

## OCCURRENCE OF RANDOM AND DIRECTIONAL MOVEMENTS IN THE PERIWINKLE, *LITTORINA LITTOREA* (L.)<sup>1</sup>

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**Abstract:** Intertidal zonation of *Littorina littorea* (L.), an intertidal herbivorous gastropod, is believed to be behaviorally maintained by a variety of environmental cues. Laboratory experiments confirm that periwinkles from Long Island Sound are geotactic, and phototactic, and are strongly directional in movement. Snails, observed under natural conditions and marked without removing them from the surface, were found to move randomly. Field experiments suggest that directional movement by *L. littorea* is initiated by dislodgement and is modified by the snail's intertidal origin and placement, and the orientation of the beach.

### INTRODUCTION

Intertidal zonation of organisms is thought to be maintained by the differing responses of organisms to changes in physical and biotic factors which vary from the low to high intertidal areas. Work on sessile organisms, in particular, has stressed the importance of physiological tolerances, settlement behavior, competition and predation (e.g. Connell, 1961) in setting these limits. Motile species present a special problem since it is conceivable that it could reach all areas throughout the intertidal zone. Yet many motile intertidal species often appear in greater abundance at a particular intertidal height (Vermeij, 1972).

Given that motile species tend to be found in particular intertidal regions, it seems likely that behavioral mechanisms must be involved (Underwood, 1979). An often cited example is the zonation pattern of the periwinkle, *Littorina littorea*, whose position in the intertidal zone is thought to be behaviorally maintained (Haseman, 1911; Gowanloch & Hayes, 1926; Smith & Newell, 1955; Gendron, 1977). Periwinkles displaced above or below their preferred habitat will move in the appropriate direction and return to that habitat (Alexander, 1960; Gendron, 1977). Phototaxis (Newell, 1958a,b), geotaxis (Kanda, 1916; Hayes, 1929; Newell, 1958a,b), hydrotaxis (Haseman, 1911), and rheotaxis (Gendron, 1977) have been reported to control *L. littorea*'s behavior. Behavior may also be modified by place of origin (Alexander, 1960), desiccation (Kanda, 1916; Hayes, 1929; Newell, 1958a) and presence of mucus of conspecifics (Dinter & Manos, 1972). For an excellent review, see Underwood (1979).

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While I found *L. littorea* (L.) to be phototactic and geotactic as reported elsewhere, the results of field observations reported in this paper suggest that periwinkles, if not dislodged from the surface, move at random. These results are inconsistent with evidence reported in the literature, and suggest dislodgment may be crucial in initiating the behavioral responses of *L. littorea*.

## MATERIALS AND METHODS

### STUDY SITES

All work was done at Port Jefferson Town Beach on the north shore of Long Island in Suffolk County, New York. Port Jefferson Town Beach is immediately west of the entrance to Mount Sinai Harbor and  $\approx 3$  km east of Port Jefferson Harbor.

Three locations were used and will be referred to as the north flat, the east flat, and the jetty. The north flat, a cobblestone beach which runs east to west with Long Island Sound to the north, has an incline of  $< 1^\circ$ . *Balanus balanoides* (L.) and *Littorina littorea* dominate the beach. The east flat is similar but faces east into Mount Sinai Harbor. The jetty runs due north into Long Island Sound. The most abundant species are *B. balanoides*, *Littorina littorea*, *Enteromorpha* spp. and *Fucus* spp.

### LABORATORY STUDIES

Newell (1958a) reported that periwinkles from horizontal and vertical surfaces responded to different taxes; snails from inclined surfaces were strongly geotactic, while snails from horizontal surfaces were phototactic.

To test for phototactic differences, periwinkles, collected on 12 July 1976 from the flats and the jetty, were placed on a level glass sheet in a darkened room with the only light from a small window. The position of each snail was noted after 3 h. Three runs were done in order to minimize the effects of trail following. The experimental surface was divided into four squares with light in the corner of one of them. Snails which moved into the square closest to light were scored as photopositive, those in the furthest square, photonegative. "No taxis" snails moved perpendicular to the light and were found in the remaining two squares. Under the assumption of random movement, equal number of snails should be found in each square.

