Spatial structure on moderately exposed rocky shores: patch scales and the interactions between limpets and algae

Mark P. Johnson¹,*, Michael T. Burrows², Richard G. Hartnoll³, Stephen J. Hawkins¹

¹School of Biological Sciences, Division of Biodiversity and Ecology, University of Southampton, Southampton SO16 7PX, United Kingdom
²Dunstaffnage Marine Laboratory, PO Box 3, Oban, Argyll PA34 4AD, United Kingdom
³Port Erin Marine Laboratory, Port Erin, Isle of Man IM9 6JA, United Kingdom

ABSTRACT: The spatial pattern of limpet grazing has been previously hypothesised to drive a mosaic of algal patches on moderately exposed shores in the northeast Atlantic. The presence of differently aged algal patches and spatial effects associated with limpets were tested for using spatially referenced data sets. Algal and limpet occurrences in 0.01 m² cells were recorded in a series of 25 m² quadrats on shores on the Isle of Man. All sites showed small-scale spatial autocorrelation for limpets and mature and juvenile algae. Hence the sites surveyed had an uneven distribution of limpets superimposed on a mosaic of differently aged patches of algae. The local density of limpets was related to the probability of a cell containing juvenile algae in 7 of the 10 quadrats surveyed. Where they had an effect, limpets generally reduced the probability of juvenile algae being recorded locally, as would be predicted by the grazer-driven mosaic hypothesis.

KEY WORDS: Limpets, Algae, Spatial statistics, Mosaic, Grazing

INTRODUCTION

Understanding the generation of pattern across different scales can be considered as the central problem in ecology (Levin 1992). On rocky shores, pattern is often discussed in terms of patchiness, where patches are generated by spatial variation in processes such as physical disturbance (Paine & Levin 1981, Sousa 1985), settlement and recruitment (Caffey 1985, Vadas et al. 1992), grazing (Hawkins & Hartnoll 1983a, Jernakoff 1983), and predation (Fairweather 1988). Given the presence of spatial pattern, it is ironic that well-designed field experiments must seek to avoid any small-scale spatial dependencies between replicates (Cressie 1993, Underwood 1997). If experiments are to be used as models of ecosystem function, some definition of the scales at which patch generating processes operate is necessary. Statistics which summarise the dependencies in spatially referenced data sets are valuable in this context (Ross et al. 1992). The use of spatial statistics clarifies decisions about the appropriate size of plots for experimentation or monitoring (Underwood & Chapman 1996). Certain hypotheses and tests only arise when spatially referenced data sets are considered (Thomson et al. 1996).

This study focuses on spatial aspects of rocky shore communities on the Isle of Man, in particular the algal mosaic (dominated by canopy-forming Fucus spp.) on the moderately exposed ledges at Port St. Mary (Jones 1948, Lodge 1948, Burrows & Lodge 1950, Southward 1956, 1964, Hartnoll & Hawkins 1980, Hawkins 1981a, b, 1983, Hawkins & Hartnoll 1983b). Time series records from a 2 x 1 m fixed quadrat at Port St. Mary show fluctuations between periods of high and low algal cover (Hartnoll & Hawkins 1985). This pattern has been interpreted, in the light of the previously
MATERIALS AND METHODS

Field data. A series of ten 25 m$^2$ quadrat surveys were made in the mid intertidal zone of 4 shores on the Isle of Man: Poyll Vaaish (U.K. Ordinance Survey grid reference: SC 239 682), Gansey (SC 215 680), Port St. Mary (SC 212 669) and Derbyhaven (SC 295 686). Four quadrats were marked out at Port St. Mary, separated by distances of at least 50 m. All the sites were level or gently sloping with no large cracks or boulders. These sources of local topographic variation were avoided as the hypothesis being tested refers to relatively level shores. The bedrock at Port St. Mary and Poyll Vaaish was smooth carboniferous limestone. In comparison, the quadrat at Gansey was marked out across an area of uneven slate. Small ridges of slate up to approximately 0.1 m in height gave the surface at Gansey a jagged appearance. The Derbyhaven site was on a concrete slab which forms part of the base of a gantry built for Ronaldsway airport.

Sites were surveyed either during spring or autumn 1996, with repeat surveys in spring 1997 at Gansey and 2 locations at Port St. Mary. A 0.5 × 0.5 m quadrat divided into 25 squares was progressively moved through each site to produce a map of 50 × 50 cells. Each 0.01 m$^2$ cell was coded for the presence or absence of algae. If algae were present, cells were divided further into ‘mature’ or ‘juvenile’ categories, a juvenile cell being one where juvenile algae were found in a cell without mature algae. Juveniles were distinguished from mature algae by frond lengths less than 0.1 m (Knight & Parke 1953) and the lack of reproductive structures. Mature Fucus individuals can grow up to approximately 0.6 m long (Knight & Parke 1953). The number of adult limpets (shell diameter >15 mm) in each 0.01 m$^2$ cell was also recorded. Limpets less than 15 mm in diameter were generally infrequent and are not considered further in the analysis presented here.

