

Food supply, grazing activity and growth rate in the limpet *Patella vulgata* L.: a comparison between exposed and sheltered shores

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Abstract

The limpet *Patella vulgata* L. is an important microphagous grazer on intertidal rocky shores of north-west Europe, occurring across the wave exposure gradient. Groups of *P. vulgata* were selected at mid-tide level of two exposed shores and two sheltered, fucoid dominated shores on the Isle of Man, British Isles, and manipulated to equivalent densities and population structure. The level of grazing activity and growth rate were determined over a 1-year period. At the same time, the abundance of epilithic microalgae, measured as the concentration of chlorophyll *a*, was determined as an estimate of food supply. Microalgal abundance showed a seasonal pattern in both exposed and sheltered conditions, with higher levels in winter compared to summer. In both seasons, the microalgal resource was more abundant on the sheltered shore studied. The level of grazing activity in *P. vulgata* showed a seasonal pattern on the exposed but not the sheltered shores. Averaged over the year, grazing activity on the exposed shores was over double that on sheltered shores. Thus, in sheltered conditions, food supply for limpets was high and grazing activity low; in exposed conditions, food supply was low and grazing activity high. The growth rate of *P. vulgata*, measured as increase in shell length, showed no significant difference between exposed and sheltered shores. Growth rate was also determined in *P. vulgata* at natural densities. Although the overall density declined with decreasing exposure to wave action, the density per unit area of grazeable substance was higher in shelter. In these populations, the mean growth rate was over twice as high on exposed compared to sheltered shores. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

The limpet *Patella vulgata* is the dominant grazer in the mid-intertidal zone of north-west Europe, and is distributed across the wave exposure gradient. On exposed shores, this microphagous grazer has an important community structuring role, regulating the recruitment of macroalgae through consumption of early macroalgal stages (see Hawkins et al., 1992 for review). With increasing shelter from wave action, the density of *P. vulgata* (Fischer-Piette, 1948; Jones, 1948; Southward, 1953; Ballantine, 1961; Lewis, 1964; Thompson, 1980), and its role in controlling community structure (Jenkins et al., 1999), decline. However, even on sheltered shores, it is relatively common beneath dense stands of macroalgae (Lewis, 1964).

The microalgal film, which coats the rocky shore, consists predominantly of organic material, diatoms and cyanobacteria and provides a food supply for microphagous grazers such as limpets. Study of this assemblage has been hampered by technical difficulties (MacLulich, 1986; Hill and Hawkins, 1990), but some progress in elucidating spatial and temporal patterns of abundance has been made. Seasonal variation in microalgal abundance (e.g. Underwood, 1984a; Fuji et al., 1991; Hill and Hawkins, 1991; Jenkins et al., in press) and spatial variation over the vertical shore gradient (e.g. Aleem, 1950; Castenholz, 1963) have been attributed to intolerance by epilithic microalgae of the physiological stresses associated with emersion (e.g. Aleem 1950; Castenholz 1963). The pattern of microalgal abundance across the wave exposure gradient is not known. However, it has been assumed in some studies in north-west Europe, that microalgal abundance increases in shelter, possibly because of the protection from environmental stress provided by an overlying fucoid canopy (e.g. Della Santina et al., 1994).

It is likely that the pattern of microalgal abundance across the wave exposure gradient will have a direct impact on the growth rate of *P. vulgata*. A number of authors have demonstrated an increase in growth rate and maximal size on sheltered, fucoid dominated shores (Fischer-Piette, 1948; Jones, 1948; Ballantine, 1961). However, more recent work showed significantly higher growth rate on exposed shores (Jenkins, 1995). None of these studies measured food supply or controlled the potentially confounding factor of conspecific density, which is an important determinant of growth rate in *P. vulgata* (Lewis and Bowman, 1975). Limpet density clearly declines with increasing shelter but owing to variability in the cover of understory species, especially turf forming algae, the effective density of limpets per unit area of grazeable substrata over the wave exposure gradient varies at different locations (Jenkins et al., 1999). Variability in the food available to *P. vulgata* across the wave exposure gradient may be a function, not only of algal production rates and density of competitors, but also of the time available to forage. At exposed sites, heavy wave action can limit the activity of predators and grazers (Menge, 1978a,b). Although the foraging activity of *P. vulgata* has been studied extensively, little is known about the effect of wave action on foraging activity (but see Della Santina et al., 1994).

Despite acknowledgement of the importance of the microalgal film in intertidal community dynamics (see Raffaelli and Hawkins, 1996 for review), relatively few studies have integrated analysis of macrofaunal ecology with analysis of the microalgal

resource. Work on intra- and inter-specific competition in microphagous gastropods in Australia and South Africa has shown that the supply of microalgae can be limiting (Underwood, 1984b,c; Bosman and Hockey, 1988; Dye and White, 1991; Lasiak and White, 1993). Bosman and Hockey (1988) showed that limpet growth rates and biomass at six different sites were significantly correlated with rates of algal production. Despite numerous studies of population dynamics in *P. vulgata* in north-west Europe (Fischer-Piette, 1948; Jones, 1948; Ballantine, 1961; Lewis and Bowman, 1975; Bowman and Lewis, 1977; Thompson, 1980; Baxter, 1982; Bowman and Lewis, 1986), none have attempted to link population parameters with food supply.