For geotactic differences, periwinkles collected on the same day (12 July 1976) and from the same locations as above were used. Snails were placed in aquaria, and the number of snails which had moved off the bottom after 3 h was noted. This experiment was repeated on 7 November 1976 but in this case the snails' positions were checked after 24 h. Consistency of periwinkle behavior was also checked, individual snails were tagged, positions were checked on 8 November, snails returned to the bottom and then checked again on 9 November.

Also examined was the geotaxis of periwinkles on wet, but not submerged surfaces.

Twenty-five snails, collected on 12 July 1976 from the jetty, were placed on a glass sheet which was covered by wet newsprint paper. The sheet was set on a 15° incline. The position of each snail was noted at 15, 30, and 60 min after the start of the experiment.

#### FIELD OBSERVATIONS

As a comparison to my laboratory studies, periwinkles were watched at Port Jefferson Town Beach during July and August of 1976 and 1977. The daily position of snails was monitored without removing the periwinkles from the surface. At low tide, periwinkles were tagged with numbered dots (Avery adhesive coding dots) which were then coated with Dekophane. Snails were tagged without removing them from the surface. The position of each snail was noted every morning at low tide and was determined by measuring the distance from each snail to three fixed points. Measurements were taken for up to 5 days or until the snail could not be found (see Fig. 2 for observational dates).

#### FIELD MANIPULATIONS

The comparative behavior of periwinkles from the flats and the jetty were examined because I assumed that geotaxis would govern the behavior on the inclined surfaces of the jetty, while on the flats phototaxis should be more important.

Inclines present a special problem since dislodged periwinkles somehow must be reattached to a surface on which they may move up or down. On 22 July and 4 September 1978, I removed a total of 25 snails, held them to the surface until they reattached, and then wetted the snails and recorded their position after 10 min. As a control, 31 snails were not removed, but otherwise treated the same.

On the flats, the interaction of periwinkle movement, beach orientation, the snail's origin, the snail's placement, and the role of dislodgment was tested with a 5-way contingency table (see Bishop *et al.*, 1975, for design). On the north and east flats, one high and one low transect line was placed. Snails were collected from above the high transect and from below the low transect, marked, and then replaced either on the high or low transect line. To control for the role of disturbance, cobbles with attached snails were moved. These snails were never dislodged from the surface. 768 snails were marked during the morning low tides of 20 and 21 July 1978. At the afternoon low tide, snails were recaptured and their positions, relative to the transect line, were noted.

### RESULTS

#### LABORATORY STUDIES

The null hypotheses of habitat differences in geotaxis and phototaxis cannot be rejected. Phototactic responses of periwinkles is independent of habitat ( $G = 2.22$ , n.s.). Of the snails which did respond, more snails, from both the jetty and the flats, move towards the light rather than away (63% of the animals from the jetty; 68% from

flats). Yet the overall distribution of periwinkles on the surface was random with respect to the light source.

The same response appears to be true for geotaxis; the response is independent of a periwinkle's origin (for July data,  $G = 2.64$ ; for November data,  $G = 0.52$ ). While many snails are strongly geotactic and begin to move up the sides of the aquaria almost immediately, the strength of this response is not dependent on whether the snail came from the flats or the jetty.

While there appear to be no differences in response due to habitat, individual snails do show consistent differences in their movement (Table I). Snails found on the sides

TABLE I

Tests of independence of *Littorina littorea*'s position on consecutive days in aquaria: 8 and 9 November 1976: snails were collected from the flats and jetty at Port Jefferson Beach; numbers in parentheses are expected counts under the assumption of independence; the  $G$  values below the tables are for tests of independence;  $K_i$  is Light's measure of agreement (Light, 1971; Petraitis, 1978) with standard deviations; this index measures consistency and may range from  $-1$  to  $+1$ ; a value of  $+1$  means all individuals found at a particular location on one day were present on the next day, while a value of  $-1$  means none were present on the next day; if movement is random, Light's measure will be zero; \*  $P < 0.01$ .