Data analysis. To characterise spatial autocorrelation at the different sites, the number of times that pairs of cells were recorded in the same state was used (join counts; Upton & Fingleton 1985). The neighbourhood for each cell included all orthogonal and diagonal connections at a specific distance. This is known as the queen’s definition of contiguity, by analogy with chess moves (Sokal & Oden 1978). If limpet or algal patches exist at a scale above 0.01 m$^2$ there will be positive spatial autocorrelation and higher than expected numbers of joins between cells. Comparing the degree of autocorrelation over successively greater distances can give an estimate of the average size of patches. When the distance between cells being compared exceeds the patch size, the number of joins will fall to a background level. Deviations from the average level of join...
counts in the absence of spatial autocorrelation can be assessed using \( z \), the standardised normal deviate (Sokal & Oden 1978, Upton & Fingleton 1985). The expected number of joins and the variance of this value were calculated using the equations presented in Upton & Fingleton (1985). The validity of using a normal approximation was confirmed using randomly generated 50 x 50 cell matrices. Join counts were compared with expected at 25 distances from the occupied cell. This involved a degree of multiple hypothesis testing, so the significance criterion for results was adjusted to reduce the chances of Type 1 error. Observed join counts were taken to be significantly more common than that expected in the absence of spatial autocorrelation only if \( z \) scores exceeded 3.0902 (a critical value of 5%, 2-tailed, in 25 tests). The magnitude of individual \( z \) scores can also be interpreted as a measure of how well-defined patches are.

An important part of the Hartnoll & Hawkins (1985) mosaic model is that aggregated limpets leave spaces between the clumps where Fucus escapes are more likely. This hypothesis was tested by examining the fits of a logistic regression (Sokal & Rohlf 1995) to the data. The fitted equation estimates the odds of an escape occurring as a function of the local limpet density:

\[
\ln \left( \frac{P_{\text{escape}}}{1 - P_{\text{escape}}} \right) = \beta_0 + \beta_1 L_0 + \beta_2 L_1 + \ldots + \beta_{N-1} L_N \tag{1}
\]

where \( L_0 \) is the number of limpets in the current cell, \( L_N \) is the total number of limpets in all cells at a distance \( N \) from the current cell, and \( \beta_0 \) to \( \beta_{N-1} \) are fitted parameters. Eq. (1) was fitted to data sets with increasing numbers of independent variables to the point where adding another distance class for limpets ceased to significantly improve the fit to data. This test for the improvement in fit with each addition of a new independent variable involved taking the difference between the log likelihood values multiplied by \(-2\) for each model. An improvement in fit was accepted if the difference in \(-2 \times \text{log likelihoods}\) exceeded the critical value of chi-squared with 1 degree of freedom. The statistically fitted models were only accepted if their overall 'goodness of fit' (sum of normalised squared residuals) did not exceed chi-squared at the 5% level (Norusis/SPSS Inc 1993).

RESULTS

Algal cover and the relative proportions of cells classified as mature or juvenile varied between quadrats (Fig. 1). Changes between successive surveys of the same quadrat imply that the patterns recorded are dynamic at an annual scale. Up to 80% of cells initially classified as juvenile were recorded as mature by the

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Fig. 1 Spatial variation of algal cover in the quadrats surveyed. Black cells: mature algae, grey cells: only juvenile algae, white cells: no algae. PSM a, b, c, and d: separate sites of quadrats at Port St Mary. PSM a and Gansey were surveyed in both 1996 and 1997.
Fig. 2. Spatial autocorrelations for cells containing (a) mature algae, (b) juvenile algae and (c) limpets. $z$ scores are calculated from the difference between the observed joint counts at the stated distance from an occupied cell and the expected number of joins in the absence of spatial autocorrelation. This difference is divided by the estimated standard deviation in the absence of autocorrelation and tested for significance using the normal distribution. Confidence limits are given by the horizontal dotted lines.
Join count statistics for cells occupied by limpets or mature or juvenile algae all showed significant spatial autocorrelation at the scale measured (Fig. 2). The tendency of all curves to stay within the confidence intervals at distances approaching 2.5 m suggests that there were few larger patterns evident in the 5 × 5 m quadrats, such as down shore gradients or regular spacing of patches. Limpet occurrences were autocorrelated over 1 or 2 cells whereas algal patch scales were more variable. The density of adult limpets recorded in surveys ranged from 8.04 to 38.36 m⁻², with the highest densities recorded in the Gansey quadrat. A maximum of 7 limpets were recorded in a single 0.01 m² cell.

