



Provided by the author(s) and University of Galway in accordance with publisher policies. Please cite the published version when available.

Title	The persistent spatial patchiness of limpet grazing
Author(s)	Johnson, Mark P.
Publication Date	2008
Publication Information	Johnson M.P., Hanley M.E., Frost N.J., Mosley MWJ, and Hawkins S.J. 2008. The persistent spatial patchiness of limpet grazing. <i>Journal of Experimental Marine Biology and Ecology</i> . 365, 136 141.
Publisher	Elsevier
Link to publisher's version	http://dx.doi.org/doi:10.1016/j.jembe.2008.08.006
Item record	http://hdl.handle.net/10379/315
DOI	http://dx.doi.org/doi:10.1016/j.jembe.2008.08.006

Downloaded 2024-04-19T11:14:13Z

Some rights reserved. For more information, please see the item record link above.



The persistent spatial patchiness of limpet grazing

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24

Mark P. Johnson^{*a}, Michael E. Hanley^b, Natalie J. Frost^c, Matthew W. J. Mosley^d, and
Stephen J. Hawkins^e

^a*The Martin Ryan Marine Science Institute, National University of Ireland, Galway,
University Road, Galway, Ireland,*

^b*School of Biological Sciences, University of Plymouth, Portland Square, Drake Circus,
Plymouth, Devon, PL4 8AA, UK,*

^c*School of Biological Sciences, University of Southampton, Bassett Crescent East,
Southampton SO16 7PX, UK,*

^d*Port Erin Marine Laboratory, Port Erin, Isle of Man, IM9 6JA,*

^e*College of Natural Sciences, Memorial Building, Bangor University, Bangor, Gwynedd,
LL57 2UW, UK.*

*Corresponding Author

mark.p.johnson@nuigalway.ie

Phone: +353 (0) 91 492325

Fax: +353 (0) 91 525005

25 **Abstract**

26 The characteristic variability of grazing has potential consequences for intertidal productivity
27 and community structure, particularly as many of the underlying functional relationships are
28 thought to be non linear. As a first approximation, it can be hypothesised that grazing is
29 patchy over short time periods before a more uniform coverage is established over longer time
30 scales. This prediction is supported by relatively short term observations previously made of
31 limpet foraging. We used eight arrays of wax disks on each of four shores to test the
32 hypothesis that grazing is patchy in the short term, but that this pattern is lost as the pattern of
33 grazing averages out over longer time scales. Wax disk arrays were exposed for two weeks at
34 a time for a period of six weeks in 2001 and in 2002 using the same set of disk holes each
35 time. Grazing at the same disk location could therefore be measured over two weeks and over
36 longer periods by averaging successive deployments. We used all three successive
37 deployments to estimate the average grazing at each disk location over a six week period in
38 2001 and 2002. All six deployments were used to characterise the pattern of grazing at longer
39 time scales. The spatial pattern of grazing in arrays was summarized using semivariogram
40 analyses. For two-week deployments, the average standardized semivariance of grazing for
41 disks separated by 20 cm was less than one. This pattern implies spatial autocorrelation of
42 grazing at this scale. There was no support for the hypothesis that small scale patchiness in
43 grazing would disappear over time. The average strength of spatial autocorrelation increased
44 when data were integrated over longer periods. A preliminary analysis indicated that the
45 degree of autocorrelation within arrays increased with grazing intensity at short time scales.
46 Surface roughness disrupted autocorrelation of grazing over both short and long time scales.
47 The persistent patchiness of grazing is likely to have implications for biofilm productivity,
48 particularly on smoother shores.

49 *Keywords: Patella vulgata; semivariogram; spatial autocorrelation; topography; wax disk*

50 **1. Introduction**

51 Grazing has frequently been shown to be an important process in determining the biomass and
52 biodiversity of organisms on rocky shores (Hawkins and Hartnoll, 1983; Chapman, 1995).

53 The often-repeated experimental approach of excluding or removing grazers (e.g., Jones,
54 1948; Coleman et al., 2005) emphasizes a lowering of the mean intensity of grazing. The
55 movements of individual grazers, however, create spatial and temporal variability in grazing
56 intensity. This variability in the pattern of trophic interactions may affect the biomass of
57 consumed species independently of changes in the mean intensity of the interaction
58 (Navarrete, 1996; Benedetti-Cecchi et al., 2005).

59 The presence of spatial and/or temporal variance effects in a system reflects the
60 underlying functional relationships among components of that system. If a linear relationship
61 exists between two variables (say grazing intensity and algal biomass) spatial or temporal
62 variation in grazing will not affect the relationship between the average level of grazing and
63 the average density of algae: changes in algal biomass only reflect changes in the mean level
64 of grazing. Variance effects occur when the underlying responses of a system to a structuring
65 process such as grazing are non-linear (e.g., Jonsson et al., 2006). In a non-linear system,
66 deviations from the mean level of grazing do not have proportional effects on algal biomass,
67 so changes in the variance of grazing can change the average algal biomass even when the
68 average level of grazing is constant. One way of expressing this is to think of the way in
69 which a system responds to a local reduction in grazing. A patch where there is a low level of
70 grazing can be a 'window of opportunity' for algae to recruit and grow to a size where
71 removal by grazing is an order of magnitude slower, if it occurs at all (Lubchenco, 1983;
72 Davies et al. 2007). If this growth is not matched by an equivalent reduction in algal biomass
73 in areas of locally increased grazing, the effects of deviations from the mean level of grazing

74 are asymmetric and the net effect of variability in grazing will be an increased algal biomass
75 (Johnson et al., 1998a; Benedetti-Cecchi et al., 2005).