November 8	November 9 Top	Side	Bottom	$K_i$
Jetty				
Top	71 (65)	11 (11)	2 (8)	$0.320 \pm 0.020$
Side	33 (35)	8 (6)	4 (4)	$0.054 \pm 0.002$
Bottom	25 (29)	3 (5)	10 (4)	$0.185 \pm 0.002$
	$G = 16.95^*$			
Flats				
Top	55 (50)	8 (7)	5 (11)	$0.303 \pm 0.017$
Side	17 (15)	2 (2)	2 (4)	$-0.010 \pm 0.005$
Bottom	16 (23)	3 (4)	14 (5)	$0.288 \pm 0.005$
	$G = 16.57^*$			

of the aquarium one day, were found there on the next. This consistency is not simply a matter of periwinkles remaining where they were since all snails were returned to the bottom after the first day.

Periwinkles, out of the water and on an incline, are geopositive rather than geonegative (Fig. 1). These snails, unlike periwinkles which are submerged, do not start moving at once. Unlike Newell (1958b), only one reversal in direction was observed.

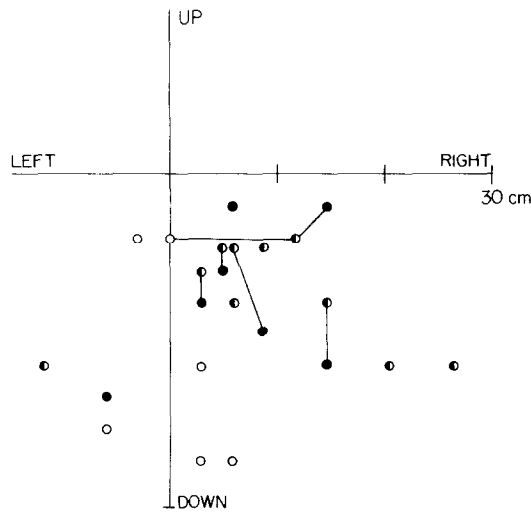


Fig. 1. Movement of *Littorina littorea* on a wet but not submerged incline: ○, positions at 15 min; ◐, positions at 30 min; ●, positions at 60 min; initial movement, assuming snails started at the origin, is not connected with a line; subsequent movement by the same snail is indicated by lines connecting circles; eight additional snails did not move at all.

#### FIELD OBSERVATIONS

A total of 654 snails were marked; 45.3% were recaptured at least once and 15.5% more than once. The low recapture rate was due to loss of tags.

While the laboratory studies indicate that periwinkles are geotactic and phototactic, the field studies of undisturbed snails (see Fig. 2) do not bear this out. Only the snails in area E1 show an average directional movement and these snails moved downwards. For all the other sites, the null hypothesis of no mean direction cannot be rejected. There are mean differences among the distances that undisturbed snails moved (Table II). Periwinkles on flat surfaces move farther than snails on inclines. There is also some variation in distances moved among the inclines. Using a priori tests, significant differences between site E1 and E2 were found, but not between W76 and W77; this result suggests that the topography of the sites are more important than the time of sampling.

It is possible that the lack of average directionality is due to consistent but different preferences of individual periwinkles. The laboratory experiments on consistency of periwinkle movement suggest such biases may be occurring among individual snails (see Table I). It was possible to check for this with my data. In three areas (S, E1, W76) enough periwinkles were seen on 3 consecutive days to test daily consistency of the angle and distance moved. There is no correlation of the distances travelled on consecutive days (using Spearman's rank correlation, S:  $r = -0.30$  for 17 pairs, n.s.; E1:  $r = +0.29$  for 25 pairs, n.s.; W76:  $r = +0.34$ , for 20 pairs, n.s.). There also seems to be no consistent day to day preference in the direction moved by undisturbed snails.

