haliotis madaka* at 30m depth of an artificial fish reef. *Bull. Jpn. Soc. Sci. Fish.*, **57**: 579-584 (in Japanese).
- 10) Nakamura, K. and T. Soh (1997). Mechanical memory hypothesized in the homing abalone *Haliotis diversicolor supertexta* under experimental conditions. *Fish. Sci.*, **63**: 854-861.
- 11) Nakamura, K. and M. V. Archdale (2001). Activity patterns of abalone under experimental conditions. *Aquacult. Res.*, **32**: 169-179.
- 12) Miller, A. C. (1968). Orientation and movement of the limpet *Acmaea digitalis* on vertical rock surfaces. *Veliger*, **11** (Suppl.): 30-44.
- 13) Frank, P. W. (1965). The biodemography of an intertidal snail population. *Ecology*, **46**: 831-844.
- 14) Nakamura, K. (2008). Individuality of locomotion habits in the small abalone *Sulculus aquatilis* Reeve. *Mem. Fac. Fish. Kagoshima Univ.*, **57**: 19-23.
- 15) Benhamou, S., J.-P. Sauve and P. Bovet (1990). Spatial memory in large scale movements: Efficiency and limitation of the egocentric coding process. *J. Theor. Biol.*, **145**: 1-12.
- 16) Uno, Y. (1976). Ecology and resources of abalones, in "Evaluation of Seed Releasing-Abalone, Prawn and Red sea bream" (ed. by Nippon Suisan Gakkai), Koseisha-Koseikaku, Tokyo, pp.39-57 (in Japanese).
- 17) Newell, R. C. (1979). Biology of Intertidal Animals, Marine Ecological Survey LTD, Kent. pp.781.
- 18) Pieron, H. (1909). Sens de l'orientation et memoire topographique de la patelle. *C. R. Acad. Sci. Paris.*, **148**: 530-532.
- 19) Hewatt, W. G. (1940). Observations on the homing limpet, *Acmaea scabra* Gould. *Am. Midl. Nat.*, **24**: 205-208.
- 20) Cook, S. B. (1969). Experiments on homing in the limpet *Siphonaria normalis*. *Anim. Behav.*, **17**: 679-682.
- 21) Gray, D. R. and A. N. Hodgson (1998). Foraging and homing behaviour in the high-shore, crevice-dwelling limpet *Helcion pectunculus* (Prosobranchia: Patellidae). *Mar. Biol.*, **132**: 283-294.
- 22) Barlow, J. S. (1964). Inertial navigation as a basis for animal navigation. *J. Theor. Biol.*, **6**: 76-117.
- 23) Beugnon, G. and R. Campan (1989). Homing in the field cricket, *Gryllus campestris*. *J. Insect Behav.*, **2**: 187-198.

Appendix I.