76 If a system of interacting species is well defined, the size of variance effects can be
77 predicted (on the basis of Jensen's inequality, Ruel and Ayres, 1999). Benedetti-Cecchi
78 (2005), however, argues that the inherent variability of ecological systems may restrict the
79 usefulness of Jensen's inequality as a predictive tool. Such potential difficulties in designing
80 and interpreting experimental investigations of variance effects emphasize how little is
81 actually known about the natural spatial and temporal variability of processes such as grazing
82 at the scale of individual foraging excursions. More recent descriptions of grazing variability
83 have tended to emphasise hierarchical patterns of spatial variability at scales from 10 m to
84 regional scales (Jenkins et al., 2005).

85 The clearest examples of spatial variation associated with individual feeding
86 excursions are generally associated with cases where consumers forage from a place of refuge
87 ('halo effects', e.g., Fairweather, 1988; Benedetti-Cecchi and Cinelli, 1995; Johnson et al.,
88 1998b). In the absence of a distinct refuge, however, it is not clear what the net result of a
89 number of foraging individuals will be. The alternatives are that either the average level of
90 grazing becomes spatially uniform at some point or that interactions between the resource and
91 the grazer maintain spatial heterogeneity in grazing effort. The large body of work on
92 individual foraging behaviour, particularly of limpets, allows some general predictions to be
93 made. Many species of limpets forage from a central home scar (Chelazzi et al., 1998).
94 Individual foraging bouts occur approximately once each day (Santini et al., 2004a) and are
95 likely to cause small-scale (approximately 20 cm) spatial autocorrelation of grazing, as
96 activity is concentrated within a section the foraging path (Chelazzi et al., 1994). A statistical
97 usage of autocorrelation is used here: describing the tendency for grazing activity in different
98 areas to be correlated. Small scale autocorrelation therefore implies that areas of relatively

99 high grazing are likely to be adjacent to other areas of relatively high grazing. This can also
100 be described as small scale (non-random) patchiness in grazing. Over longer periods of time,
101 however, the overall pattern of grazing may be relatively uniform due to the overlaying of
102 foraging paths from different limpets and the lack of directional bias in foraging excursions
103 (Chelazzi et al., 1998).

104 The topographic complexity of the shore is likely to modify the spatiotemporal pattern
105 of grazing. As previously mentioned, distinct physical refuges may create haloes of grazing or
106 predation. More generally, surface irregularities may disrupt foraging patterns, increasing the
107 complexity of individual grazing excursions on rougher surfaces (Little et al., 1988;
108 Erlandsson et al., 1999). These more elaborate foraging paths could reduce the spatial
109 patchiness of grazing. Alternatively, particular topographic features could focus grazing in
110 restricted areas during different foraging excursions (c.f., Matthiopoulos, 2003), leading to
111 increases in grazing patchiness on rougher shores.

112 Arrays of wax disks were used (Thompson et al., 1997) to examine the spatial and
113 temporal variability of grazing. This allowed a test of the hypothesis that the net effect of
114 overlaying successive foraging excursions is a relatively uniform spatial distribution of
115 grazing. By using successive deployments of disks we hoped to define the duration of the
116 ‘window of opportunity’ for algae to recruit in areas of relatively low grazing. Topographic
117 complexity was measured in all areas where disk arrays were laid out. These measurements
118 were used to identify any changes in the spatiotemporal pattern of grazing with surface
119 complexity.

120

121

122 2. Methods

123 Measurements of grazing activity were made in arrays of wax disks placed on four separate
124 shores. These shores were Poyll Vaaish (54°04' N, 4°41' W) and Port St Mary (54°04' N,
125 4°44' W) in the Isle of Man along with Wembury (50°18' N, 4°06' W) and Heybrook (50°19'
126 N, 4°07' W) in the southwest of England All four shores contained expanses of littoral rock
127 that differed in complexity from smooth to rough. Surface features included ridges formed by
128 erosion-resistant sedimentary layers, pits and crevices. Wave activity at all the shores was
129 moderate for British coasts. The shores can be considered as semi-exposed (Lewis, 1964;
130 Southward, 1956) with a midshore composed of limpets and barnacles with a patchy
131 distribution of brown macroalgae (mostly *Fucus vesiculosus* L.). Mid shore limpets in the Isle
132 of Man are *Patella vulgata* L., but *P. depressa* Pennant and *P. vulgata* coexist on shores in
133 southwest England (Jenkins et al., 2001). Removal and exclusion experiments have repeatedly
134 demonstrated the regulation of algal cover by limpet grazing on moderately exposed shores
135 (Jones 1948, Coleman et al., 2006). Other grazing gastropods on these shores are not thought
136 to have the same magnitudes of effects as limpets. In part this may reflect average population
137 densities. For example, *Littorina littorea* (L.) is often found at densities an order of magnitude
138 lower on moderately exposed British coasts compared to the north west Atlantic (Lubchenco,
139 1983; Norton et al., 1990).