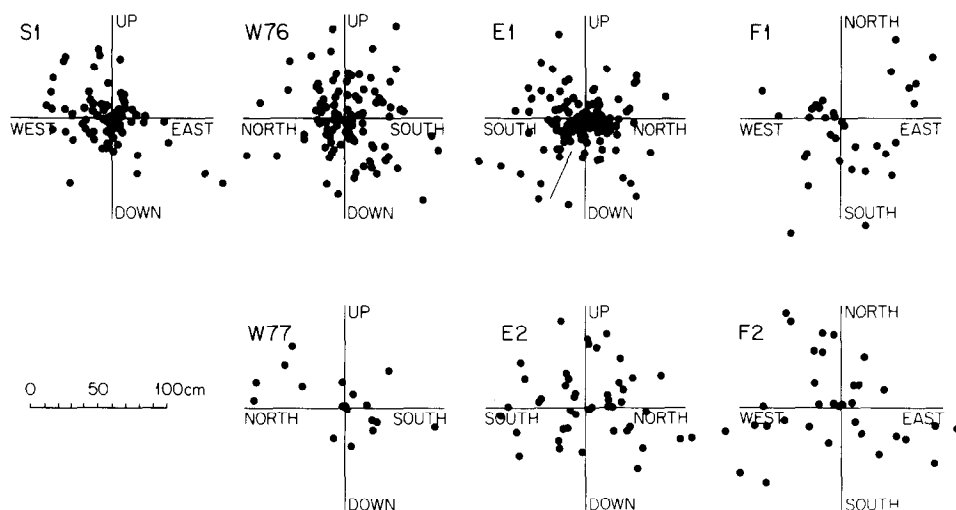


Fig. 2. Movement of undisturbed *Littorina littorea* in the field: letter code denotes the direction of the surface (e.g. E for East-facing, F for flats); W76 and W77 are the same west-facing surface sampled in 1976 and 1977; points are positions of snails after two tidal cycles assuming all started at the origin; line in E1 gives mean angle which is significant; the sampling dates are: 11–15 June 1976 for W76, 5–7 June 1977 for W77, 11–14 June 1976 for E1, 11–13 August 1976 for E2, 11–14 June 1976 for S, 26–28 June 1976 for F1, and 11–13 August 1976 for F2; a total of 654 snails were marked: 45.3% were recaptured at least once and 15.5% more than once; the low recapture rate was due to loss of tags.

TABLE II

Analysis of variance of mean distances in mm moved by *Littorina littorea* in the field: for further details, see Fig. 2; \*  $P < 0.05$ .

	Locations						
	F1	F2	W76	W77	E1	E2	S
Mean	352	422	267	284	230	243	218
SD	213	255	170	220	175	186	170
N	35	34	99	18	130	42	75
Source		MS		d.f.		F	
Locations		276,153		6		7.91*	
A priori tests							
Inclines vs. flats		1,031,601		1		29.55*	
Among inclines		135,700		4		3.89*	
W76 vs. W77		4,238		1		0.12	
E1 vs. E2		411,286		1		11.78*	
Error		34,913		426			

## FIELD MANIPULATIONS

Periwinkles, living on the inclined surface of the jetty which are dislodged, are more likely to commence moving within the 10-min observation period than those snails left undisturbed: 69.2% of the dislodged snails moved, while only 18.8% of the controls did, a significant difference (test of equality of percentages,  $t = 4.05$ ,  $P < 0.001$ , see Sokal & Rohlf, 1969).

The behavior of the snails on the two sampling dates differed. Of the snails which were dislodged did move, most moved upwards in July, while most moved downwards in September. Fisher's exact test of sampling date against direction of movement is significant ( $P = 0.001$ ). The July field result is particularly surprising since the laboratory experiments for July 1976 (see Fig. 1) show dislodged periwinkles moving downwards, the opposite of the field results.

