FACTORS AFFECTING CLIMBING IN THE COASTAL GASTROPOD *HYDROBIA ULVAE*

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(Fig. 1)

In a series of laboratory experiments designed to create conditions under which the dispersal and feeding hypotheses of climbing in *Hydrobia ulvae* would predict opposing results, significantly larger numbers of snails climbed (*a*) food-bearing sticks than non-food-bearing sticks, (*b*) in 100 % sea water than in 41 % sea water, and (*c*) in the dark than in the light. The first two of these results are in accordance with the hypothesis that climbing is not a distinct behavioural activity but is merely normal crawling/browsing behaviour carried out in a vertical plane; they are in disagreement with the hypothesis that climbing is undertaken in order to facilitate dispersal away from unfavourable conditions. The third result is neutral in respect of the two hypotheses, but is explicable in terms that activity during the night is advantageous because of lowered rates of vertebrate predation.

INTRODUCTION

In the preceding paper (Barnes, 1981) it is argued that the climbing behaviour of *Hydrobia ulvae* (Pennant) may be regarded as an extension of normal browsing and food-seeking activity into the vertical plane rather than a special behavioural pattern subserving a role in dispersal of the population. The present paper describes laboratory experiments in which the conditions were controlled to distinguish those factors which act as a stimulus to climbing behaviour.

METHODS

The basic laboratory apparatus, animals and methodology were as described earlier (Barnes, 1981), except as indicated below; the experiments formed a direct continuation of the previous studies, over the period January–March 1980.

After an interval of 38 days after the completion of the last set of experiments described in Barnes (1981) – during which time the snail population was provided with one six-hour period of 'tidal' cover per week to keep it alive – the reaction of the same population of snails to the presence or absence of light during tidal cover was investigated. Snails were subjected to two experimental tides per day in two series. In the first series, extending over five days, the morning tide occurred from 0900 to 0930 hours (British Standard Time) under the ambient daylight, whilst the early evening tide, from 1700 to 1730 hours, took place in the dark (the aquarium being blacked out by two, double-folded, black PVC bags). Because time of day acted as a confounding variable, a second series was conducted, after an interval of two tideless days, in which the morning tide occurred in the dark (from 0900 to 1000 hours) and the early evening tide (from 1700 to 1800 hours) took place in the light, provided by a daylight neon tube mounted directly above the aquarium.

After a further interval of 22 days, experiments involving two different salinities were carried out. The snails were again subjected to two tides per day, each of 60 minutes duration, the aquarium being blacked out as described above. The two salinities used were 34‰ and 14‰ (see Discussion). Tides 1, 4, 5, 8 and 9 were of full-strength sea water, and tides 2, 3, 6, 7 and 10 were of the sea water diluted to 41 %: the experiment therefore lasted five days.

On 2 March 1980 a fresh batch of *H. ulvae* were collected from the vicinity of Site 1 on Cockle Bight, the Scolt Head N.N.R., Norfolk (see Barnes, 1981), together with a supply of green 'blanket weed' (*Rhizoclonium riparium* (Roth) Harv.) from the dried bed of the creek draining Hut Gap Marsh, on which *Hydrobia* were abundant, and the snails from Site 1 were added to the aquarium system. The sticks used in all previous experiments were discarded and replaced by three more from those originally recovered from Site 3 (see Barnes, 1981). These had been stored, dry, in the laboratory for more than 3 months. All three were scrubbed in sea water before use and as a result of this treatment and their storage they were considered to be devoid of suitable food for *H. ulvae*. A rectangle cut from the harvested blanket of green algae, from which all snails had been removed, was wrapped round one of the three sticks. Then, in a third experiment, snails were provided with a choice between climbing the sticks without food and the one with a covering of algal food. Tests were run in the dark (as above), with full-strength sea water, and with high tides of 90 min duration at the rate of one per day (0900–1030 hours) for six days. The position in the aquarium of the food-bearing stick was changed after each tide so that it twice occupied each of the three positions in the sod of sediment in a random order.

As in the experiments reported previously, snails were displaced back to the sediment surface after each period of tidal cover. In all the experiments described here, the numbers of snails on the sticks were recorded only at the end of each of the stated periods of tidal cover.

RESULTS

Climbing activity was markedly greater in 100 % than in 41 % sea water (Table 1), the totals of 264 and 2 snails, respectively, standing on their own without the need for statistical analysis.