140 Grazing intensity was recorded as the percentage of wax surface marked by the radula
141 scrapes of grazing limpets (Thompson et al., 1997). Disks are 14 mm in diameter and are set
142 into pre-formed holes in the shore. The technique has been validated in a study of limpet
143 grazing across Europe (Jenkins et al., 2001) and for grazers in Australia (Forrest et al., 2001).
144 Trials using video have established that *Patella vulgata* does not tend to alter behaviour when
145 encountering disks (> 80% of cases, Jenkins et al. 2001). To characterize the spatiotemporal
146 pattern of grazing, arrays of thirty-six disks were set out in evenly spaced square grids. Disks

147 were separated by 20 cm from each other in the arrays, as a previous spatial study indicated
148 that this was an appropriate scale for observing the effects of grazers (Johnson et al., 1997).
149 Following the recommendations of Thompson et al. (1997), wax disks were left out for 2
150 weeks at a time. This avoids any problems with variation in foraging activity associated with
151 the spring neap cycle. Disks were laid out for three successive 2 week deployments to
152 examine short term consistency in foraging. A 6 week long sequence of deployments was
153 repeated in May 2001 and February 2002. The design allows grazing to be integrated across
154 different time periods (Figure 1). The data are summarized by three different periods:
155 'Fortnightly' data calculate spatial statistics (see below) from individual two week
156 deployments and represent the average of six deployments overall. 'Six week' data average
157 grazing over three successive deployments before calculating spatial statistics. Six week
158 values for 2001 and 2002 were averaged per array for further analysis. The longest period of
159 integration ('all data') was to average the grazing at each disk position over all six
160 deployments before calculating spatial statistics.

161 Arrays were placed in four 'smooth' and four 'rough' areas in the mid-shore level at
162 each shore. These areas were randomly chosen from a larger number of areas initially
163 assessed as rough or smooth on each shore. This subjective positioning of arrays was intended
164 to provide a range of variable topographies within arrays at each shore. Surface topography
165 was subsequently quantified for each array by running a metal chain (link size 1.5 cm) across
166 the rock surface such that it conformed as closely as possible to all contours and crevices. The
167 chain link size is about the length of a juvenile limpet (Orton, 1928), so irregularities
168 measured at this scale are likely to affect the foraging paths of limpets. The ratio of chain
169 length to linear distance between the ends of the chain gives an index of surface complexity
170 (Luckhurst and Luckhurst, 1978). Chain length ratios have been found to correlate with other
171 measures of surface complexity, such as fractal dimensions (Frost et al., 2005). Chain length

172 measurements were repeated four times for each array to give an average ratio. On a
173 completely smooth surface the chain ratio will be one, with values greater than one indicating
174 increasing levels of complexity.

175 The strength and scale of spatial pattern in grazing was estimated by calculating
176 standardized semivariograms (Rossi et al., 1992). Distance was measured as the number of 20
177 cm steps between disks using rook's moves only (no diagonals). This produces an
178 omnidirectional variogram with 120 data pairs at the 20 cm lag and 200 pairs at the largest lag
179 presented (100 cm). In the presence of autocorrelation (small scale non random spatial
180 patchiness) the standardized semivariance will be lower than the overall variance, leading to
181 values below 1 at the smallest lags (20 cm between disks). If there is no consistent spatial
182 pattern, semivariograms stochastically fluctuate around the background variance (equal to one
183 in standardized semivariograms). Under the hypothesis that grazing is correlated at the scale
184 of individual foraging bouts, but becomes spatially random over long time scales, the
185 predicted pattern is for the standardized semivariance to be below one for the fortnightly
186 estimates rising to one when grazing is integrated across all data.

187 Inferential statistics are not traditionally applied to individual semivariograms. Unlike
188 many (single data set) uses of semivariograms, the current study generates a number of
189 replicated estimates of spatial dependence (standardized semivariances at lag 20 cm). This
190 allows conventional inferential statistics to be applied to this derived variable. Individual
191 semivariogram values were normally distributed, implying that averaging does not introduce
192 biases in the estimate of central tendency and that the use of simple inferential statistics is
193 valid.

194 There was little variation between regions or shores in the lag 20 cm semivariances.
195 Nested ANOVA (2 shores nested within 2 regions, variances were considered homogenous
196 following non-significant Bartlett's tests) suggested that most of the variation in semivariance

197 was within shores. There were no significant differences at the level of shore(region) or
198 region with a minimum of 85 % of the variance at the within shores level. Semivariance data
199 were therefore pooled for a regression-based analysis of array scale variables that may
200 influence the degree of autocorrelation in grazing intensity. Predictor variables in this analysis
201 included surface roughness (given the rationale presented in the introduction). Further
202 potential predictor variables were the overall level of grazing, the number of limpets and the
203 clumping of limpet home scars.

204 A number of arguments can be proposed *a priori* for the additional potential predictor
205 variables of grazing patchiness. For example, if grazing is infrequent, this reduces the scope
206 for an average grazing pattern to be defined through successive foraging excursions. An
207 ‘undersaturation’ of grazing may therefore prevent the loss of patchiness through averaging
208 out. The clumping of limpet home scars may influence the spatial pattern of grazing, if
209 proximity to conspecifics alters foraging behaviour. An index of the degree of limpet
210 aggregation was estimated from maps of limpet home scar locations around each wax disk
211 array during the February deployment (including limpets in a 20 cm buffer zone extending
212 beyond the edges of the disk array). Nearest neighbour statistics were calculated using the
213 average distance from one individual to the nearest neighbouring limpet, divided by the
214 expected distance based on a random distribution (Clark and Evans, 1954; including the
215 Donnelly (1978) correction for maps without a boundary strip). A Clark and Evans nearest
216 neighbour index of one implies a random distribution of limpets, with values below one
217 indicating a degree of aggregation. There were significant positive correlations between
218 limpet density (mean 138 m⁻², SE 15.4), roughness (mean 1.106, SE 0.0168) and nearest
219 neighbour statistics (mean 0.607, SE 0.0144). Hence arrays in areas with rougher surfaces
220 tended to have more limpets and these limpets were less aggregated than in smoother areas.
221 These variables were not, however, correlated with the average grazing per disk (mean 10.84

222 %, SE 0.965). The colinearity between potential predictor variables potentially complicates
223 statistical inference, but the results of an exploratory analysis are presented to indicate
224 variables that may influence the spatial pattern of grazing. This exploratory analysis used best
225 subsets regression to identify combinations of predictor variables that explained variation in
226 the semivariance at lags of 20 cm. The most informative regressions were identified on the
227 basis of maximum r^2 values (adjusted for degrees of freedom) and minimum Mallows Cp
228 scores (Quinn and Keough, 2002).

