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Foraging in the limpet *Patella vulgata*: the influence of rock slope on the timing of activity

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Preliminary observations of limpet activity at Lough Hyne, in south-west Ireland, showed that individuals on steep slopes were primarily active at night, when emersed; while those on near-horizontal rocks were often active during daytime submersion. Observations over an 11 d period of limpet populations on a near-vertical and a near-horizontal site, only 45 m apart, confirmed that animals on the near-vertical site were active on nocturnal low tides, whilst those on the near-horizontal site were active on daytime high waters. A short-term survey at ten sites, which had limpets on both extremes of slope (i.e. either near-vertical or near-horizontal), showed that limpets on near-horizontal surfaces were, on average, more active at daytime high waters than those on near-vertical faces. In 1996 and 1997 surveys of activity at daytime high, and nocturnal low waters were conducted at sites (14–15) with varying rock slopes (~3–87°). In all cases, limpets on more steep slopes were active at nocturnal emersion whilst animals on more gentle slopes were active on daytime submersion periods. In most cases these trends were significant and explained between 22–40% and 37–44% of the variation in activity with site in 1996 and 1997 respectively. Analysis of the head orientation of limpets on their home scars showed that animals orientated in a down shore direction at all sites (1997 data) suggesting that limpets do perceive and respond to slope. Whilst slope does appear to influence the timing of limpets' activity (and especially on very steep or gently sloping sites) it does not account for a large degree of the variation in activity and, on sites with slopes between 30 and 60°, is likely to work in combination with other factors.

INTRODUCTION

The activity of intertidal grazing molluscs is usually restricted to certain periods of the tidal cycle and to particular stages of the day/night cycle. Some species feed when submerged, others when emersed, and a few when they are washed by the rising or falling tide. Some species are nocturnal, others are diurnal or feed at dusk and dawn (see reviews by Hawkins & Hartnoll, 1983; Little, 1989; Chapman & Underwood, 1992). These patterns of behaviour have been associated with a number of factors, for example predator avoidance (Levings & Garrity, 1983; Warren, 1985); amelioration of physical extremes (e.g. Garrity, 1984; Branch & Cherry, 1985) or minimizing foraging times (Evans & Williams, 1991).

Many species are active only during one particular combination of conditions. The limpet, *Patella vulgata* L. has, however, been reported at different localities to be active at a variety of stages of the tidal and day/night cycles (reviewed by Hartnoll & Wright, 1977; Branch, 1981; Hawkins & Hartnoll, 1983; Little, 1989; Williams & Morritt, 1991; Della Santina et al., 1994). Possible explanations for the timing of these different behavioural rhythms, such as predation pressure or food availability, have been proposed (Little, 1989; Della Santina et al., 1994). There is also evidence for the endogenous control of limpet behaviour, possibly entrained by tidal emersion or a combination of tidal and day/night cycles (Little & Stirling, 1985; Della Santina & Naylor, 1993). Individual (intrapopulation) variation in behavioural patterns has, however, been recorded with tidal height (Little et al., 1988) and also between individuals seemingly under the same environmental conditions (Della Santina et al., 1994).

One of the most striking differences between behavioural rhythms in populations of *P. vulgata* appears to be related to the slope of the rock substrate. Animals on near-vertical rock surfaces tend to be active at nocturnal low waters (e.g. limpets on vertical pier walls; Della Santina et al., 1994). It is known, however, from work on the Isle of Man, that animals on near-horizontal surfaces are more active during daytime submergence (Hartnoll & Wright, 1977) than animals on vertical surfaces where observations suggest that activity occurs when the tide is out (Hawkins & Hartnoll, 1982). Such comparisons of behaviour of limpet populations at different sites are usually confounded by geographic differences (e.g. different tidal ranges etc.; see Gray & Naylor, 1995) and temporal variation in observation periods (i.e. being unable to survey different sites at the same time; see Della Santina et al., 1994). Observations, in general, are also short-term, not allowing for temporal variation in

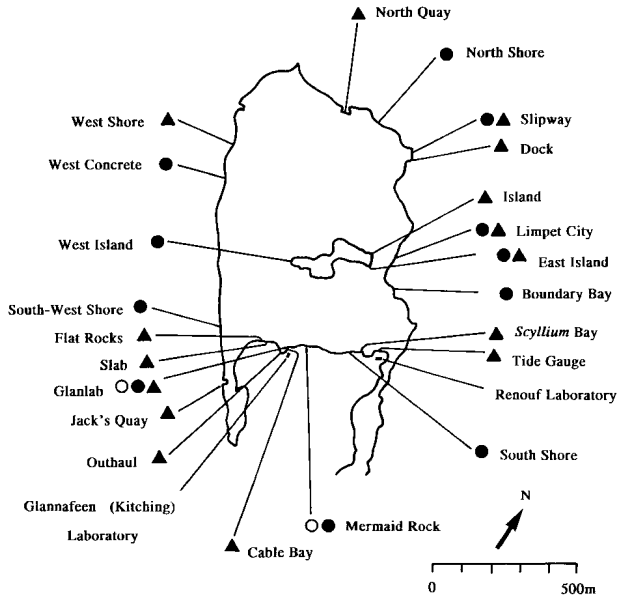

Figure 1. Map showing study sites at Lough Hyne, southern Ireland. Open circles represent those sites at which activity was monitored over several days in 1992; closed circles represent those sites used in the 1992 survey and triangles those used in 1996 and 1997.

behaviour (e.g. with phases of the tide) and are conducted on small spatial scales (e.g. investigating only one or two populations; Little et al., 1988). The comparative value of these different records of limpet behaviour is therefore limited by these confounding problems.