The overall aim of this study was to determine the level of food supply, foraging activity and growth rate in an important intertidal species, *P. vulgata*, in two contrasting environments— sheltered and exposed rocky shores. In order to provide an insight into the effects of these different habitats, the confounding influence of limpet density must be removed. To achieve this, the density and length frequency of limpets on the sheltered shores, where density per unit area of grazeable substrate was higher, were manipulated to match those on exposed shores, and food supply, grazing activity and growth rate were determined. Growth rate was also measured in patches of natural density to confirm the importance of intraspecific competition in growth of this species. The abundance of the microalgal film, which forms the food supply for *P. vulgata*, was estimated in summer and winter in both environments, to test the hypothesis that where limpet densities are equivalent, microalgal abundance is higher on sheltered shores. Large-scale temporal and spatial variability in grazing activity of *P. vulgata* was assessed over a 13-month period on both sheltered and exposed shores, using the frequency of radula scrapes on wax surfaces to provide an index of grazing intensity (Thompson et al., 1997). We tested the hypothesis that limpet grazing activity is higher on sheltered shores where desiccation stress and risk of dislodgement from wave action is lower. In addition, the growth rate of marked *P. vulgata* individuals was determined at sheltered and exposed shores, with the aim of linking growth in an intertidal mollusc to its food supply and level of grazing activity.

2. Methods

2.1. Study sites

Four shores were chosen in the south of the Isle of Man, British Isles (Fig. 1) to represent the two extremes of exposure to wave action found in this area. The two exposed shores at Port St. Mary (A) and Derbyhaven (B) were dominated at mid tide level by a fucoid–barnacle mosaic described in detail by Hawkins (1981). The two sheltered shores (C and D) were dominated over the full tidal range by fucoids with the mid-shore covered in dense uninterrupted stands of *Ascophyllum nodosum* (L.) Le Jolis. Beneath this cover of *Ascophyllum*, the substratum was covered by a red algal turf within which patches of ‘bare’ substratum grazed by *P. vulgata* occurred. Observations made during high water using SCUBA and video, and during low water, showed limpets to be permanently restricted to these patches. These ‘bare’ patches consisted of a mosaic

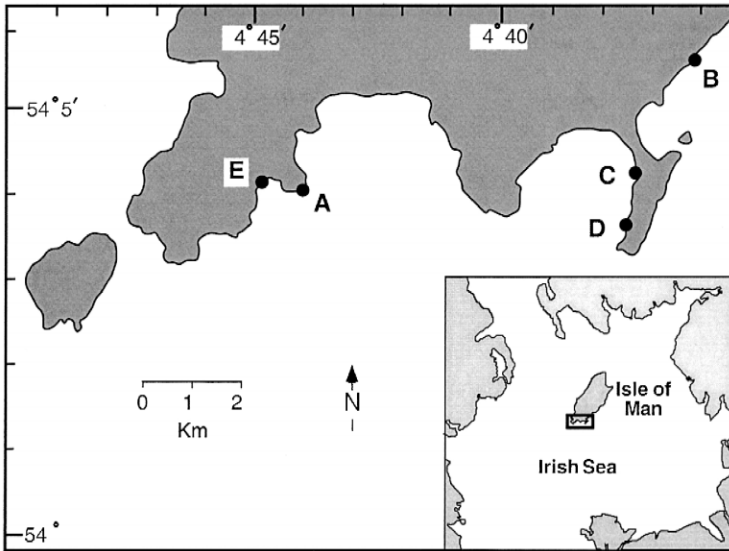


Fig. 1. Map showing the location of the Isle of Man and study sites. Exposed sites: (A) Port St. Mary, (B) Derbyhaven; sheltered sites: (C) Inner Langness, (D) Outer Langness; site of preliminary study: (E) Perwick Bay. Inset map shows the position of the Isle of Man in the Irish Sea; the black rectangle depicts the area covered by the main map.

of bare rock and encrusting algae, predominantly *Phymatolithon lenormandii*, and will subsequently be referred to as 'bare substratum'. For a full description of the sheltered shores studied, see Jenkins et al. (1999).

2.2. Experimental design

At both exposed shores, six well drained 2×2 m plots, at least 10 m apart, were selected at mid-tide level (Port St. Mary, 2.7–4.0 m above LAT; Derbyhaven, 2.65–3.9 m above LAT). Areas with a high density of barnacles and/or fucoids were avoided. At both sheltered shores, six patches of limpets of between 0.2 and 1.25 m^2 in area were selected beneath the dense *Ascophyllum* canopy at mid-tide level (inner Langness 3.0–4.2 m above LAT; outer Langness 2.8–4 m above LAT). The density and length frequency of limpets at all selected plots and patches were determined. Density was higher in the sheltered shore patches, and thus, the limpet population in each patch could be manipulated to closely resemble the density and length frequency of the exposed shore limpet population.