229

230 **3. Results**

231 Semivariograms for all combinations of time periods showed evidence for small scale
232 autocorrelation of grazing (Figure 2). For each of the three time periods, the average
233 standardized semivariance was significantly lower than 1 (1 sample t test, $p < 0.05$, $n = 32$).
234 Grazing was therefore patchy at lags of 20 cm. Spatial dependence was absent from the larger
235 lag distances, where the semivariances were close to one, the background level of variability.
236 The relative spatial dependence of grazing at small scales actually increased when integrating
237 data over longer time periods (although this increase was not significantly greater than zero,
238 paired t-test, mean difference = 0.03, $p > 0.05$). This is contrary to the hypothesis that
239 successive grazing bouts should smooth out the spatial pattern of grazing over time.

240 Variation among arrays in the patchiness of grazing was partially explained by the
241 predictor variables of average grazing and surface roughness (Table 1). On short time scales,
242 the best predictors of the size of the standardized lag 20 cm semivariance were grazing and a
243 combination of grazing and surface roughness. The stability of slope estimates in the fitted
244 models and relatively low Variance Inflation Factors indicate that the models in Table 1 are
245 not affected by colinearity in grazing and roughness. Higher average grazing reduced the lag
246 semivariance at small spatial scales (Figure 3). This can be interpreted as an indication that

247 patches were more sharply defined when an array had relatively high grazing. Arrays in
248 increasingly rougher areas had higher lag 20 cm semivariances. Hence rougher surfaces
249 appear to disrupt the processes leading to patchiness in grazing. This effect was significant in
250 fortnightly data and when all data were averaged across disks. Patterns for the six week
251 averaged data were consistent with the patterns in Table 1, but the individual regressions were
252 not significant.

253

254 **4. Discussion**

255 The results support a view of grazing as a characteristically patchy process (Adler et al. 2001).
256 Furthermore, this patchiness does not appear to ‘average out’ over time. The grazing
257 behaviour of limpets and probably also the features of the exploited resource cause persistent
258 patterns of high and low grazing at the 20 cm spatial scale. This persistent patchiness was not
259 expected given the existing information on foraging behaviour in limpets.

260 Surface roughness was associated with less distinct spatial patchiness of grazing.
261 Topographic irregularities did not appear to focus grazing consistently in particular areas. It
262 may be that the effect of topography reflects the disruption of individual foraging bouts as
263 limpets move around surface features. The patchiness of limpet grazing is probably linked to
264 home scar clumping so that the more dispersed home scars on rougher surfaces lead to a more
265 even pattern of grazing. This effect does not, however, seem to offer a full explanation as
266 home scars were still relatively clumped on rougher surfaces (the maximum nearest neighbour
267 statistic was 0.74) and nearest neighbour ratios were not particularly clear predictors of
268 grazing patchiness. The focusing of grazing into certain areas on smooth surfaces may reflect
269 previously unrecognised topographic cues, not identified by chain link methods of measuring
270 topography. For example, gentle depressions in the rock could act as foraging cues or as sites
271 of enhanced microalgal productivity.

272 The patterns of grazing activity can be considered as the net result of successive
273 individual foraging bouts or they may reflect behavioural interactions between foraging
274 individuals. Individuals following the mucus trails left by foraging conspecifics may reinforce
275 any established grazing patterns. Both Littorinids and limpets are thought to follow recent
276 trails (Della Santina et al., 1995; Edwards and Davies, 2002). The network of such trails could
277 create a small scale 'map' that concentrates grazing in particular areas. In smooth areas, where
278 individual foraging paths are less convoluted, the integrity of mucous trail networks may be
279 greater in comparison to rough surfaces. If this is the case, trail following could lead to more
280 spatially consistent foraging tracks on smooth surfaces.

281 The results are consistent with limpets following a marginal value strategy where the
282 resource is autocorrelated, as previously suggested by Santini et al. (2004b). Under this type
283 of strategy limpets return to the high (food) value areas and therefore maintain spatial
284 heterogeneity in grazing effort. However, both the available field data and the modelling
285 approach of Santini et al. (2004b) leave a number of areas unexplored. Little is known about
286 how grazing affects the productivity (as opposed to the biomass) of epilithic algae, so the
287 dynamics of resource renewal in grazed patches are poorly understood. Furthermore the
288 approach of Santini et al. (2004b) does not include the scope for interactions between
289 conspecifics, reflecting how little is known about how interactions among individuals shape
290 processes like grazing at the population level.

291 Studies of foraging by intertidal grazers have been criticized for inadequate replication
292 (Chapman, 2000). Limited observations of individual foraging excursions have suggested that
293 successive grazing bouts are spatially independent (e.g., Chelazzi et al., 1994) and that the
294 distribution of foragers can be random despite aggregated home scar locations (Coleman et
295 al., 2004). The results presented were used to summarize the spatial patterns of grazing over a
296 more extensive range of timescales than has been possible before. The results from wax disks

297 indicate that, not only was the small scale pattern of grazing not random, the degree of
298 patchiness tended to increase over time.