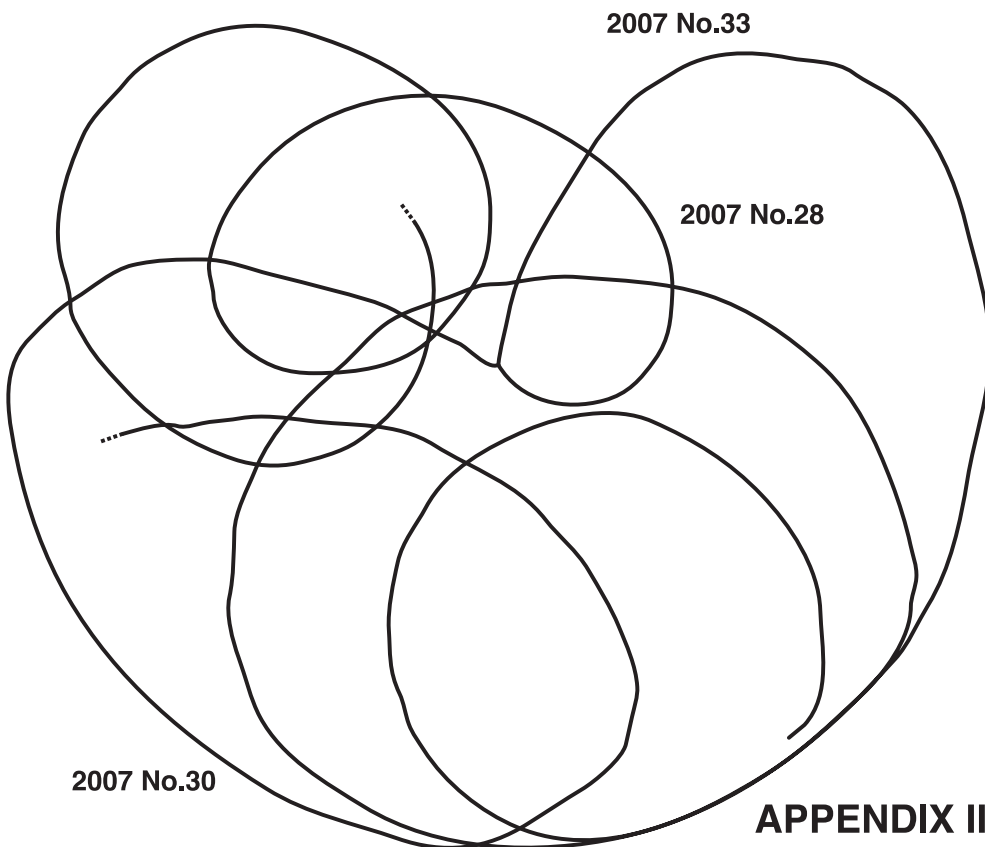
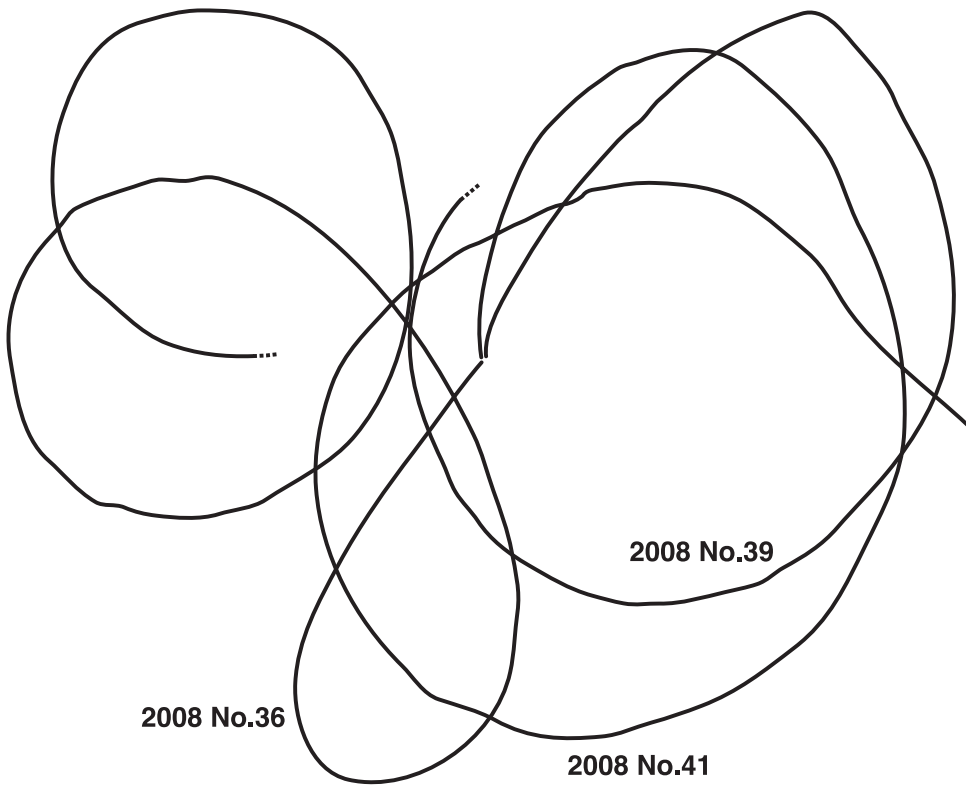
Four tracks of the return type, observed in the tank of 1 m ø. Each tracing is prolonged to examine the locomotion habit in detail. Numerals added to each track indicate the observation year and specimen No. Upper, previous datum on No.7, 2006 and present datum on No.26, 2008; lower, previous data on No.3 and 7, both 2006.

Appendix II.

Six tracks of the moving type, observed in the tank of 1 m ø. Numerals added to each track indicate the observation year and specimen No. Upper, present data on No.36, 39 and 41, each 2008; lower, previous data on No. 28, 30 and 33, each 2007.



APPENDIX I



APPENDIX II