The proportion of limpets in each 10-mm size class over 15 mm in length was calculated for all exposed shore plots, and mean values determined. In each sheltered shore patch, these mean values were used to determine the number of limpets in each size class needed. Those sheltered shore patches where the size distribution did not allow manipulation to the correct size frequency were rejected, and a new patch selected. Limpets were removed from patches to obtain the correct size distribution and

density. The cryptic nature of juvenile limpets (< 15-mm length) meant manipulation to equivalent densities at all shores was very difficult. Therefore, this size class was removed from all plots at the start of the experiment and new recruits were removed at subsequent sampling dates. The density and population structure of limpets in all plots on both sheltered and exposed shores were assessed at three monthly intervals. Rate of loss of limpets was low and equivalent among shores over the study period. No attempts were made to replace lost limpets, owing to the difficulty of transplanting this species (pers obs). Thus, over the period of study, densities declined by approximately 15% but the overall population structure at all shores remained equivalent. In addition to the manipulated patches, six further patches were selected at both sheltered shores where limpet density was not manipulated.

2.3. Sampling

The grazing activity of *P. vulgata* at all four shores was assessed using the method developed by Thompson et al. (1997), which relies on the distinctive marks made by the feeding apparatus of marine molluscan herbivores. These grazing marks can be recorded on discs of wax placed into pre-formed holes in the rock surface, and grazing activity quantified by assessing the area of wax surface scraped during a given time. In the centre of each plot of the exposed shores, an array of nine equally spaced holes was drilled over an area just less than 1 m². The positioning of wax discs in this way ensured they were within the grazing range of *P. vulgata* from inside the 2 × 2 m plot, but were unlikely to be influenced greatly from those outside. In the manipulated patches of the sheltered shores with a minimum area of 0.75 m², nine holes were drilled, while in smaller patches, between five and nine holes were drilled to obtain a similar hole spacing. For details on the preparation of holes and of wax discs, see Thompson et al. (1997). From November 1997 to November 1998, at approximately monthly intervals, wax discs were placed in the prepared holes and retrieved 14 days later. Discs were examined under a binocular microscope, using an eyepiece graticule with 25 dots regularly spaced over a circular area. Grazing marks of limpets were recognized from the description of Thompson et al. (1997), and the area covered by such marks on each disc estimated by using the graticule dots as 'point intercepts'.

Previous work had shown that the occurrence of grazing marks from grazers other than *P. vulgata* on wax discs, placed on the exposed shores studied, was highly infrequent (Thompson, 1996). In north-west Europe, the density of non-limpet grazers in the mid-shore intertidal zone increases with shelter from wave action (Moyses and Nelson-Smith, 1963). Thus, to give an indication of the likelihood of grazing marks from grazers other than *P. vulgata* occurring on wax discs placed on sheltered shores, preliminary work was undertaken at a sheltered site, Perwick Bay (Fig. 1, site E). Six patches of limpets were selected at mid-tide level, and at three of these patches, all limpets were removed. Nine wax discs were deployed in each patch for a period of 14 days. Analysis of wax discs from patches with no limpets showed no sign of any grazing marks.

The growth of *P. vulgata* was assessed at all four shores by monitoring the increase in shell length of marked individuals over a period of approximately 1 year. This was

carried out at both manipulated and non-manipulated patches. At each plot or patch, between 10 and 20 limpets with a minimum shell length of 20 mm were labeled. Two small areas of shell were carefully filed smooth and micro-marker number labels fixed in position using superglue. Two micro-markers were attached to each limpet to allow for loss. At intervals of approximately 3 months, limpets were relocated and lost numbers re-applied. In order to relate shell length to biomass, 100 limpets were taken from mid-tide level at one exposed (Port St. Mary) and one sheltered (inner Langness) shore. The shell lengths were measured and dry weight of the body (including the shell) was determined by drying at 60°C until constant weight was obtained.

The abundance of the microalgal film was determined using chlorophyll *a* as an index of standing crop at one exposed shore (Port St. Mary) and one sheltered shore (inner Langness). Only the patches with manipulated densities of limpets were sampled at inner Langness. Two sampling dates were chosen at random from within each of two seasons, summer (June–August 1998) and winter (December 1998–March 1999). Three chips of rock with a minimum surface area of 4 cm² were taken randomly using a hammer and fine chisel (blade size, 1–2 cm) from within the area of each plot and patch. Barnacle and algal (including lithothamnion) encrusted rock was avoided. This amount of rock represented only 0.1% of exposed shore plots and between 0.4% and 2.4% of patches on sheltered shores over the whole year of sampling. The level of chlorophyll *a* in each sample was estimated using the method for rock substrata described by Thompson et al. (1999). Samples were initially washed and hydrated in filtered sea water. Extraction was made using cold methanol over a period of between 5 and 24 h and absorbance of the resulting solution determined at 665 and 750 nm. The surface area of each rock sample was determined by image analysis and the level of chlorophyll *a* per unit area of rock surface calculated using the following equation:

$$\text{Chlorophyll } a \text{ concentration } \mu\text{g cm}^{-2} = \frac{13.0 \times \overset{\circ}{A}665v}{dV}$$

where $\overset{\circ}{A}665$ = net absorbance of solution at 665 nm, v = volume of solution (ml), d = path length of cell (cm), V = surface area of sample (cm²).