In Lough Hyne, a sheltered sea lough in south-west Ireland, Little et al. (1988, 1990, 1991) have shown at a number of sites over a period of seven years that limpets on steep surfaces are primarily active at times of nocturnal low tides. Casual observations, however, suggested between site variation in this pattern, which appeared to be related to the slope of the rock surface. The present paper, therefore, investigates activity patterns of limpet populations on rock substrates of varying slope, at a number of time intervals, to ascertain whether rock slope plays a role in influencing behavioural patterns.

MATERIALS AND METHODS

Preliminary observations on near-vertical and near-horizontal surfaces

Observations were made at several sites (Figure 1) in Lough Hyne, a marine lough 80 km west of Cork, Ireland between 1992 and 1997. Initial observations revealed very different behavioural patterns for limpets, *Patella vulgata*, on horizontal and vertical rock surfaces. Animals on vertical surfaces were consistently active when emersed during low water periods at night or occasionally during the daytime (reviewed by Williams & Morritt, 1991). Field observations, however, suggested animals on horizontal surfaces moved whilst submerged in the daytime. To investigate whether these patterns were predictable for a population (i.e. a number of animals within the same tidal range and at the same locality) at a given site, limpet populations were monitored at two sites over a period of 11 d. In September 1992, over a neap–spring–neap cycle (see Kitching, 1987 for a description of tidal conditions in the lough) limpet activity in populations at the Glannafeen Laboratory (Glanlab), a near-horizontal (i.e. slope $<20^{\circ}$), and Mermaid Rock, a near-vertical site ($>60^{\circ}$) were monitored (see Figure 1 for site locations). Both sites were almost bare of macroalgae ($<5\%$ cover) and had only a sparse barnacle (*Elminius modestus, Chthamalus montagui* and *Semibalanus balanoides*) cover.

Patella vulgata is a homing species, returning to orientate exactly at the same location on the rock surface when inactive. A number was painted on the shell of each limpet with white Tipp-Ex^{TM} (Tipp-Ex GmbH & Co KG) and on the rock surface so that the two numbers aligned. A break in this alignment signified that the limpet had moved (see Little & Stirling, 1985). Limpets were defined as active if they were not on their home scar, or had turned upon it. Positions of each limpet were recorded every 15 min using time-lapse photography (Ricoh XRX cameras, Ricoh Europe B.V.). Wide-angle lenses (24 or 28 mm) were used to include a field of view of $\sim 2\times1$ m. In daylight the lenses were fitted with polarizers to improve underwater visibility, and at night electronic flash was used. In general Fuji Neopan 400 film (Fuji Photo Film Co. Ltd) was employed, to ensure adequate resolution. Cameras were mounted on extended tripods, and protected with weather shields.

Time-lapse photography worked well during emersion, and during submersion when the water surface was calm. During rough wave action limpet activity was monitored visually by using a viewing box to supplement camera records. Movement patterns (percentage population active) were recorded graphically.

Activity patterns during submergence on near-horizontal and near-vertical sites

To investigate whether activity underwater in daylight was a common behaviour of animals on horizontal rock surfaces, activity was monitored during daytime submersion at ten sites in the lough in September 1992 (Figure 1). At each site 30–40 limpets were measured (±0.1 mm) on both near-vertical (defined as $>60^{\circ}$) and near-horizontal (defined as $<20^{\circ}$) rocks and their shells and home scars numbered with Tipp-Ex^{TM}. All limpets were at heights between $+15$ and $+45$ cm above standard level (SL, approximately the lowest level reached by tides; Bassindale et al., 1948), but individual heights were not recorded.

Observations of activity were carried out over a period of 1 h at high water, and the activity expressed as percentage of the population active. Animals were scored as active if the Tipp-Ex^{TM} number on the home scar and the shell did not align. The survey was initially conducted on 5 September 1992 (at mean neap tides) and repeated on 11 September (neap–spring tides) and on 15 September (mean spring tides), at which times some of the readings (for sites at East Island and Boundary Bay) were taken from automatic recording devices (as used by Little et al., 1991; $N=23$).

Differences in percentage activity between horizontal and vertical populations at the same tidal period were tested using Mann–Whitney tests. Differences between the same populations at different times were not tested as the same individuals were used on different days, therefore violating assumptions of independence of the data.