More *Hydrobia* were present on sticks bearing blanket weed after 90 min than on those without (Table 2), the mean number on the food-bearing sticks being 3·0 times that on the plain wooden ones. The probability that the stick with food supported the largest number of snails in all six trials by chance is 0·0014; the probability that the

Table 1. *Numbers climbing in 100 % versus 41 % sea water*

Time of day	100 %					41 %				
	a.m.	p.m.	a.m.	p.m.	a.m.	p.m.	a.m.	p.m.	a.m.	p.m.
Tide number	1	4	5	8	9	2	3	6	7	10
Stick 1	21	12	9	9	16	0	0	0	0	0
Stick 2	6	14	11	17	10	1	0	0	0	0
Stick 3	19	28	18	41	33	0	0	0	1	0
Total	46	54	38	67	59	1	0	0	1	0
Grand total	264					2				

Table 2. *Numbers climbing on food-bearing (FB) versus non-food-bearing (NFB) sticks*

In each trial, the food-bearing stick is asterisked.

	Stick number			NFB max.:FB
	1	2	3	
Trial 1	76	508*	92	1:5·5
Trial 2	51	50	238*	1:4·7
Trial 3	52	206*	112	1:1·8
Trial 4	67	86	226*	1:2·6
Trial 5	130*	110	86	1:1·2
Trial 6	115*	86	94	1:1·2

numbers of snails on the six replicate food-sticks formed the six largest totals of the eighteen in the experiment by chance is much less than 0·001 (Mann–Whitney $U = 0$). The orientation of *H. ulvae* on the plain sticks also indicated, just as observed previously (Barnes, 1981), that many were climbing down as the period of cover ended. The significant difference in numbers of snails on the two types of stick therefore presumably reflects the fact that *Hydrobia* climbed down the plain sticks before the end of the experimental high tide, whereas those on the food-stick remained on their edible substratum.

More *H. ulvae* climbed the experimental sticks in the dark than in the light (Table 3): Wilcoxon matched-pairs, signed-ranks test on the individual-stick light/dark pairings, $P < 0.005$, one-tailed test. This was the case in both series (series 1, $T = 10$, $N = 14$; series 2, $T = 1.5$, $N = 12$) and it is evident that the asymmetry is greatest in the second series, in which it was also apparent that the ambient light intensity under the neon tube was greater than in the (indoor) natural daylight regime of the first series. On average, 42 % more snails climbed in the dark than in the light in series 1, and 84 % more in series 2.

Table 3. *Climbing activity in darkness versus in light*

Series 1: natural daylight, a.m.; blacked-out, p.m.

Replicate no. ...	1		2		3		4		5	
	l	*d*	*l*	*d*	*l*	*d*	*l*	*d*	*l*	*d*
Stick 1	29	28	21	20	21	28	24	18	4	18
Stick 2	21	30	26	58	30	43	31	27	15	15
Stick 3	32	62	54	75	37	68	37	50	20	31
Total	82	120	101	153	88	139	92	95	39	64

Grand total 402:571

Series 2: blacked-out, a.m.; overhead neon 'daylight' tube, p.m.

Replicate no. ...	1		2		3		4	
	l	*d*	*l*	*d*	*l*	*d*	*l*	*d*
Stick 1	13	38	28	51	28	62	9	27
Stick 2	22	36	26	50	22	51	17	22
Stick 3	28	49	44	80	23	38	25	20
Total	63	123	98	181	73	151	51	69

Grand total 285:524

DISCUSSION

Muus (1967), Anderson (1971) and others have concluded that the climbing behaviour of *H. ulvae* is related to dispersal; Muus, for example, stating that 'the tendency of the Hydrobiae to crawl upwards under unfavourable conditions provides them with especially good possibilities for passive dispersal to other biotopes'. Barnes (1981), however, considered the pattern of climbing activity manifested in relation both to an individual period of tidal cover and to the spring tidal cycle (Fig. 1) to be inappropriate for a dispersal mechanism, and suggested that dispersal was achieved mainly through the larval stages and, in adults, by being rolled over the sediment surface by flooding tides. He

related climbing activity to feeding behaviour, postulating that climbing should not be considered as distinct from normal crawling/browsing.