2.4. Data analysis

Data were analysed, where possible, using ANOVA. Prior to using ANOVA, Cochran's test (Winer, 1971) was used to test for heterogeneity of variance. Multiple comparisons of levels within significant factors were made using Student Newman Keuls (SNK) tests.

For limpet growth rates, data from each individual patch or plot were used to construct a Ford–Walford plot of initial limpet length against the growth increment over 1 year. This enabled an estimate to be made of the growth increment for a standard limpet of initial length 35 mm for each patch or plot. These data were then analysed using ANOVA. In one patch on each sheltered shore, there were insufficient limpets (< 10) at the end of the experimental period to accurately estimate growth. Thus, the number of replicate plots on the exposed shores was randomly reduced to five to match the five replicates on the sheltered shores.

3. Results

3.1. Limpet grazing activity

The seasonal pattern of grazing activity of *P. vulgata* differed over the wave exposure gradient (Fig. 2). On the two exposed shores studied, there were marked seasonal changes in the level of limpet grazing activity, which were on the whole consistent between shores. Grazing activity was markedly depressed during late winter/early spring and for a period at the end of the summer. On the sheltered shores, there was no obvious seasonal pattern and the two shores showed little consistency. A formal comparison of grazing levels between seasons was not possible owing to the lack of independence between observations over time.

A comparison of total grazing effort between exposed and sheltered shores was made by taking an average value for each of the six plots on each shore over the 13-month experimental period (November 1997–November 1998). Grazing activity was signifi-

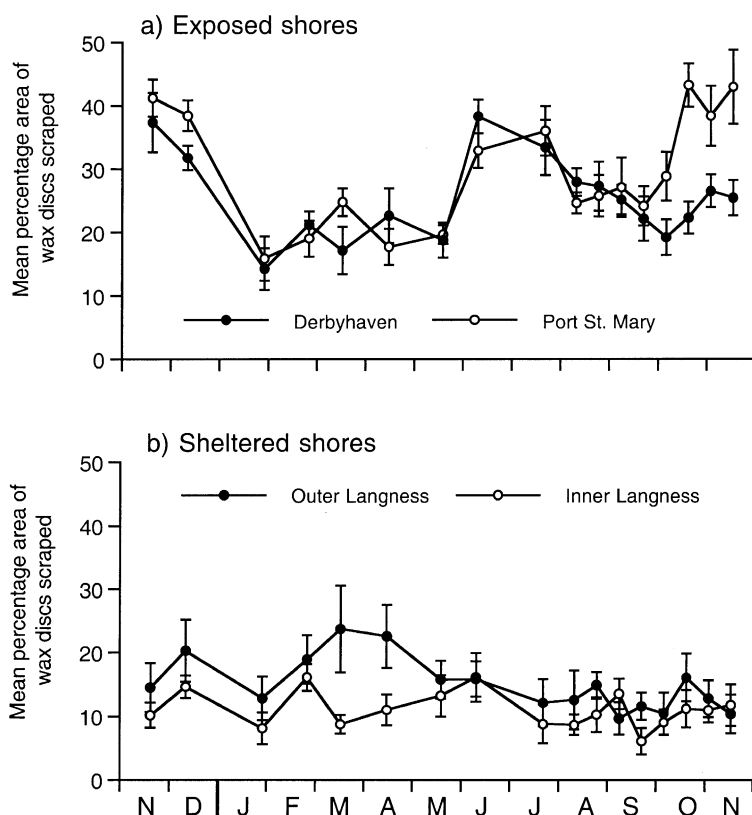


Fig. 2. Pattern of grazing activity in *P. vulgata* over a 13-month period at mid-tide level of two sheltered and two exposed rocky shores. Error bars = ± 1 SE.