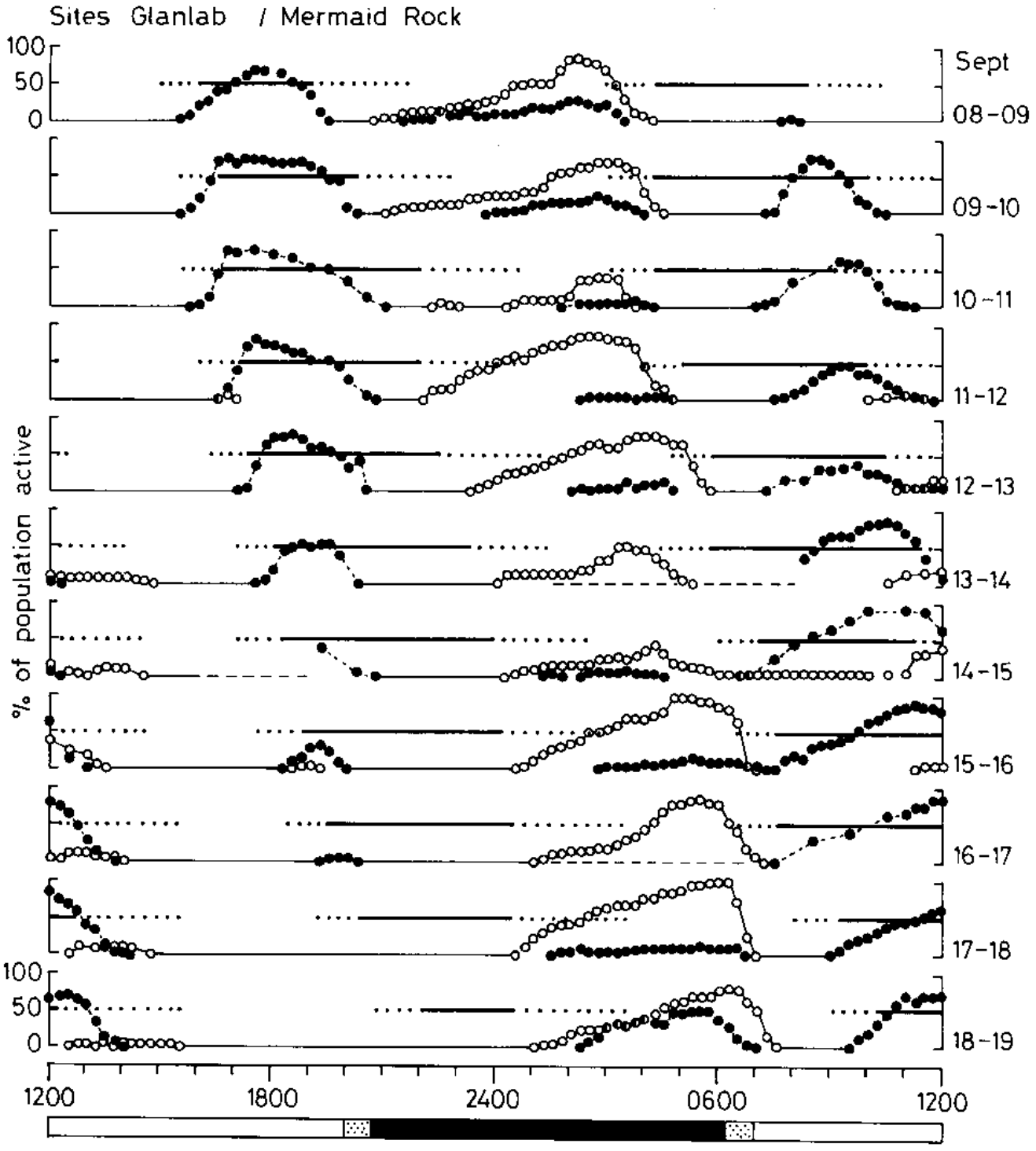

Figure 2. Activity of limpets on near-horizontal and near-vertical surfaces at Glannafeen Laboratory and Mermaid Rock in September 1992. Closed circles show limpets on near-horizontal surfaces; open circles show animals on near-vertical surfaces. Horizontal bar shows periods of water cover, and dots show partial cover. Bottom bar shows day (white) night (black) and dawn/dusk (stipple).

Activity patterns on a range of slopes

In August–September 1996 and 1997, limpet activity was recorded at 14 (1997) and 15 sites (1996) respectively around the lough (Figure 1). As opposed to examining the extreme ranges of possible slope, sites were selected to represent a range of slopes from near-horizontal to near-vertical, to detect whether there was any trend in activity over the entire slope gradient. In 1996, at each site, $\geqslant 20$ limpets were selected which had home scars on similar slopes (within $\sim 10^{\circ}$, as measured by clinometer). Where possible the same sites were used in 1997, although often with reduced sample sizes ($N \geqslant 12$) due to difficulties in locating animals on appropriate slopes. In 1997 the head orientation of the limpets on their home scar was also recorded. Head orientation was scored as an angular bearing relative to the slope of the rock (i.e. a limpet facing directly up-slope would score a value of 0° and one

Table 1. *Percentage activity of limpets during diurnal high tide (N=30–40 animals) on near horizontal (<20°) and near vertical (>60°) rock surfaces at ten sites around Lough Hyne, southern Ireland in September 1992.*

		Percentage activity				Percentage activity		
Site	Vertical Mean size (mm ±SD)	05/09 mean neap	11/09 neap–spring	15/09 mean spring	Horizontal Mean size (mm ±SD)	05/09 mean neap	11/09 neap–spring	15/09 mean spring
South Shore	33.5 ±5.2	0	3	3	32.0 ±5.6	43	58	85
Glanlab/Mermaid	27.2 ±3.2	0	0	31	41.1 ±5.2	37	63	90
South-west Shore	32.0 ±6.4	0	3	16	35.0 ±8.0	9	42	57
West Island	34.5 ±4.6	0	0	0	36.2 ±7.3	0	29	61
West Concrete	34.0 ±4.9	6	0	0	34.0 ±6.7	6	19	30
North Shore	30.4 ±4.2	0	6	7	33.5 ±4.8	5	18	17
Slipway	29.9 ±4.7	20	7	46	34.5 ±8.9	14	6	55
Limpet City	31.4 ±4.8	0	6	7	38.5 ±8.0	9	44	53
East Island	31.0 ±4.4	23	10	15	38.2 ±5.0	14	17	30
Boundary Bay	36.3 ±4.3	0	0	26	39.7 ±4.6	34	40	68
Mean	32.2 ±2.6				36.3 ±3.0			
Mean (arc-sine)		1.4	2.0	11.0		11.8	32.2	55.2

facing down-slope 180°). In both years animals and their home scars were numbered using Tipp-Ex™, and maximum shell length measured (±0.1 mm). Activity was monitored at four times at daytime high waters and once at nocturnal low water during neap to spring tides in 1996 and twice at high water and once at low water in 1997. The number of planned surveys in 1997 had to be reduced as compared to 1996 due to heavy rainfall which inhibits limpet movement (Little et al., 1990) hence a number of surveys were terminated or were eliminated from analysis as freshwater was running over the rock surface (e.g. Tide Gauge on 2 September) in 1997.