299 The patchiness of limpet grazing can change the structure and turnover of algal
300 canopies (Johnson et al., 1998a), leading to changes in macrophyte plant diversity and
301 biomass (c.f., Weber et al., 1998; Adler et al., 2001). The temporal and spatial autocorrelation
302 in grazing may also affect the composition and productivity of microalgal biofilms (Sommer,
303 2000). Both field and aquarium experiments suggest that grazing patchiness on time scales
304 equivalent to the wax disk exposures (between two and six weeks) is sufficient to generate
305 heterogeneity in the biofilm (Sommer, 2000; Thompson et al., 2004). These effects are most
306 clear in territorial limpets, where grazing is highly structured in space. For example, the high
307 degree of spatiotemporal organization of foraging by *Lottia gigantea* is associated with
308 'gardens' of enhanced microbial productivity (Stimson, 1973; Davies and Hawkins, 1998).
309 Given such influences on biofilms, it seems reasonable to suggest that differences in the
310 consistency of grazing will lead to changes in microbial community structure. Heterogeneity
311 in resources can also feed back into the structure of limpet populations, increasing intra-
312 individual variability in growth rates (Pfister and Peacor, 2003).

313 The observed patterns indicate that 'scaling-up' from individual foraging behaviour to
314 population-level grazing patterns is not necessarily straightforward. In the absence of models
315 of resource renewal including interactions between foraging limpets, there is no basis for
316 predicting the degree of patchiness, while the best existing model (a uniform grazing pattern
317 predicted on the basis of short term observations, see introduction) has been rejected. The
318 population-level approach leads to new hypotheses about grazers (e.g., the potential role of
319 trail following and subsequent 'gardening' on smooth surfaces) that may not have been
320 apparent from observations of individuals. Techniques analogous to the wax disk arrays can
321 be used to characterize the spatiotemporal 'fingerprint' of grazing in different systems and

322 with different consumers. Wider use of such techniques in experiments is the next step in
323 understanding how autocorrelation of foraging affects interactions between consumers and
324 how this process scales up to landscape and ecosystem processes, as predicted by simulation
325 models (Moloney and Levin, 1996).

326

327

328 **Acknowledgements**

329 Research funded by grant from the Natural Environment Research Council. L. Hanley
330 assisted with fieldwork. D. Cookson assisted with analysis of limpet spatial data.

331 **References**

- 332 Adler, P.B., Raff, D.A., Lauenroth, W.K., 2001. The effect of grazing on the spatial
333 heterogeneity of vegetation. *Oecologia*, 128, 465-479.
- 334 Benedetti-Cecchi, L., 2005. The importance of the variance around the mean effect size of
335 ecological processes: Reply. *Ecology* 86, 265-268.
- 336 Benedetti-Cecchi, L., Cinelli, F., 1995. Habitat heterogeneity, sea-urchin grazing and the
337 distribution of algae in littoral rock pools on the west coast of Italy (western
338 Mediterranean). *Mar. Ecol. Progr. Ser.* 126, 203-212.
- 339 Benedetti-Cecchi, L., Vaselli, S., Maggi, E., Bertocci, I. 2005. Interactive effects of spatial
340 variance and mean intensity of grazing on algal cover in rock pools. *Ecology* 86,
341 2212-2222.
- 342 Chapman, A.R.O., 1995. Functional ecology of furoid algae - 23 years of progress.
343 *Phycologia* 34, 1-32.
- 344 Chapman, M.G., 2000. Poor design of behavioural experiments gets poor results: examples
345 from intertidal habitats. *J. Exp. Mar. Biol. Ecol.* 250, 77-95.
- 346 Chelazzi, G., Santini, G., Parpagnoli, D., Della Santina, P., 1994. Coupling motographic and
347 sonographic recording to assess foraging behaviour of *Patella vulgata*. *J. Moll. Stud.*
348 60,123-128.
- 349 Chelazzi, G., Santini, G., Della Santina, P., 1998. Route selection in the foraging of *Patella*
350 *vulgata* (Mollusca:Gastropoda). *J. Mar. Biol. Ass. UK*, **78**,1223-1232.
- 351 Clarke, P.J., Evans, F.C. (1954) Distance to nearest neighbour as a measure of spatial
352 relationships in populations. *Ecology*, 35, 455-453.
- 353 Coleman, R.A., Underwood, A.J., Chapman, M.G., 2004. Absence of costs of foraging
354 excursions in relation to limpet aggregation. *J. Anim. Ecol.* 73, 577-584.