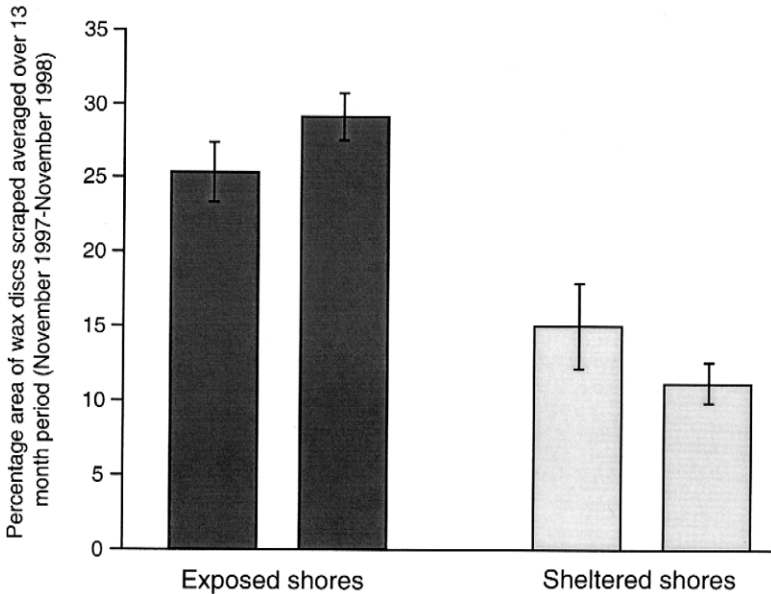


Fig. 3. Mean monthly grazing activity *P. vulgata* averaged over a 13-month period at mid-tide level of two sheltered and two exposed rocky shores. Error bars = ± 1 SE.

cantly greater at the exposed sites (Fig. 3, Table 1) with over twice the area of wax discs scraped by limpet radulae.

In order to examine variability at smaller spatial scales, four sampling dates were selected at random. At each date, analysis of variance was used to test differences due to the effect of exposure and the spatial scales of shore and plot. At one date (November 1997), data were heterogenous even after transformation, and thus results should be treated with caution. From the mean squares estimates, ANOVA allows a quantitative measure of the variation associated with each factor in the analysis, and thus allows determination of variability among individual replicate wax discs. Components of variation were calculated for random factors only using the hierarchical model described by Winer (1971). The fixed factor exposure was not included in this analysis owing to the illogicality of comparisons between fixed and random variance components (Underwood, 1997).

Table 1

ANOVA of *P. vulgata* grazing activity averaged over a 13-month period (November 1997–November 1998) on two exposed and two sheltered shores

Source	df	MS	F	P	F test denominator
Exposure	1	1193.4	27.8	< 0.05	Shore (Exposure)
Shore (Exposure)	2	42.9	1.7	< 0.2	Residual
Residual	20	24.7			

$C = 0.498$, $P > 0.05$.

Table 2
ANOVA of *P. vulgata* grazing activity at four dates throughout the experimental period

	Source	df	MS	F	P	Variance component	%variance component
November 1997; $C = 0.1468$, $P < 0.05$	Exposure	1	27338.11	115.54	< 0.01		
	Shore (Exposure)	2	236.61	0.44	> 0.6	0 ^a	0 ^a
	Plot (Shore (Exposure))	20	535.23	2.14	< 0.01	40.68	14.0
	Residual	144	250.47			250.47	86.0
April 1998; $C = 0.1184$, $P > 0.05$	Exposure	1	402.80	0.29	> 0.6		
	Shore (Exposure)	2	1402.18	2.44	> 0.1	19.68	7.6
	Plot (Shore (Exposure))	20	575.83	3.17	< 0.001	56.34	21.9
	Residual	144	181.47			181.47	70.5
July 1998; $C = 0.1079$; $P > 0.05$	Exposure	1	28393.80	87.17	< 0.05		
	Shore (Exposure)	2	325.75	0.56	> 0.5	0 ^a	0 ^a
	Plot (Shore (Exposure))	20	579.80	1.88	< 0.05	38.67	11.1
	Residual	144	309.13			309.13	88.9
September 1998; $C = 0.1052$; $P > 0.05$	Exposure	1	9638.94	25.85	< 0.05		
	Shore (Exposure)	2	372.82	1.02	> 0.3	0.20	0.1
	Plot (Shore (Exposure))	20	364.44	1.43	> 0.1	15.67	5.8
	Residual	144	254.78			254.78	94.1

Owing to occasional losses in the field, the number of wax disc replicates was randomly reduced to seven at all dates.

^aNegative estimates were set to zero.

At three of the four dates, grazing activity was significantly greater on exposed shores (Table 2). There was no significant effect of the spatial scale of shore at any date and of the three spatial scales, shore, plot and replicate wax discs, differences between shores contributed by far the least to overall variability (Table 2). There were significant

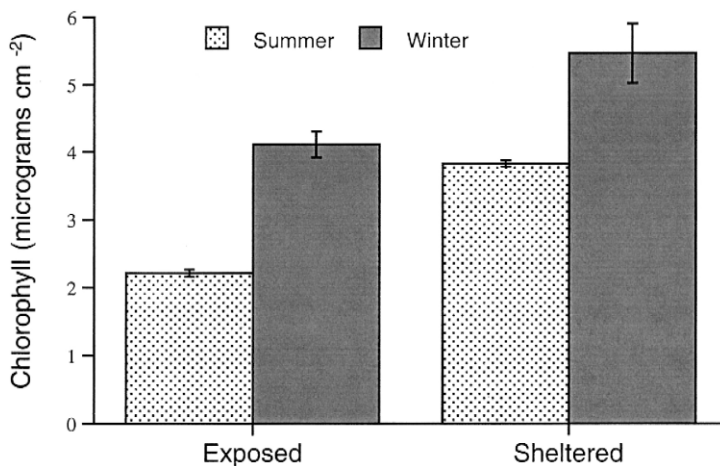


Fig. 4. Mean concentration of chlorophyll *a* on rock substrata from two sampling dates in summer and winter on one sheltered and one exposed rocky shore. Error bars = ± 1 SE.