Percentage activity of limpets was arc-sine transformed (to account for the constraints on percentage data) and regressed against slope for each observation period. Head orientation (1997 only) was analysed using circular statistics to investigate whether animals were orientated in a downshore (i.e. 180°), rather than a random direction (*V*-test; Zar, 1996).

RESULTS

Patterns of activity on near-vertical and near-horizontal surfaces

At the Glanlab and Mermaid Rocks (Figure 2), there was a clear distinction between activity of limpets on near-horizontal and near-vertical surfaces. On near-horizontal surfaces (Glanlab), activity was greatest during daytime submergence. A peak of activity on the afternoon tide was gradually replaced by a peak on the morning tide, so that at times there were two underwater

Table 2. *Mean size, slope and percentage activity for limpets (N=20–30 animals) from sites with varying slope in Lough Hyne, southern Ireland during August–September 1996.*

				Percentage activity				
Site	Mean size (mm ±SD)	Slope (°)	N	29/08 DHW	30/08 NLW	30/08 DHW	01/09 DHW	04/09 DHW
Slipway	46.9 ±5.7	2.8	20	30	5	0	15	60
Glanlab	42.9 ±8.7	10.0	30	73.3	10	10	56.7	43.3
Outhaul	46.7 ±6.0	15.5	30	6.7	50	10	3	0
East Island	46.8 ±5.2	20.3	24	37.5	0	4	37.5	50
Flat Rocks	39.7 ±7.0	25.7	25	24	52	0	0	4
Island	45.7 ±5.8	35.1	30	6.7	0	3.3	50	73.3
Limpet City	34.7 ±5.6	40.1	20	35	5.3	0	25	42.9
Slab	34.8 ±4.1	47.1	25	0	68	0	0	4
West Shore	42.1 ±5.2	53.2	23	30.4	48	0	0	40
North Quay	33.5 ±4.9	59.6	20	0	5	0	0	0
Scyllium Bay	35.6 ±5.2	65.5	26	23.1	50	0	23.1	24
Cable Bay	40.7 ±5.8	70.5	20	10	65	0	0	0
Tide Gauge	35.9 ±4.5	70.4	25	0	84	0	0	0
Dock	38.3 ±3.9	81.7	21	23.8	52.4	0	4.8	28.6
Jack's Quay	36.5 ±5.5	87.4	30	0	93.3	0	0	0

29 August, daytime high water (DHW); 30 August, nocturnal low water (NLW); 30 August, daytime high water; 1 September, early morning high water; 4 September, high water, springs.

Table 3. *Mean size, slope, percentage activity and head orientation (mean angle (°) where 180°=head orientated down shore and 0°=head orientated upshore, and mean resultant vector, r) (N values for size and head orientation varied as orientation measurements were not always possible due to rock topography) for limpets (N=12–17 animals) from sites in Lough Hyne, Southern Ireland during August–September 1997.*

				Percentage activity			Mean head orientation		
Site	Mean size (mm ±SD)	Slope (°)	N	26/08 DHW	29/08 DHW	02/09 NLW	(°)	r	N
Slipway	47.9 ±4.5	4.2	15	73.3	40	6.6	173	0.666	13
Glanlab	41.8 ±9.3	8.4	15	73.3	73	0.0	173	0.654	12
Outhaul	41.3 ±8.5	15.9	14	21.4	7.1	7.1	172	0.738	13
Flat Rocks	36.5 ±6.3	22.5	12	75	25	16.7	185	0.860	11
Island	49.9 ±5.4	37.5	16	100	25	#	202	0.551	16
Limpet City	40.5 ±3.7	38.5	15	37.5	31	#	193	0.856	16
West Shore	44.0 ±3.8	51.6	12	51.6	42	33	165	0.747	12
Slab	38.9 ±4.8	53.0	16	43.8	19	0	177	0.718	16
North Quay	38.5 ±4.3	56.6	14	14.3	0	0	175	0.594	13
Scyllium Bay	34.9 ±5.1	66.0	14	50	14	42.9	190	0.827	14
Cable Bay	41.5 ±5.4	68.2	12	0	8	33	178	0.740	12
Tide Gauge	39.6 ±4.1	69.4	14	21.4	7	*	189	0.857	14
Dock	39.9 ±2.9	80.1	17	11.8	24	52.9	184	0.886	17
Jack's Quay	33.7 ±5.8	87.1	14	7.1	0	100	161	0.818	14

26 August, daytime high water (DHW); 29 August, daytime high water; 2 September, nocturnal low water (NLW); #, sites not sampled due to lack of boat access; *, site not included due to freshwater running over the rock surface.