- 355 Coleman, R.A., Underwood, A.J., Benedetti-Cecchi, L., Aberg, P., Arenas, F., Arrontes, J.,
356 Castro, J., Hartnoll, R.G., Jenkins, S.R., Paula, J., Della Santina, P., Hawkins, S.J.,
357 2006. A continental scale evaluation of the role of limpet grazing on rocky shores.
358 *Oecologia* 147, 556-564.
- 359 Davies, A.J., Johnson, M.P., Maggs, C. A. 2007. Limpet grazing and the loss of *Ascophyllum*
360 canopies on decadal time scales. *Mar. Ecol. Progr.Ser.* 339,131-141.
- 361 Davies, M.S., Hawkins, S.J., 1998. Mucus from marine molluscs. *Adv. Mar. Biol.* 34, 1-71.
- 362 Della Santina, P., Santini, G., Chelazzi, G., 1995. Factors affecting variability of foraging
363 excursions in a population of the limpet *Patella vulgata* (mollusca, gastropoda). *Mar.*
364 *Biol.* 122, 265-270
- 365 Donnelly, K., 1978. Simulations to determine the variance and edge effect of total nearest
366 neighbor distance. In: I. Hodder (ed.) *Simulation Methods in Archaeology*. Cambridge
367 University Press, London, pp. 91-95.
- 368 Edwards, M., Davies, M.S., 2002. Functional and ecological aspects of the mucus trails of the
369 intertidal prosobranch gastropod *Littorina littorea*. *Mar. Ecol. Progr. Ser.* 239,129-
370 137.
- 371 Erlandsson, J., Kostylev, V., Williams, G.A., 1999. A field technique for estimating the
372 influence of surface complexity on movement tortuosity in the tropical limpet *Cellana*
373 *grata* Gould. *Ophelia* 50,215-224.
- 374 Fairweather, P.G., 1988. Predation creates haloes of bare space among prey on rocky
375 seashores in New South Wales. *Aust. J. Ecol.* 13, 401-409.
- 376 Forrest, R.E., Chapman, M.G., Underwood, A.J., 2001. Quantification of radular marks as a
377 method for estimating grazing of intertidal gastropods on rocky shores. *J. Exp. Mar.*
378 *Biol. Ecol.* 258, 155-171.

- 379 Frost, N.J., Burrows, M.T., Johnson, M.P., Hanley M.E., Hawkins S.J., 2005. Measuring
380 surface complexity in ecological studies. *Limnol. Oceanogr. Methods* 3, 203-210.
- 381 Hawkins, S.J., Hartnoll, R.G., 1983. Grazing of intertidal algae by marine invertebrates.
382 *Oceanogr. Mar. Biol. Ann.Rev.* 21 195–282.
- 383 Jenkins, S.R., Arenas, F., Arrontes, J., Bussell, J., Castro, J., Coleman, R.A., Hawkins, S.J.,
384 Kay, S., Martinez, B., Oliveros, J., Roberts, M.F., Sousa, S., Thompson, R.C.,
385 Hartnoll, R.G., 2001. European-scale analysis of seasonal variability in limpet grazing
386 activity and microalgal abundance. *Mar. Ecol. Progr. Ser.* 211, 193-203.
- 387 Jenkins, S.R., Coleman, R.A., Della Santina, P., Hawkins, S.J., Burrows, M.T., Hartnoll, R.G.
388 2005. Regional scale differences in the determinism of grazing effects in the rocky
389 intertidal. *Mar. Ecol. Progr. Ser.* 287, 77-86.
- 390 Johnson, M.P., Burrows, M.T., Hartnoll, R.G., Hawkins, S.J., 1997. Spatial structure on
391 moderately exposed rocky shores: patch scales and the interactions between limpets
392 and algae. *Mar. Ecol. Progr. Ser.* 160, 209-215.
- 393 Johnson, M.P., Burrows, M.T., Hawkins, S.J., 1998a. Individual based simulations of the
394 direct and indirect effects of limpets on a rocky shore *Fucus* mosaic. *Mar. Ecol. Progr.*
395 *Ser.* 169, 179-188.
- 396 Johnson, M.P., Hughes, R.N., Burrows, M.T., Hawkins, S.J. 1998b. Beyond the predation
397 halo: small scale gradients in barnacle populations affected by the relative refuge
398 value of crevices. *J. Exp. Mar. Biol. Ecol.* 231, 163-170.
- 399 Jones, N.S., 1948. Observations and experiments on the biology of *Patella vulgata* at Port St.
400 Mary, Isle of Man. *Proc. Trans. Liv. Biol. Soc.* 56, 60-77.
- 401 Jonsson, P.R., Granhag, L., Moschella, P.S., Aberg, P., Hawkins, S.J., Thompson, R.C., 2006.
402 Interactions between wave action and grazing control the distribution of intertidal
403 macroalgae. *Ecology* 87, 1169-1178.

- 404 Lewis, J.R., 1964. The Ecology of Rocky Shores. English Universities Press, London, UK.
- 405 Little C., Williams, G.A., Morrill, D., Perrins, J.M., Stirling, P., 1988. Foraging behaviour of
406 *Patella-vulgata* L in an Irish sea-lough. J. Exp. Mar. Biol. Ecol. 120, 1-21.
- 407 Lubchenco, J., 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity,
408 and plant escapes during succession. Ecology 64, 1116-1123.
- 409 Luckhurst, B.E., Luckhurst, K., 1978. Analysis of the influence of substrate variables on coral
410 reef fish communities. Mar. Biol. 49, 317-323.
- 411 Matthiopoulos, J., 2003. The use of space by animals as a function of accessibility and
412 preference. Ecol. Mod. 159, 239-268.
- 413 Moloney, K.A., Levin, S.A., 1996. The effects of disturbance architecture on landscape-level
414 population dynamics. Ecology 77, 375-394.
- 415 Navarrete, S.A., 1996. Variable predation: effects of whelks on a mid-intertidal successional
416 community. Ecol. Monogr. 66, 301-321.
- 417 Norton, T.A., Hawkins, S.J., Manley, N.L., Williams, G.A., Watson, D.C., 1990. Scraping a
418 living: a review of littorinid grazing. Hydrobiologia 193, 117-138.
- 419 Orton, J.H., 1928. Observations on *Patella vulgata*. Sex-phenomena, breeding and shell
420 growth. J. Mar. Biol. Ass. UK 15, 851-862.
- 421 Pfister, C.A., Peacor, S.D., 2003. Variable performance of individuals: the role of population
422 density and endogenously formed landscape heterogeneity. J. Anim. Ecol. 72, 725-
423 735.
- 424 Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists.
425 Cambridge University Press, Cambridge.
- 426 Rossi, R.E., Mulla, D.J., Journel, A.G., Franz, E.H., 1992. Geostatistical tools for modeling
427 and interpreting ecological spatial dependence. Ecol. Monogr. 62, 277-314.