The local density of limpets was estimated to affect the probability of juvenile algal cells being recorded in 7 of the 10 quadrats (Table 1). Limpets affected the chance of encountering juvenile algae at ranges up to 4 cells, depending on the site. The impact that a unit change in limpet number has on the odds of an escape can be seen by examining the effects of multiplication by the values in the column for exp(β). In all but 1 case (Port St. Mary b2), increasing the local density of limpets reduced the odds of finding juvenile algae. However, the standard error for the positive estimate of β is fairly large so the difference from a negative value may not be significant. The effect of limpets on the probability of a cell containing juvenile algae generally decreased with increasing distance class.

**DISCUSSION**

The analysis of spatially referenced data sets demonstrated patch structures of limpets and algae at all sites with scales between 0.1 and 2 m. The distinct autocorrelations of cells classed as mature or juvenile algae indicate that algal recruitment varied in space as well as time. Local limpet density was related to the probability of a cell containing juvenile algae in 7 of the 10 surveys. Where they had an impact, limpets generally reduced the probability of local algal recruitment.

The results support the hypothesis (Hartnoll & Hawkins 1985) of a role for limpet grazers in the generation of algal patch structure on moderately exposed rocky shores. However, the generality of such a grazer-driven mosaic is unclear. Limpets had an impact at some sites but not all. The proportion of
Table 1. Logistic regressions for the odds of a cell containing juvenile algae dependent on the sum of limpet numbers in 0.01 m² cells at different distances from the current cell (see Eq. 1 in text). The goodness of fit (sum of normalised squared residuals) is compared to chi-squared, with degrees of freedom dependent on the number of parameters fitted in the model. If the residuals from the fitted model are large the goodness of fit will exceed the critical value of chi-squared: ns: not significant at the 5% level.

<table>
<thead>
<tr>
<th>Site</th>
<th>Constant</th>
<th>Limpet distance class from current cell</th>
<th>Goodness of fit</th>
<th>df</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>3</td>
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<tr>
<td>PSM a1</td>
<td>(\beta)</td>
<td>0.7336</td>
<td>-0.5386</td>
<td>-0.1926</td>
<td>-0.1687</td>
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<td></td>
<td>SE of (\beta)</td>
<td>0.1733</td>
<td>0.1929</td>
<td>0.0512</td>
<td>0.0449</td>
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<td>Exp((\beta))</td>
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<td>0.1950</td>
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<td></td>
<td>Exp((\beta))</td>
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<tr>
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<td>Exp((\beta))</td>
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<td>0.7841</td>
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</table>

Limpets remaining faithful to a single home scar over the course of a year would certainly affect the spatial relationships with juvenile algae. The effect of limpets also varied in presence and extent from year to year at the same site. One potential reason for the absence of any detected limpet effect is that grazers may have been 'swamped' by an exceptionally good algal recruitment. This may have happened between the 2 surveys at Port St. Mary a, where 65% of cells not originally occupied by algae contained algae on the second survey.

It is not clear what site-specific factors could have been responsible for the differences between quadrats in the extent and degree of limpet effects on juvenile algal occurrence. Surface roughness may interfere with the grazing of limpets, reducing their local effects on algal recruitment probabilities (cf. Lubchenco 1983). The surface roughness of quadrats in this study was crudely estimated using the ratio of a length of a tape stretched out across a quadrat to the length of the same line after the tape had been pressed into surface irregularities. The average of 5 such ratios was used for each quadrat. This estimate of surface irregularity confirmed Gansey as the roughest site. Autocorrelations and limpet impacts at Gansey were generally amongst the weakest found. However, rank correlations of quadrat surface roughness with limpet grazing effects did not show any significant trends.

Statistics which examine the spatial dependencies in ecosystems represent methods of expanding and testing hypotheses which complement, but do not replace, more traditional experimental approaches. The additional information available from spatially referenced data sets are of interest in their own right. This study reinforces the view of considerable small-scale patchiness linked to the behaviour patterns of intertidal organisms (Underwood & Chapman 1996). Further work is required to distinguish between the roles of limpet grazing and other potential causes of algal patchiness such as microhabitat heterogeneity, other grazers, algae-algae interactions and algae-barnacle interactions.

Acknowledgements. This research was funded by a grant in the NERC special topic: 'Testable models of aquatic ecosystems' We thank Prof. R. N. Hughes and P. C. Watts for comments on an earlier draft of this manuscript. Simon Bray assisted with fieldwork in the autumn survey.

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Submitted: June 2, 1997; Accepted: October 21, 1997

Proofs received from author(s): December 2, 1997