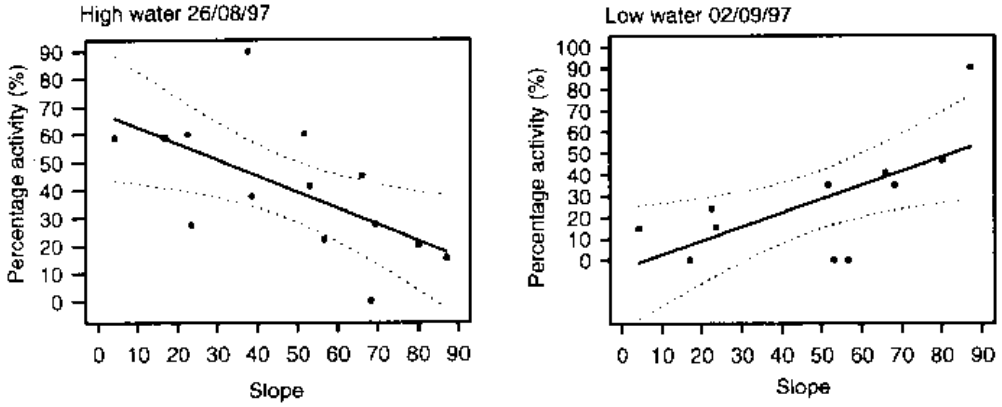

Figure 3. Examples of regression lines (±95% confidence limits) for percentage activity (arc-sine transformed) of limpet populations against rock slope during diurnal high water and nocturnal low water tides at Lough Hyne in 1997 (regression equations are given in Table 4).

Table 4. *Regression analysis for limpet activity (y) vs rock slope (x) in September 1996 and August–September 1997. Percentage activity was arc-sine transformed prior to analysis.*

Date	High/low water	Equation	r^2	ANOVA	
1996					
29/08	High	y= 38.36−0.35 x	0.29	F=5.34, 1, 13 df	P=0.038
30/08	High	y= 11.23−0.16 x	0.37	F=7.77, 1, 13 df	P=0.015
30/08	Low	y= 9.91+0.56 x	0.40	F=8.62, 1, 13 df	P=0.012
01/09	High	y= 31.95−0.36 x	0.28	F=4.95, 1, 13 df	P=0.044
04/09	High	y= 42.21−0.38 x	0.22	F=3.68, 1, 13 df	P=0.077
1997					
26/08	High	y= 68.46−0.58 x	0.38	F=7.46, 1, 12 df	P=0.018
29/08	High	y= 43.86−0.38 x	0.37	F=7.01, 1, 12 df	P=0.021
02/09	Low	y=−3.79+0.65 x	0.44	F=7.20, 1, 9 df	P=0.025

activity peaks each day. There was only limited activity at night during emersion, except on 18–19 September. In contrast, the limpets on near-vertical surfaces (Mermaid Rock) were almost exclusively active at night during emersion for the full 11 d. Animals did, however, show some activity on two daytime high tides (14 and 15 September), and very slight activity during the falling tide on several days. At these sites, only 45 m apart, the difference in behaviour on the two rock slopes was clearly maintained for 11 days.

Activity patterns during submergence on near-horizontal and near-vertical sites

At ten sites around the lough, overall percentage activity during daytime high tides was significantly greater on near-horizontal surfaces than on near-vertical surfaces on all three occasions when surveys were carried out (Table 2; Mann–Whitney tests, $P<0.05$ for all three tidal cycles). The pattern of activity under water was not, however, uniform at all sites and tides (Table 2). Only on a mean spring tide were limpets on all near-horizontal rocks more active than those on all near-vertical rocks. On a mean neap tide, limpets on near-horizontal rocks at West Island showed no activity, while at Slipway and East Island, limpets on near-vertical surfaces showed more activity than those on near-horizontal surfaces.

Activity patterns on a range of slopes

Limpets were, in general, larger at near-horizontal sites than near-vertical sites (Tables 1–3). There was a significant negative relationship between size and slope (1996 size=45.72–0.1245 slope; 1,13 df; $F=11.61$; $P=0.005$; $r^2=47.2\%$; 1997 size=45.2–0.095 slope; 1,12 df; $F=4.79$; $P=0.049$; $r^2=28.5\%$) with larger limpets being found on more gently sloping surfaces. Although size of animals did vary between sites (Tables 2 & 3), only once in the eight surveys was there a significant relationship between size and activity patterns (30 August High water survey 1996; regression, activity $-33.6+0.938$ slope; 1,13 df; $F=9.53$; $P=0.009$; $r^2=42.3\%$; all other regressions, $P>0.05$).

There was a consistent trend for limpet activity to increase with slope steepness at times of nocturnal low water (i.e. animals on steeper slopes were more active, a positive relationship of slope vs activity; Figure 3, Table 4) whereas activity at daytime high waters was greater on more gently sloping surfaces (a negative relationship with slope steepness; Figure 3, Table 4). Whilst these relationships were significant in most cases (Table 4; except 4 September 1996), the regression only explained between 22 and 40% in 1996 and between 37 and 44% in 1997 of the variation in activity in the respective data sets (Table 4). Animals at some sites were consistent in their behaviour patterns (e.g. Jack's Quay, Glanlab) whereas others were more variable (e.g. Outhaul) or showed very little activity during either year (e.g. North Quay). Activity was generally greater during spring tide periods (Table 2). For most sites, therefore, there was a negative relationship between activity and steepness of the rock during daytime high waters and a positive relationship during nocturnal low waters; however these relationships did not explain the activity patterns of all the sites.

In 1997 at all sites, irrespective of slope, animals were orientated on their homescars with their heads in a down-shore direction (Table 3; *V*-test for circular uniformity, Zar 1996, to test whether animals head orientations were not uniformly distributed, but had a mean direction of 180°, in all cases $P<0.01$).