- 428 Ruel, J.J., Ayres, M.P., 1999. Jensen's inequality predicts effects of environmental variation.
429 Trends Ecol. Evol. 14, 361-366.
- 430 Santini, G., Thompson, R.C., Tendi, C., Hawkins, S.J., Hartnoll, R.G., Chelazzi, G., 2004a.
431 Intra-specific variability in the temporal organisation of foraging activity in the limpet
432 *Patella vulgata*. Mar. Biol. 144, 1165-1172.
- 433 Santini, G., Burrows, M.T., Chelazzi, G., 2004b. Bioeconomics of foraging route selection by
434 limpets. Mar. Ecol. Progr. Ser. 280, 189-198.
- 435 Sommer, U., 2000. Benthic microalgal diversity enhanced by spatial heterogeneity of grazing.
436 Oecologia 122, 284-287.
- 437 Southward, A.J., 1956. The population balance between limpets and seaweeds on wave
438 beaten rocky shores. Ann. Rep. Mar. Biol. Stat. Port Erin 68, 20-29.
- 439 Stimson, J., 1973. Role of territory in ecology of intertidal limpet *Lottia gigantea* (Gray).
440 Ecology 54, 1020-1030.
- 441 Thompson, R.C., Johnson, L.E., Hawkins, S.J., 1997. A method for spatial and temporal
442 assessment of gastropod grazing intensity in the field: the use of radula scrapes on wax
443 surfaces. J. Exp. Mar. Biol. Ecol. 218, 63-76.
- 444 Thompson, R.C., Norton, T.A., Hawkins, S.J. 2004. Physical stress and biological control
445 regulate the producer–consumer balance in intertidal biofilms. Ecology 85: 1372–
446 1382.
- 447 Weber, G.E., Jeltsch, F., Van Rooyen, N., Milton, S.J., 1998. Simulated long-term vegetation
448 response to grazing heterogeneity in semi-arid rangelands. J. Appl. Ecol. 35, 687-699.

449 Table 1. Results of best subsets regressions on standardized semivariances calculated at a lag
 450 of 20 cm. Predictor variables for each array (n = 32) were surface roughness (rough), mean
 451 limpet density (limpets), nearest neighbour ratio (nn ratio) and mean grazing per disk
 452 (grazing). Only regressions with significant overall fits to the data are shown. Variance
 453 Inflation Factors for the variables in the multiple regression shown were both equal to 1.
 454
 455

Dependent variable	Mallow's Cp	Adj r ² (%)	p	Predictor variable	Slope	SE of slope
Fortnights	0.964	10.4	0.041	grazing	-0.006	0.0029
Fortnights	1.048	13.4	0.047	grazing	-0.005	0.0029
				rough	0.235	0.1639
All data	0.461	10.8	0.037	rough	0.576	0.2641

456 **Figure captions**

457 **Figure 1.** Summary of averaging process for all the two-week deployments at a single array
458 location. The largest scale of averaging ('all data') uses the mean grazing intensity at each
459 location over all six deployments before calculating a semivariogram. 'Six weeks' averaging
460 splits the data into a mean for 2001 and a mean for 2002 before calculating a semivariogram.
461 These two semivariograms are then averaged to create a single semivariogram for this
462 temporal scale. The shortest period for calculating semivariograms is 'Fortnightly'. This
463 produces six semivariograms. Semivariances at each lag distance are averaged for the six
464 deployments to produce a consensus semivariogram for short term deployments.

