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The persistent spatial patchiness of limpet grazing

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Abstract

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

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

1. Introduction

Grazing has frequently been shown to be an important process in determining the biomass and biodiversity of organisms on rocky shores (Hawkins and Hartnoll, 1983; Chapman, 1995). The often-repeated experimental approach of excluding or removing grazers (e.g., Jones, 1948; Coleman et al., 2005) emphasizes a lowering of the mean intensity of grazing. The movements of individual grazers, however, create spatial and temporal variability in grazing intensity. This variability in the pattern of trophic interactions may affect the biomass of consumed species independently of changes in the mean intensity of the interaction (Navarrete, 1996; Benedetti-Cecchi et al., 2005).

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

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

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

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

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

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

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

2. Methods

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

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

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

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

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

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

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

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

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

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

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

3. Results

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

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

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

4. Discussion

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

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

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

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

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

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

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

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

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

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

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

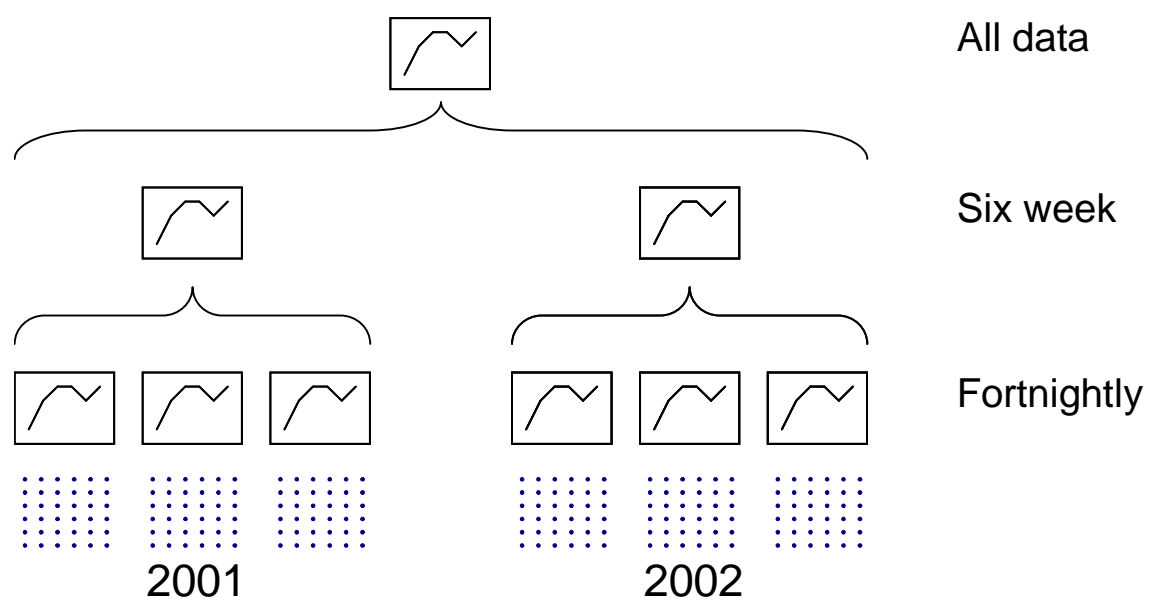
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Figure 1. Summary of averaging process for all the two-week deployments at a single array location. The largest scale of averaging ('all data') uses the mean grazing intensity at each location over all six deployments before calculating a semivariogram.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