DISCUSSION

General patterns

Limpets at all sites studied in Lough Hyne appear to be sensitive to slope, or a slope-related variable, and align their heads on their home scar in a down-shore direction. Slope is presumably detected by statocysts (Fretter & Graham, 1962). Limpets may orientate in this direction so that their head and nuchal cavity will sense the incoming/outgoing tide and will, therefore, experience the first waves of the flooding tide and the remains of the ebbing tide. Orientation in a downshore direction may be advantageous to aid flushing of the nuchal cavity to remove accumulated faeces as well as other excretory products (CO_2 etc.) and also the storage of water in the mantle/nuchal cavity prior to emersion.

Although *Patella vulgata* at Lough Hyne moves predominantly at night during emersion on near-vertical shores, many populations on near-horizontal surfaces forage under water during daylight. Limpets on near-vertical and near-horizontal rock surfaces at the Glanlab and Mermaid Rock sites showed relatively constant behaviour patterns for 11 d. Apart from the general increase in activity as tides changed from neaps to springs, the Glanlab population (near-horizontal) were active on daytime high waters, whilst the near-vertical population at Mermaid Rocks moved on nocturnal low waters. Such behaviour is consistent with reports for other populations of *P. vulgata* on near-horizontal (e.g. Hartnoll & Wright, 1977; Hawkins & Hartnoll, 1982; reviewed by Hawkins & Hartnoll, 1983; Little, 1989) and near-vertical surfaces (e.g. Hawkins & Hartnoll, 1982; Little & Stirling, 1985; Della Santina & Naylor, 1993; Della Santina et al., 1994; Gray & Naylor, 1995; reviewed by Little 1989; Williams & Morritt, 1991). The activity of both populations followed daily tidal fluctuations, for example animals at Glanlab switching from the evening high water tide to the morning tide and not being active on nocturnal high tides (18–19 September). This tracking of the tide and 'switching' between tides has previously been recorded for animals on vertical surfaces in Lough Hyne (switching from the early morning low water tide to the late evening low water tide; Little & Stirling, 1985; Little et al., 1988) and North Wales (Della Santina et al., 1994). Activity during daytime submergence for animals on near-horizontal rocks at Glanlab has been consistently observed on annual September visits between 1990 and 1997.

Variability in foraging behaviour with slope

In general, limpets on near-horizontal rock surfaces, within a few metres of animals on near-vertical surfaces,

showed greater activity during daytime submersion. When comparing sites with a range of slopes, there was a positive relationship between slope steepness and increasing population activity when limpets were emersed at night, and a negative relationship of activity with increasing slope at daytime high water. At some sites this relationship was very strong; for example Jack's Quay and Glanlab, the most vertical and horizontal sites, had consistent patterns for all years studied.

There is no clear explanation why limpets on varying rock slopes show different behaviour patterns. It is tempting to assign the cause of differing behaviour to some other influence such as predation, either by marine predators during nocturnal high waters (e.g. crabs and fish) or terrestrial predators during day time low waters (e.g. birds). There was little evidence of predator activity underwater during the day, but crabs (especially *Necora puber* L.) were abundant at night (personal observation). Naylor (1958) observed, however, that some individuals of *Carcinus maenas* L. showed a tendency to be active at every high tide, and therefore would prey on animals moving during the day (see also McGaw & Naylor, 1992). It is, therefore, possible that on some slopes avoidance of predation prevents activity underwater during the day. There are few avian predators on limpets in Lough Hyne, although hooded crows (*Corvus corone cornix* L.) have been observed to prey on limpets experimentally removed from their home scars (Little et al., 1990), and limpets are a minor natural dietary item for these birds (Berrow et al., 1991).

Limpets on most near-horizontal surfaces showed more activity at spring tides than at neaps, as do limpets on near-vertical surfaces when emersed (Little et al., 1991; Williams & Morritt, 1991). Little et al. (1991) speculated that time of submersion might be the cue for degree of activity, but depth of water cover could be as important. Since the shore height of each individual was not recorded in the present study, but limpets were used within a height band, some of the variation between sites may be related to either duration of water cover, or depth.

Limpets on vertical surfaces showed longer overall feeding times than those on horizontal surfaces (Figure 2; unpublished data). In a preliminary survey of chlorophyll levels (A. Miles, unpublished data) no consistent difference in food supply was found between horizontal and vertical surfaces. Mucus feeding trails were, however, more obvious on near-horizontal rock surfaces (personal observation). Mucus is persistent and may be important in energy balance if re-ingested (Davies et al., 1992). If total food supply varied between horizontal and vertical rocks then limpets might have variable foraging times in order to obtain the same food supply and, on more rough surfaces (e.g. barnacle cover) individuals may take longer to reach areas to feed in. Variation in food supply has been cited as a possible cause of differences in foraging duration between exposed and sheltered shore populations of *P. vulgata* in north Wales (Della Santina et al., 1994) although, as in the present study, no evidence was presented to support this case.

Lability of foraging patterns

Spatial and temporal variability in foraging behaviour of marine grazers has been emphasized by Chapman & Underwood (1992). Although the most steep and most gently sloping sites showed predictable, consistent foraging rhythms, other sites showed more labile patterns, especially sites of intermediate slope (e.g. Flat Rocks, Outhaul). The relationship between behaviour and slope, although explaining a considerable amount of the variation in the present data set, is likely to be only one of a variety of factors which limpets may use to cue their activity. Some authors have noted, for example, the role of wave action, rainfall and possible individual-orientated cues (e.g. energy requirements) which may influence activity (Little et al., 1990; Williams & Morritt, 1991). In their study of the Mediterranean limpet, *Patella rustica*, Della Santina & Chelazzi (1991) showed a marked positive correlation between activity and sea roughness and many tropical species are active whilst awash (Garrity, 1984; Williams & Morritt, 1995). Wave action is variable around the lough, for example, a west or south-west wind produces increased wave action in the north-east corner of the lough. At the Slipway site, limpets on near-vertical surfaces were very active underwater during such wave action (e.g. 5 and 15 September 1992). At Mermaid Rock, activity on the falling tide was often observed when wave action alternately wetted and uncovered limpets on near-vertical slopes (see 14 and 15 September 1992; Figure 2). Part of the variation in activity shown by near-vertical limpets may be ascribed to variation in wave action.