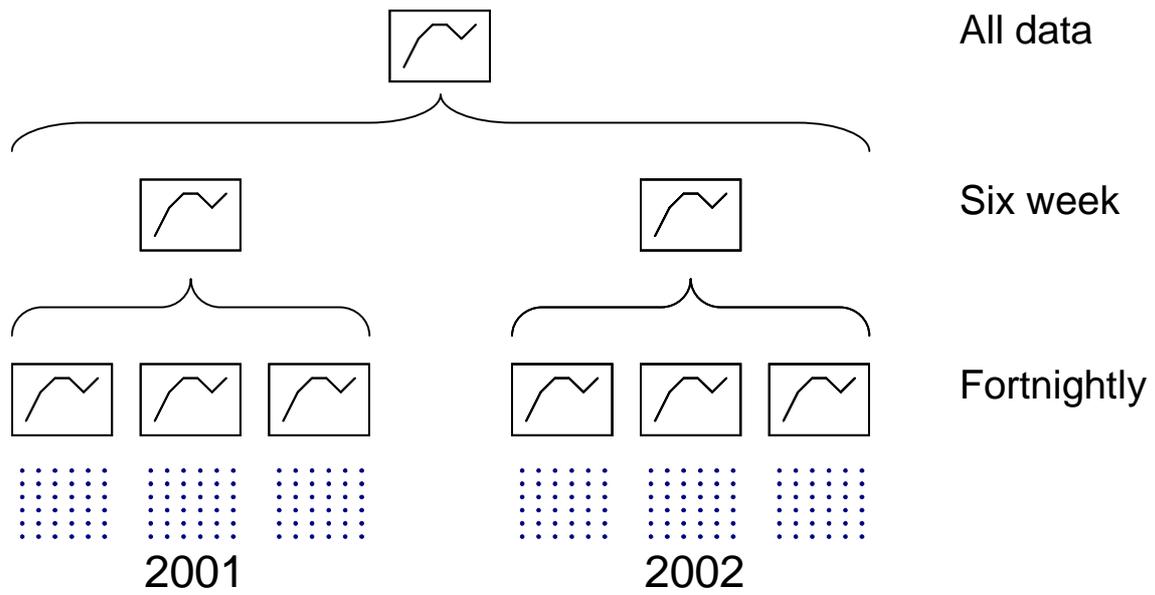
465

466 **Figure 2.** Standardized semivariograms for grazing in wax disk arrays using data aggregated
467 over different time periods (fortnights, six weeks and all data). Points at each lag distance are
468 the average of 32 arrays. Variability equal to the background variance at each site occurs
469 when the semivariance is one (dotted line shown for reference). Error bars are SE.

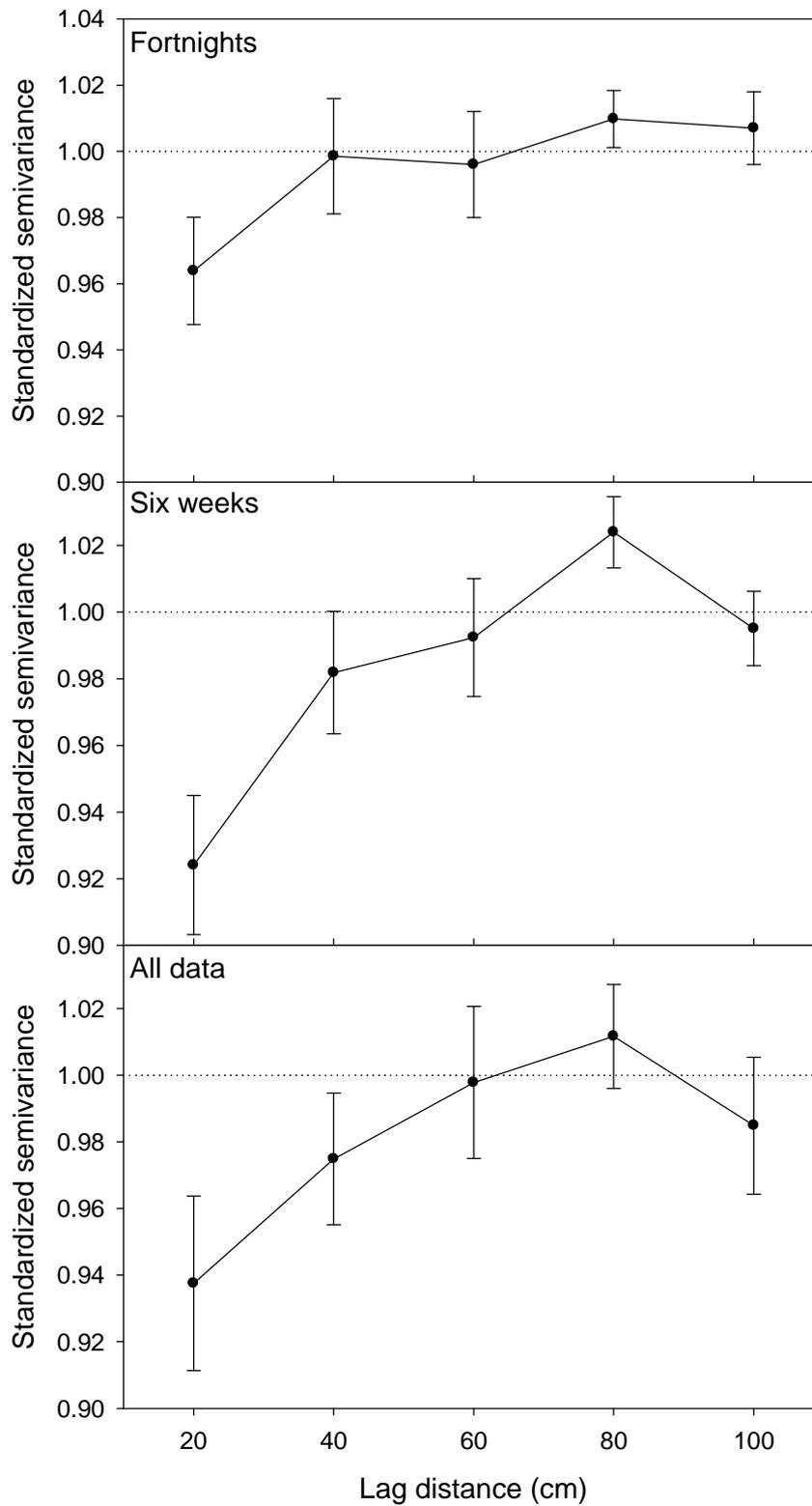
470

471 **Figure 3.** Relationships between (a) average grazing and standardized semivariance when
472 patterns were analysed using single two week deployments fortnights; (b) surface roughness
473 and standardized semivariance when using the average grazing at each disk integrated across
474 all deployments. Both fits are significant with adjusted r^2 between 10 and 11 % (Table 1).

475 Figure 1



476 Figure 2



477 Figure 3