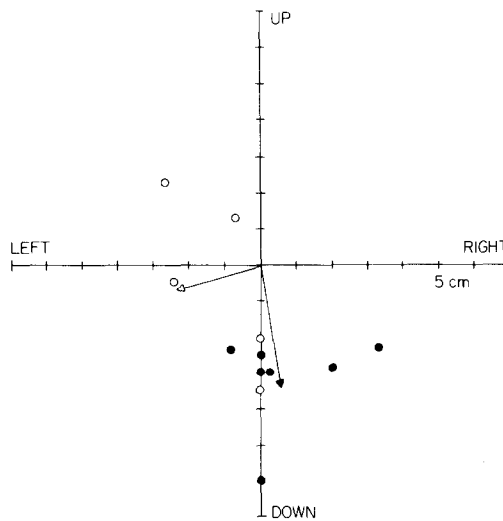


Fig. 3. Movement of dislodged and undisturbed *Littorina littorea* on a wet but not submerged incline: ○, undisturbed periwinkles; ●, dislodged individuals; vectors give mean distance and angle moved by each group.

In Fig. 3, the relative position of each snail recorded in September is plotted. The dislodged periwinkles show a mean direction of movement (Rayleigh's test of mean angle of direction,  $P < 0.01$ ), move farther ( $t$ -test,  $t = 4.72$ , d.f. = 10,  $P < 0.001$ ), and in a very different direction than the control snails (Watson-Williams two-sample test,  $P < 0.05$ , see Madria, 1972).

When comparing data for animals from the flats, the four-way interaction of positions  $\times$  origin  $\times$  placement  $\times$  orientation is the highest order interaction which is significant (Table IV). The pattern of the residuals (Bishop *et al.*, 1975) shows that periwinkles, replaced in the same location that they came from, move downwards on the north-facing beach, but upwards on the east-facing beach.

Two of the three-way interactions are significant and by conditional breakdown of *G*-tests (Bishop *et al.*, 1975) these interactions can be tested in the presence of other, higher-order interactions. The position  $\times$  placement  $\times$  orientation effect, given the

TABLE III

Movement of *Littorina littorea* on the flats: snail's position, relative to the transect line, was noted after one tidal cycle. The data from the flats were analyzed by *G*-tests of goodness of fit for the five-way table: position (snails recovered above or below the transect line), origin (*Littorina* from high or low in the intertidal), placement (*Littorina* replaced high or low in the intertidal), dislodgment (periwinkles attached or not to cobbles) and beach orientation (north versus east facing); only the interaction effects involving the position of *Littorina* were calculated since the number of snails placed on a particular beach and transect and of a particular origin are fixed; all other interactions reflect sampling effects (e.g., interaction of orientation versus placement would reflect differing recovery success on the four transects: north-high, north-low, east-high and east-low).

Dislodged?	Placement	Origin	Beach orientation			
			North position		East position	
			Above	Below	Above	Below
Yes	High	High	15	32	30	10
		Low	31	38	18	22
	Low	High	32	15	16	15
		Low	27	23	29	31
No	High	High	23	28	35	11
		Low	26	21	34	18
	Low	High	16	14	14	14
		Low	26	20	24	26

position  $\times$  origin  $\times$  placement  $\times$  orientation interaction, remains significant ( $G = 20.37 - 7.56 = 12.81$ , d.f.  $4 - 2 = 2$ ,  $P < 0.005$ ). This interaction cannot simply be explained in terms of the four-way interaction. Examination of the residuals shows snails placed in the high intertidal move downwards on the north facing beach but upwards on the east-facing beach.

The conditional breakdown of the position  $\times$  origin  $\times$  orientation interaction given the four-way interaction is not significant ( $G = 12.41 - 7.56 = 4.85$ , d.f.  $4 - 2 = 2$ , n.s.). Here, the three-way interaction is better explained by the higher-order effect which has already been described.

All other three-way interactions are not significant and removal of any possible four-way interaction has no effect.

Since the interaction of position  $\times$  placement  $\times$  orientation is significant, it is not surprising that the two-way interactions of position  $\times$  placement and of position  $\times$  orientation are also significant (Table IV). In both cases the conditional breakdown, given the three-way interaction, is not significant (for position  $\times$  placement:  $G = 25.27 - 20.37 = 4.90$ , d.f.  $9 - 4 = 5$ , n.s.; for position  $\times$  orientation:



$G = 30.80 - 20.37 = 10.43$ , d.f. =  $9 - 4 = 5$ , n.s.). These second-order effects can be explained by the three-way interactions of position  $\times$  placement  $\times$  orientation.