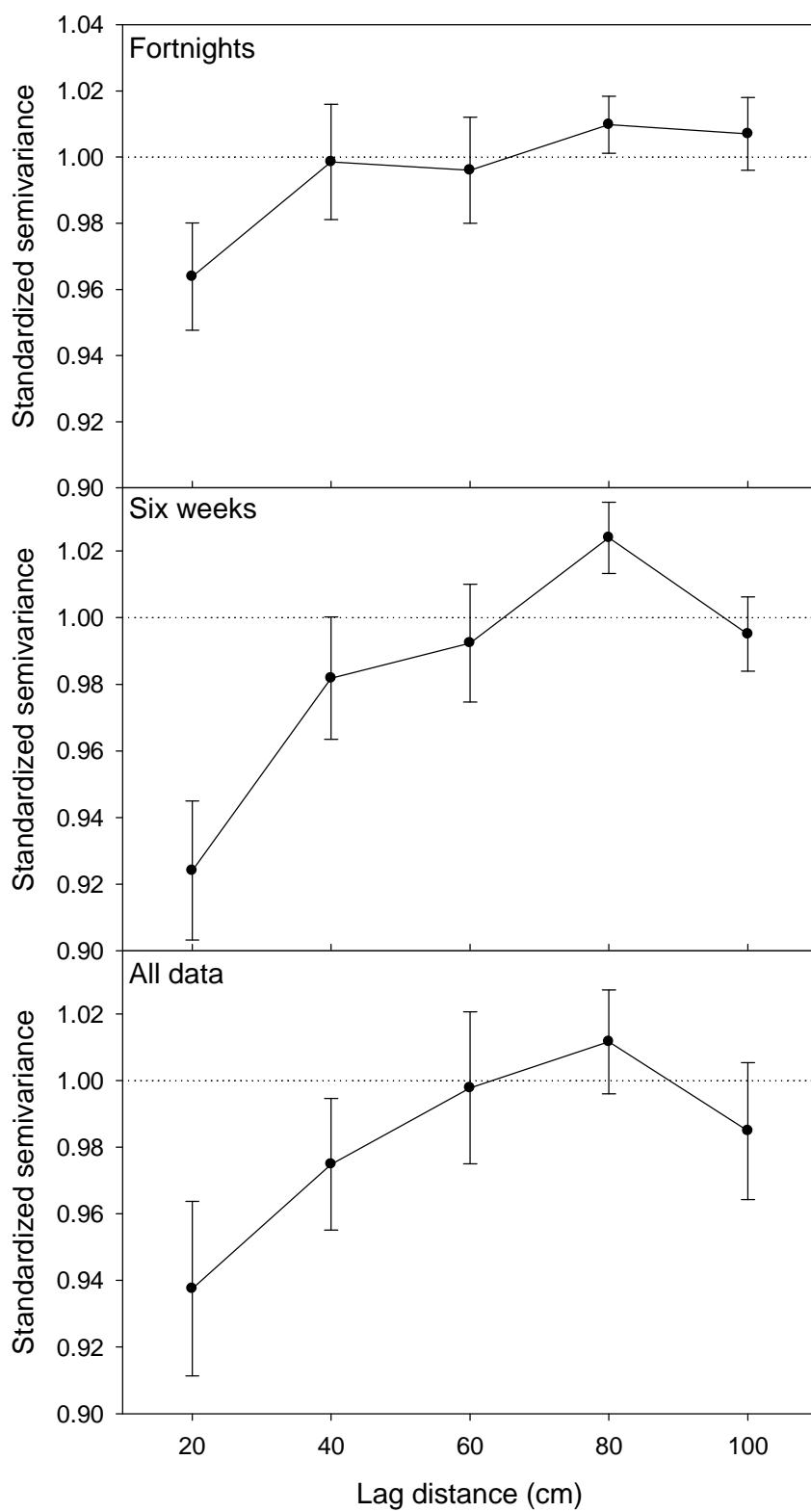
Figure 2. Standardized semivariograms for grazing in wax disk arrays using data aggregated over different time periods (fortnights, six weeks and all data). Points at each lag distance are the average of 32 arrays. Variability equal to the background variance at each site occurs when the semivariance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

Figure 3. Relationships between (a) average grazing and standardized semivariance when patterns were analysed using single two week deployments fortnights; (b) surface roughness and standardized semivariance when using the average grazing at each disk integrated across 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