Table 3

ANOVA of chlorophyll *a* levels on rock substrata at mid-tide level of an exposed and sheltered shore

Source	df	MS	F	P	F test denominator
Shore	1	26.30	140.03	< 0.01	Shore × Date (Season)
Season	1	37.50	30.67	< 0.05	Date (Season)
Date (Season)	2	1.22	0.94	> 0.3	Residual
Shore × Season	1	0.21	1.11	> 0.4	Shore × Date (Season)
Shore × Date (Season)	2	0.19	0.15	> 0.8	Residual
Residual	40	1.30			

$C = 0.2576$, $P > 0.05$.

differences among plots at all four dates and these differences accounted for between 6% and 22% of variability. By far, the most variability (between 71% and 94%) was a result of differences among individual wax discs. This indicates that over short time scales, there are substantial differences in the degree to which the rock substrate is grazed over small spatial scales (10s of cm).

3.2. Microalgal abundance

Unlike the other factors measured, the analysis of microalgal food supply was only carried out at one shore for each exposure level, and thus conclusions regarding the general influence of exposure on microalgal abundance should be treated with caution. Microalgal abundance, measured in plots with equivalent limpet densities, was signifi-

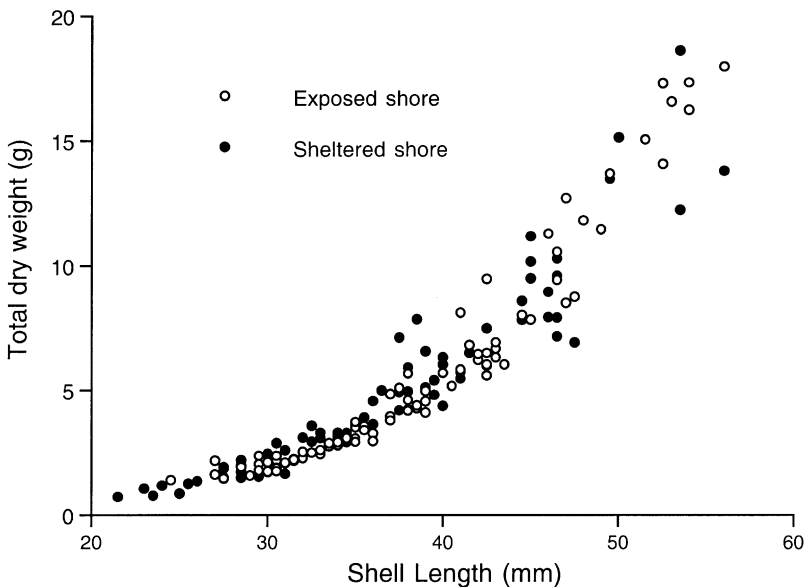


Fig. 5. Relationship between shell length and total dry weight of *P. vulgata* from one exposed (Port St. Mary) and one sheltered (Inner Langness) shore.

cantly greater on the sheltered compared to the exposed shore (Fig. 4, Table 3). Averaged over the two seasons, summer and winter, there was 47% greater abundance of chlorophyll on the sheltered shore. Season had a significant effect on chlorophyll levels with greater abundance in the winter compared to the summer on both shores. The effect of season was consistent over both shores with a non-significant interaction between the two factors (Table 3).

3.3. Limpet growth

There was no difference in the relationship between limpet shell length and biomass (measured as the total dry weight of shell and soft body parts) between the exposed and sheltered shore sampled (Fig. 5). Therefore, it was assumed that change in limpet shell

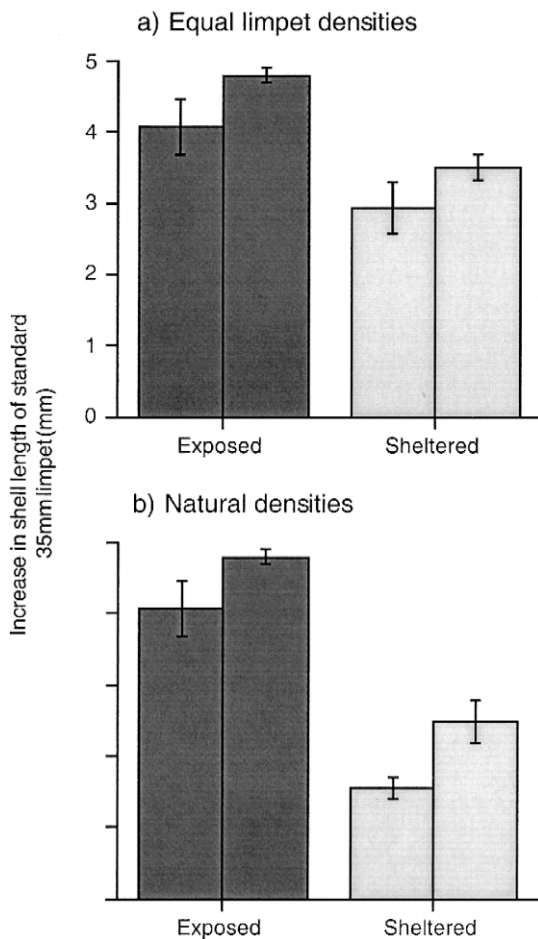


Fig. 6. Mean growth, measured as increase in shell length, of *P. vulgata* from two exposed and two sheltered shores. Increase in shell length of a 'standard' 35-mm limpet extracted from a Ford–Walford plot for each replicate. Error bars = ± 1 SE. (a) Comparisons of growth in manipulated populations with equal densities. (b) Comparisons of growth in non-manipulated populations with natural densities.