Population differences between years may also be a function of variation in site characteristics. The near-vertical North Quay site has been under observation since 1986, and activity patterns were consistent (animals in mid-high shore being active on nocturnal low waters; Little et al., 1988, 1990; Evans & Williams, 1991) from 1986 to 1990. During observations in 1996 and 1997 very little activity was recorded on nocturnal low waters (present and unpublished data) and limpet density was much lower than in previous years. This site now supports a more dense cover of barnacles, macroalgae (mostly *Fucus vesiculosus*) and also patches of mussels (*Mytilus edulis*) than in previous years (personal observations) and it is possible that this change in community composition may influence limpet behaviour. Limpets forage more easily over smooth surfaces than barnacle-covered rocks (Underwood, 1979, also see Little et al., 1988), and some species of limpets grow faster in more homogeneous, smooth areas (Fletcher & Underwood, 1987). Roughness, or habitat complexity, could therefore be a major determinant of activity and subsequent success in *P. vulgata*.

Rainfall has a clear inhibitory effect on limpet behaviour, especially during nocturnal low waters (Little et al., 1990). In 1997 rainfall was heavy during the observation period and freshwater influx to the lough was high. A number of nocturnal low water surveys during this period had to be terminated due to rainfall, or even when rain was not falling, due to freshwater runoff over the rock surface which inhibited limpet movement.

Implications for populations on different slopes

Della Santina & Naylor (1993) have shown *P. vulgata* in north Wales (vertical populations) to have a strong circatidal and weak circadian endogenous clock. If the same is true for individuals in Lough Hyne, and if slope is an

important exogenous determinant of activity, limpets on horizontal and vertical surfaces must either use different cues to set their clocks, or interpret these cues in a different fashion to effect the differences in behaviour. As all patellid limpets recruit from planktonic larvae, the development of these different rhythms must occur after settlement, again suggesting that these animals are sensitive to slope (or some related variable). The influence of these cues is presumably most pronounced on steep or horizontal surfaces, and cues derived from slopes between these extremes are not likely to be such strong entrainment factors. Exogenous factors such as light have been suggested to override certain components of the endogenous clock (e.g. daylight inhibiting daytime foraging at low water, Della Santina et al., 1994). These exogenous factors, such as rainfall, are important, as they can override endogenous cues for activity and inhibit activity for long time periods (possibly days). Under such conditions animals may become physiologically stressed, a further condition which may influence timing and duration of activity.

It is likely that a variety of factors influence the timing of activity of individuals, which may or may not work in combination with each other. The relationship with slope appears to be quite strong, especially on either very steep or slight slopes, and activity patterns on rocks of intermediate slope are more labile. Some environmental factors may assume greater importance in determining the possible windows of foraging activity (e.g. tides, rainfall) at the population level whilst other variables (e.g. food intake, foraging times) will influence the behaviour of individuals within these constraints (see Williams & Morritt, 1991; Della Santina et al., 1994; Santini et al., 1995). Intrapopulation variation in behaviour is, therefore, likely to be greater on sites where environmental factors are more variable (possibly accounting for the very strong patterns recorded from sites with very uniform habitats, e.g. pier walls and horizontal platforms). The different rhythms of behaviour for populations on steep, or nearly-horizontal, environmentally uniform sites suggests very different controlling factors. Individuals in these populations must also experience different constraints on their energy budgets as a result of their different behavioural rhythms. Calculation of the different energy budgets and potential foraging strategies for animals on vertical and horizontal rocks (see Evans & Williams, 1991; Santini & Chelazzi, 1996 for studies on vertical populations) might lead to explanations for such divergent timing in behaviour of animals sometimes no more than 2–3 m apart.

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REFERENCES

Bassindale, R., Ebling, F.J., Kitching, J.A. & Purchon, R.D., 1948. The ecology of the Lough Ine rapids with special reference to water currents. I. Introduction and hydrography. *Journal of Ecology*, **36**, 305–322.

Berrow, S.D., Kelly, T.C. & Myers, A.A., 1991. The impact of hooded crows *Corvus corone cornix* L. on populations of intertidal molluscs. In *The ecology of Lough Hyne* (ed. A. Myers et al.), pp. 79–88. Dublin: Royal Irish Academy.

Branch, G.M., 1981. The biology of limpets: physical factors, energy flow, and ecological interactions. *Oceanography and Marine Biology. Annual Review*, **19**, 235–380.

Branch, G.M. & Cherry, M.I., 1985. Activity rhythms of the pulmonate limpet *Siphonaria capensis* Q. & G. as an adaptation to osmotic stress, predation and wave action. *Journal of Experimental Marine Biology and Ecology*, **87**, 153–168.

Chapman, M.G. & Underwood, A.J., 1992. Foraging behaviour of marine benthic grazers. In *Plant–animal interactions in the marine benthos* (ed. D.M. John et al.), pp 289–317. Oxford: Clarendon Press. (Systematics Association, Special vol. 46.)