Water of 14‰ constitutes a suboptimal or unfavourable milieu for *H. ulvae* (Muus, 1967; Fenchel, 1975; Hylleberg, 1975); in water of that salinity at a temperature of 20 °C (the ambient temperature of the present study), for example, the feeding rate of this gastropod is depressed by more than 80% of its optimum value (Hylleberg, 1975). Yet salinities of this order are not so low as to interfere with locomotion (Newell, 1964; Muus, 1967): Newell (1964) suggested that flotation continued down to salinities of 3‰. Therefore, if the upward crawling of *H. ulvae* is a preliminary to dispersal which 'can
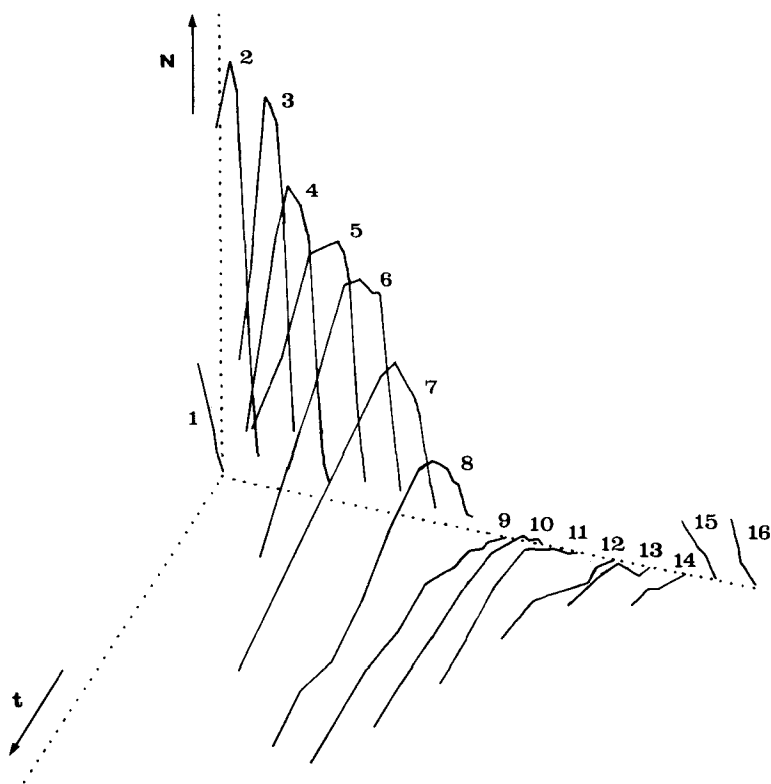

Fig. 1. Three-dimensional representation illustrating the pattern of climbing activity of *Hydrobia ulvae* collected in the field towards the end of a period of emersion during neap tides and subjected, in the laboratory, to a series of sixteen tides approximately corresponding to a spring tidal cycle. The N-axis displays the different numbers of snails up vertical structures at different times within each period of tidal cover, duration of cover being displayed on the *t*-axis. The sixteen tides (numbered in sequence) are equally spaced along the third axis. Note the variation both within and between periods of tidal cover. (From a computer plot kindly produced from the data of Barnes, 1981, by Dr A. E. Friday.)

be induced by any unfavourable environmental factor' or is a reaction to 'a new milieu not directly suiting it' (Muus, 1967), one would predict that numbers climbing the experimental sticks in these experiments would be larger under the 14‰ salinity regime than under that of the normal sea water. If, on the other hand, the behaviour pattern is related to feeding, as suggested by Barnes (1981), one would predict on the basis of the

findings of Hylleberg (1975) – see above – that the numbers climbing should be smaller under the 14‰ regime. The results presented here (Table 1) clearly support the latter interpretation.

Barnes (1981) also suggested that snails climbed down the experimental sticks in advance of the tidal ebb on finding them nutritionally to be suboptimal: a specific case of the general thesis argued by Underwood (1979) that herbivorous gastropods move (and on surfaces oriented vertically, move upwards) until they encounter suitable food, and move less rapidly when food is located. Therefore, if *H. ulvae* climbs intertidal objects during its normal browsing activity, one would also predict that the numbers of snails remaining on the experimental sticks with added abundant food would be larger than on those without suitable edible material. On the dispersal hypothesis, however, the numbers of snails climbing or remaining on individual sticks would not be influenced by the nutritional status of those sticks. Here again (Table 2), the present experiments clearly support the postulated relationship with feeding and refute the predictions from the dispersal hypothesis.

Neither, on the dispersal hypothesis, is there any reason to expect a differential level of activity in relation to the presence or absence of light (Table 3): snails presumably can disperse equally well on daytime and night-time high tides. Bird predators hunting visually and consuming those *Hydrobia* on the surface of intertidal expanses of sediment tend to feed more during daytime low tides than at night; Goss-Custard (1969), for example, suggested that redshank (*Tringa totanus*) only feed at night when they cannot obtain sufficient food during the day. It also seems intuitively likely that the success rate of any visually hunting predator is lower at night than in the day. Therefore the greater surface activity of *Hydrobia* during darkness may have a marked selective advantage in respect of decreased predation, especially perhaps from plovers (see Evans, 1979).

The evidence presented in this and the earlier paper is thus inimical to the hypothesis that climbing activity is related to dispersal, but is compatible with an explanation based on feeding activity.

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