Table 4

ANOVA of growth (increase in shell length) in populations of *P. vulgata* from exposed and sheltered shores

Source	df	MS	F	P	F test denominator
<i>(a) Manipulated populations of equal density; C = 0.467, P > 0.05</i>					
Exposure	1	7.57	7.08	> 0.1	Shore (Exposure)
Shore (Exposure)	2	1.07	2.57	> 0.1	Residual
Residual	16	0.42			
<i>(b) Natural non-manipulated populations; C = 0.562, P > 0.05</i>					
Exposure	1	29.28	17.16	< 0.06	Shore (Exposure)
Shore (Exposure)	2	1.71	4.94	< 0.03	Residual
Residual	16	0.35			
SNK test for Shore (Exposure)					
SE = 0.2629					
Exposed: shore 1 v shore 2 NS					
Sheltered: shore 1 v shore 2 S					

length was a consistent measure of growth in *P. vulgata* across the wave exposure gradient. Ford–Walford plots, of initial shell length against shell length increase over 1 year, were plotted for all plots/patches. For all plots, there were between 10 and 20 limpets. The increase in shell length for a standard 35-mm limpet was extracted from all plots.

There was no significant effect of exposure on limpet growth rates when limpet density and population structure were equivalent (Fig. 6, Table 4). In addition, there was no difference between replicate shores within each level of exposure (Table 4). For the comparison between sheltered and exposed shores at natural non-manipulated densities, there was more variability between individual shores, indicated by the significant effect of shore (exposure). This was a result of a difference between the two replicate sheltered shores (Table 4(b)). The mean growth rate of the standard 35-mm limpet at natural densities on the sheltered shores was only 2 mm/year compared to 4.4 mm/year at the exposed shores. This difference was just insignificant at the 5% level (Table 4(b), $P < 0.06$).

Table 5

ANOVA of growth (increase in shell length) in populations of *P. vulgata* of differing density on sheltered shores

Source	df	MS	F	P	F test denominator
Density	1	7.08	21.07	< 0.001	Pooled data
Shore	1	2.81	8.37	< 0.02	Pooled data
Density × Shore	1	0.14	0.42	> 0.5	Residual
Residual	16	0.35			
Pooled data	17	0.34			

NB Density × Shore was non-significant ($P > 0.25$) and was thus pooled with the residual to increase the power of the test for density.

$C = 0.472$ $P > 0.05$.

Comparison between manipulated and non-manipulated patches on the two sheltered shores allows determination of the effect of limpet density on growth rates. The density of limpets over 15 mm in length in manipulated patches was standardised at 25 m^{-2} , with little variability between individual patches. In contrast, the patches selected as natural density showed great variability, with a range of densities of limpets over 15 mm length from 35–84 m^{-2} (mean = 65 m^{-2}) at inner Langness, and a range of 40–83 m^{-2} (mean = 72 m^{-2}) at outer Langness. Mean growth rate of limpets in manipulated low density patches was significantly greater than in non-manipulated high density patches (Fig. 6, Table 5). There was also a significant difference between the two replicate sheltered shores.

4. Discussion

The standing stock of microalgae, measured as the concentration of chlorophyll *a* on the substratum, was used as an estimate of food supply for *P. vulgata*. Estimates of the availability of food for intertidal grazers should ideally be based on the rate of production of microalgae, in addition to estimates of standing crop (Underwood, 1984a). Unfortunately, there are serious difficulties in accurately assessing epilithic microalgal production in the field (see Jenkins et al., in press, for discussion), and hence estimation of standing crop was considered a more reliable measure of limpet food supply.