Davies, M.S., Jones, H.D. & Hawkins, S.J., 1992. Physical factors affecting the fate of pedal mucus produced by the common limpet *Patella vulgata*. *Journal of the Marine Biological Association of the United Kingdom*, **72**, 633–643.

Della Santina, P. & Chelazzi, G., 1991. Temporal organization of foraging in two Mediterranean limpets, *Patella rustica* L. and *P. coerulea* L. *Journal of Experimental Marine Biology and Ecology*, **153**, 75–85.

Della Santina, P. & Naylor, E., 1993. Endogenous rhythms in the homing behaviour of the limpet *Patella vulgata* Linnaeus. *Journal of Molluscan Studies*, **59**, 87–91.

Della Santina, P., Naylor, E. & Chelazzi, G., 1994. Long term field actography to assess the timing of foraging excursions in the limpet *Patella vulgata* L. *Journal of Experimental Marine Biology and Ecology*, **178**, 193–203.

Evans, M.R. & Williams, G.A., 1991. Time partitioning of foraging in the limpet *Patella vulgata*. *Journal of Animal Ecology*, **60**, 563–575.

Fletcher, W.J. & Underwood, A.J., 1987. Interspecific competition among subtidal limpets: effect of substratum heterogeneity. *Ecology*, **68**, 387–400.

Fretter, V. & Graham, A., 1962. *British prosobranch molluscs*. London: The Ray Society.

Garrity, S.D., 1984. Some adaptations of gastropods to physical stress on a tropical shore. *Ecology*, **65**, 559–574.

Gray, D.R. & Naylor, E., 1995. Foraging and homing behaviour of the limpet, *Patella vulgata*: a geographical comparison. *Journal of Molluscan Studies*, **62**, 121–124.

Hartnoll, R.G. & Wright, J.R., 1977. Foraging movements and homing in the limpet *Patella vulgata* L. *Animal Behaviour*, **25**, 806–810.

Hawkins, S.J. & Hartnoll, R.G., 1982. The influence of barnacle cover on the numbers, growth and behaviour of *Patella vulgata* on a vertical pier. *Journal of the Marine Biological Association of the United Kingdom*, **62**, 855–867.

Hawkins, S.J. & Hartnoll, R.G., 1983. Grazing of intertidal algae by invertebrates. *Oceanography and Marine Biology. Annual Review*, **21**, 195–282.

Kitching, J.A., 1987. Ecological studies at Lough Hyne. *Advances in Ecological Research*, **17**, 115–186.

Levings, S.C. & Garrity, S.D., 1983. Diel and tidal movements of two co-occurring neritid snails: differences in grazing patterns on a tropical shore. *Journal of Experimental Marine Biology and Ecology*, **67**, 261–278.

Little, C., 1989. Factors governing patterns of foraging activity in littoral marine herbivorous molluscs. *Journal of Molluscan Studies*, **55**, 273–284.

Little, C., Morritt, D., Paterson, D.M., Stirling, P. & Williams, G.A., 1990. Preliminary observations on factors affecting foraging activity in the limpet *Patella vulgata*. *Journal of the Marine Biological Association of the United Kingdom*, **70**, 181–195.

Little, C., Partridge, J.C. & Teagle, L., 1991. Foraging activity of limpets in normal and abnormal tidal regimes. *Journal of the Marine Biological Association of the United Kingdom*, **71**, 537–554.

Little, C. & Stirling, P., 1985. Patterns of foraging activity in the limpet *Patella vulgata* L.—a preliminary study. *Journal of Experimental Marine Biology and Ecology*, **89**, 83–296.

Little, C., Williams, G.A., Morritt, D., Perrins, J.M. & Stirling, P., 1988. Foraging behaviour of *Patella vulgata* L. in an Irish sea-lough. *Journal of Experimental Marine Biology and Ecology*, **120**, 1–21.

McGaw, I.J. & Naylor, E., 1992. Distribution and rhythmic locomotor patterns of estuarine and open-shore populations of *Carcinus maenas*. *Journal of the Marine Biological Association of the United Kingdom*, **72**, 599–609.

Naylor, E., 1958. Tidal and diurnal rhythms of locomotory activity in *Carcinus maenas* (L.). *Journal of Experimental Biology*, **35**, 602–610.

Santini, G. & Chelazzi, G., 1996. Energy maximization vs. time minimization in the foraging of the limpet *Patella vulgata*. *Journal of Animal Ecology*, **65**, 599–605.

Santini, G., Chelazzi, G. & Della Santina, P., 1995. Size-related functional and energetic constraints in the foraging of the limpet *Patella vulgata* (Mollusca, Gastropoda). *Functional Ecology*, **9**, 551–558.

Underwood, A.J., 1979. The ecology of intertidal gastropods. *Advances in Marine Biology*, **16**, 111–210.

Warren, J.H., 1985. Climbing as an avoidance behaviour in the saltmarsh periwinkle, *Littorina irrorata* (Say). *Journal of Experimental Marine Biology and Ecology*, **89**, 11–28.

Williams, G.A. & Morritt, D., 1991. Patterns of foraging in *Patella vulgata* (L.). In *The ecology of Lough Hyne* (ed. A. Myers et al.), pp. 61–69. Dublin: Royal Irish Academy.

Williams, G.A. & Morritt, D., 1995. Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata*. *Marine Ecology Progress Series*, **124**, 89–103.

Zar, J.H., 1996. *Biostatistical analysis*, 3rd ed. New Jersey: Prentice Hall.

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