TABLE IV

Analysis of data from Table III: main effects are coded as follows: POST, position; ORIG, origin; PLAC, placement; DISL, dislodgment; OREN, beach orientation; \*  $P < 0.05$ ; \*\*  $P < 0.01$ .

	d.f.	<i>G</i>
Complete independence	16	44.92**
Two-way interactions		
POST $\times$ ORIG	9	14.56
POST $\times$ PLAC	9	25.27**
POST $\times$ DISL	9	13.75
POST $\times$ OREN	9	30.80**
Three-way interactions		
POST $\times$ ORIG $\times$ PLAC	4	7.63
POST $\times$ ORIG $\times$ DISL	4	2.79
POST $\times$ ORIG $\times$ OREN	4	12.41*
POST $\times$ PLAC $\times$ DISL	4	5.96
POST $\times$ PLAC $\times$ OREN	4	20.37**
POST $\times$ DISL $\times$ OREN	4	2.15
Four-way interactions		
POST $\times$ ORIG $\times$ PLAC $\times$ DISL	2	1.94
POST $\times$ ORIG $\times$ PLAC $\times$ OREN	2	7.56*
POST $\times$ ORIG $\times$ DISL $\times$ OREN	2	1.95
POST $\times$ PLAC $\times$ DISL $\times$ OREN	2	2.01
Five-way interaction		
POST $\times$ ORIG $\times$ PLAC $\times$ DISL $\times$ OREN	1	1.93

The other second-order interactions are not significant. However, removal of position  $\times$  dislodgment  $\times$  orientation interaction from the position  $\times$  dislodgment interaction is significant ( $G = 13.75 - 2.15 = 11.60$ , d.f. =  $9 - 4 = 5$ ,  $P < 0.05$ ). While the orientation of the beach masks the effect of dislodgment, the conditional breakdown suggests dislodgment makes a difference. From the residuals it appears that periwinkles which are dislodged move downwards while those which are attached to cobbles tend to move upwards. Partition of the *G* values shows that 77% of the value is accounted by the dislodgment treatment; periwinkles which are dislodged show a stronger effect.

Finally, the model of independence of position from all other factors does not fit (Table IV). Checking the higher order effects it can be seen that the position  $\times$  orientation interaction has the highest *G* value. Yet the conditional breakdown of the model of independence given the position  $\times$  orientation interaction remains significant ( $G = 44.92 - 30.80 = 14.12$ , d.f. =  $16 - 9 = 7$ ,  $P < 0.05$ ). The effect of beach orientation on position does not account for all the variation; other interactions must be important too.

## DISCUSSION

The behavior of *Littorina littorea* depends on whether or not the periwinkle has been disturbed; snails left undisturbed move randomly while the behavior of those snails which are dislodged from the substratum seems to be governed by various taxes. While I found no habitat differences among snails as reported by others (e.g. Newell, 1958a,b), the non-random movement of periwinkles does seem to be modified by the snail's origin and placement (high versus low intertidal), by the orientation of the beach and by the time of year. The explanation that periwinkles if displaced return to their original position (Gendron, 1977) is too simplistic since other factors play an important role and confound the actual movement of the snails.

*L. littorea* behavior appears to be an either/or situation which depends, in part, on dislodgment. In this context, it is interesting to note if other researchers handled the periwinkles before making their observations. It appears all reports of taxis in *L. littorea* involve periwinkles that have been handled, i.e. dislodged from the surface before the observations began (Haseman, 1911; Kanda, 1916; Gowanloch & Hayes, 1926; Newell, 1958a,b; Alexander, 1960; Gendron, 1977). In two other cases, periwinkles not removed from the surface seemed to move randomly (Dexter, 1943; Smith & Newell, 1955).

The effect of dislodgment on intertidal zonation of periwinkles is not known, but poses an interesting problem. Given that wave action varies from beach to beach, the risk of dislodgment should also vary. If this is the case, zonation patterns of periwinkles may, in part, be controlled by the frequency with which a snail is dislodged and its behavioral responses are brought into play.

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