Microalgal standing crop showed a seasonal pattern consistent with previous studies (Aleem, 1950; Nicotri, 1977; Underwood, 1984a; MacLulich, 1987; Fuji et al., 1991; Hill and Hawkins, 1991; Thompson, 1996); chlorophyll *a* levels were significantly higher in winter compared to summer. This pattern was consistent over both the exposed and sheltered shore studied. Thus, the seasonal pattern of microalgal abundance was the same, irrespective of the level of wave action and the cover of furoid macroalgae. Although the seasonal pattern was the same, microalgal abundance, averaged over both winter and summer, was nearly 50% greater on the sheltered compared to the exposed shore when limpet density was equivalent. There are a number of factors which may account for this observation. Reduced levels of grazing activity, amelioration of physical extremes by the furoid canopy, and reduced levels of wave action, may all be important. The physiological stresses associated with insolation, desiccation, and high temperatures, experienced by epilithic microalgae during periods of emersion, have been proposed as one of the main limiting factors to microalgal abundance (e.g. Aleem, 1950; Castenholz, 1963). It is clear that desiccation stress will be far lower at the substratum on sheltered shores. In north-west Europe, such shores are dominated by furoid macroalgae (Lewis, 1964), which protects the substratum from direct sunlight during low water, and hence maintains a relatively damp cool environment. Interestingly, no effect of furoid cover on microalgal abundance was found by Hill and Hawkins (1991) on exposed shores, although this might be explained by the confounding effect of limpet density. Although furoid cover may be important in enhancing microalgal abundance on sheltered shores, it seems unlikely it is the sole cause, since this effect would occur primarily in the summer. However, the difference between exposed and sheltered shores was consistent between seasons.

Differences in the level of grazing activity of *P. vulgata* on exposed and sheltered shores could be the cause of the distinct difference in microalgal abundance. The level of grazing activity on the sheltered shores, averaged over a 13-month period, was less than half of that found at the exposed sites. Lower levels of grazing activity on sheltered shores are likely to allow levels of microalgal standing stock to increase. However, it could also be argued that lower levels of grazing activity on sheltered shores are a result of higher food supply. It is not possible from this study to determine if reduced levels of grazing activity on sheltered shores are a cause of, or an effect of, the higher microalgal abundance. Evans and Williams (1991) developed a predictive model of foraging in *P. vulgata*, which suggested that limpets do not forage to maximise energetic gain but to minimise the time spent away from the home scar. During foraging periods, limpets are more vulnerable to predators and desiccation stress. Given this argument, it seems likely that the higher grazing activity on exposed shores is caused by lower levels of food. This was the conclusion of Della Santina et al. (1994), who showed that on each foraging excursion, *P. vulgata* spent a longer period away from the home scar on an exposed compared to a sheltered shore. This conclusion was based on an assumption of higher food supply on the sheltered shore; microalgal abundance was not measured.

The direct effect of wave action on foraging in *P. vulgata* is not known. Hawkins and Hartnoll (1982) noted the cessation of foraging in *P. vulgata* while awash, and postulated that risk of dislodgement was the cause. *P. vulgata* forages predominantly during daytime high water on the exposed shores studied (Hartnoll and Wright, 1977; personal communication R.C. Thompson), and thus could be at potential risk of dislodgement if foraging during high wave action. The higher levels of foraging activity on the exposed shores studied, clearly show that in the long term at least, higher levels of wave action did not inhibit foraging in *P. vulgata*. This does not preclude the inhibition of foraging by heavy wave action over short time scales. Occasional inhibition of foraging is unlikely to limit the average yearly foraging activity. This is especially true in an area such as the Irish Sea, which due to its enclosed nature, is not subject to the continuous swell of the Atlantic.

The growth rate of *P. vulgata* showed no significant difference between exposed and sheltered shores when at equivalent densities, despite a higher level of food supply in shelter. The absence of elevated growth rates in sheltered sites may be a result of the low level of grazing activity observed there. These observations provide support for the theoretical predictions of Evans and Williams (1991), that the foraging strategy of *P. vulgata* is based on minimising the time away from the home scar, so as to minimise mortality, rather than maximising energetic gain. It is not clear how the risk of mortality during foraging changes over the wave exposure gradient. The level of predation by birds, which can be an important source of mortality in *P. vulgata* (Coleman et al., 1999), is probably lower on sheltered shores owing to the dense cover of fucoids but predation from crabs may increase owing to higher densities in shelter (Crothers, 1970).

At natural densities, the mean growth rate of a standard 35-mm limpet at the sheltered sites was only 2 mm/year, compared to 4.4 mm/year at the exposed sites. These data clearly show that the general assumption of enhanced growth rates on sheltered shores is not universal. The overall density of *P. vulgata* declines as shelter increases (Fischer-Piette, 1948; Jones, 1948; Southward, 1953; Ballantine, 1961; Lewis,

1964; Thompson, 1980). However, at mid-tide level of many sheltered shores, there is a reduction in the area of free space on which limpets can graze owing to an increase in turfing algae (Lewis, 1964; Jenkins et al., 1999). On the shores studied, this results in an actual increase in density of limpets per unit area of grazeable substrate. Comparison of growth rate in sheltered shore limpets, from manipulated low density patches and non-manipulated high density patches, further demonstrates the importance of conspecific density and intraspecific competition in *P. vulgata*. The growth rate in low density patches was significantly higher.

In summary, in populations of *P. vulgata* with similar density and size structure, there was no difference in growth rate between sheltered and exposed shores. However, food supply was much higher and grazing activity much lower in sheltered than in exposed conditions. Whether the higher level of microalgal standing stock in shelter was a result of low grazing pressure, or whether a high food supply allowed individuals to graze less, needs to be ascertained in future manipulative experiments.

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