Spatial pattern of rocky intertidal barnacle recruitment: comparison over multiple tidal levels and years

DAPHNE M. MUNROE AND TAKASHI NODA

Faculty of Environmental Science, Hokkaido University, N10 W5, Kita-ku, Sapporo, Hokkaido, 060-0810, Japan

*Recently developed methods allow quantification and examination of point patterns. Understanding patterns of aggregation or regularity of larval recruits at various spatial scales can help in identifying underlying ecological and biological processes determining their distribution. A rocky shore plot (30 cm wide × 100 cm tall) in southern Hokkaido, Japan was cleared each summer. Barnacle (*Chthamallus challengeri*) recruitment, after a period of approximately 134 days, was recorded using 40 photographs (25 cm²); 8 photographs per 20 cm horizontal band of tidal height, 5 bands total. Barnacle recruits within each photograph were mapped and co-ordinates used to analyse aggregation at scales from 0–2 cm using Ripley's K statistic and neighbourhood density function (NDF) (both models assumed heterogeneity of first-order density). Quadrat density counts at scales from 20–50 cm provided estimates of aggregation using Morisita's standardized index. These analyses showed that barnacle recruits demonstrate ordered spacing up to a distance of 6 mm. From 6 mm to 2 cm recruits show random spacing based on NDF, but ordered distribution based on the Ripley's K statistic. This discrepancy is likely a result of the cumulative nature of the Ripley's K statistic. At larger scales, Morisita's standardized index indicated aggregation. This result may be explained biologically by the trade off between maximizing need for space at small spatial scales, however being constrained by copulation with neighbours, resulting in aggregation at scales larger than the maximum penis length. The observed pattern was consistent among years with different recruitment densities and among tidal levels, indicating site specific characteristics and interspecific interactions may have a larger influence than desiccation stress or density dependence on spacing of recruits.*

Keywords: spatial point pattern, barnacle recruitment, rocky intertidal, Ripley's K, tide height, *Chthamallus challengeri*

Submitted 21 May 2008; accepted 7 October 2008

INTRODUCTION

Ecologists have been increasingly incorporating spatial pattern analysis into research aimed at understanding processes underlying observed ecological patterns (Wiegand & Moloney, 2004; Perry *et al.*, 2006). The utility of these methods is broad and they offer a unique opportunity to examine patterns while considering underlying processes to develop more informed hypotheses about those patterns (Perry *et al.*, 2006).

Second-order statistics, such as neighbourhood density function (Stoyan & Stoyan, 1994; Wiegand *et al.*, 1999) or Ripley's K (Ripley, 1977), are desirable because they can characterize mapped point patterns over a range of spatial scales (Wiegand *et al.*, 2007), null models can be used to determine if points are aggregated, random or ordered distributions and replication of plots can be used to increase power and summarize results (Diggle, 2003). Appropriate null model selection has been used to separate and understand the role of environmental heterogeneity in observed patterns of trees (Wiegand *et al.*, 2007) and bird nest sites (Cornulier & Bretagnolle, 2006). In ecological applications of spatial

Corresponding author:
D.M. Munroe
Email: munroe@ees.hokudai.ac.jp

point pattern analysis methods, examination of patterns over a range of scales is important because underlying processes that shape patterns can change with spatial scale (Le Tourneux & Bourget, 1988; Wiegand & Moloney, 2004). Replication is essential for statistical inference; however, in spatial point pattern analysis few studies include replicate point patterns. An exception is neuroanatomical studies involving replicate tissue samples and mapped locations of cells (Beasley *et al.*, 2002).

Once settled, barnacles live permanently fixed to rocky intertidal surfaces (Anderson, 1994) and therefore are ideal organisms with which to investigate spatial patterns. Permanent attachment combined with obligatory sexual reproduction creates a trade off between increased spacing between individuals to reduce competition and aggregation of individuals to ensure reproductive success (Kent *et al.*, 2003). Permanent attachment and the importance of conspecific proximity mean that spatial patterns of barnacles established by settling cyprids determine subsequent adult fitness (Satchell & Farrell, 1993; Hills & Thomason, 1996).

In rocky intertidal environments, annual variability in larval recruitment is high (Crisp, 1974) and strong environmental and biological gradients exist vertically in the tidal zone. Density of recruits can vary greatly from year to year and from upper intertidal to lower. Satchell & Farrell (1993) proposed that spatial patterns of recruits may be

density-dependant such that the above trade off between competition and reproductive success shifts at high recruitment density (higher density would lead to greater tendency for maximal spacing while lower density would mean greater aggregation). While investigating territorial behaviour of settling cyprids, Crisp (1961) observed a decrease in territorial spacing of individuals at higher density. Thus, density-dependant changes in recruitment patterns may be evident between years and among tide levels in a rocky intertidal population. In addition, environmental gradients in the tidal zone may cause changes in the spatial patterns of recruits.

Although other studies have examined spacing of barnacle recruits (Wethey, 1984; Hills & Thomason, 1996; Kent *et al.*, 2003; Hayashi & Tsuji, 2008), shortcomings still exist concerning examination of patterns over multiple years, densities and tide levels. Hills & Thomason (1996) used settlement patterns of barnacles on different surfaces to investigate effect of surface type on settlement with nearest neighbour and Morisita's index methods. Unfortunately, the form of Moristita's index used in their study suffers from inaccuracies at low densities and therefore generality of their results are questionable. Wethey (1984) described changes in nearest neighbour distance for recently settled barnacles over a single settlement season and found high aggregation between concurrent settlers and also affinity to settle in cracks; however, these results were confounded. López Gappa *et al.* (1997) used similar methods as in the present study (repeated mapping of barnacles on an intertidal plot over 3 years and analysis involving nearest neighbour and Ripley's K), however, their focus was not on recent settlers and no clearing of plots occurred. Previous studies have examined spacing of barnacle recruits, yet few have investigated spatial patterns over multiple years and densities and none (to our knowledge) have examined aggregation patterns over tidal levels, all questions that can be accurately examined by employing replicated and complementary techniques described above.

In this study it is our intention to: (1) use spatial point pattern analysis in combination with quadrat density methods to examine spatial patterns of barnacle recruitment over a range of spatial scales from 0–50 cm; (2) compare spatial patterns of mapped points of barnacle recruits over 4 years to determine if annual changes in density correspond to changes in spatial pattern; and (3) compare spatial patterns of mapped points of barnacle recruits among tidal levels to determine if tidal changes in density and environmental gradients correspond to changes in spatial pattern.

This study is the first of its kind to address spatial point patterns of barnacle recruits using recent and novel spatial point pattern analysis methods. Future research should involve study of these patterns in multiple regions, with more species and on a greater scale of mapping to allow more factors to be examined and larger spatial scale questions to be tested.

MATERIALS AND METHODS

A rocky intertidal plot in the southern region of Hokkaido, Japan ($41°56'29.8''$N $140°56'5.2''$E) was used to study barnacle recruitment (Figure 1). The shore plot was permanently marked using screws drilled into a roughly vertical volcanic basalt rock face (average angle $64°$ from horizontal) at an
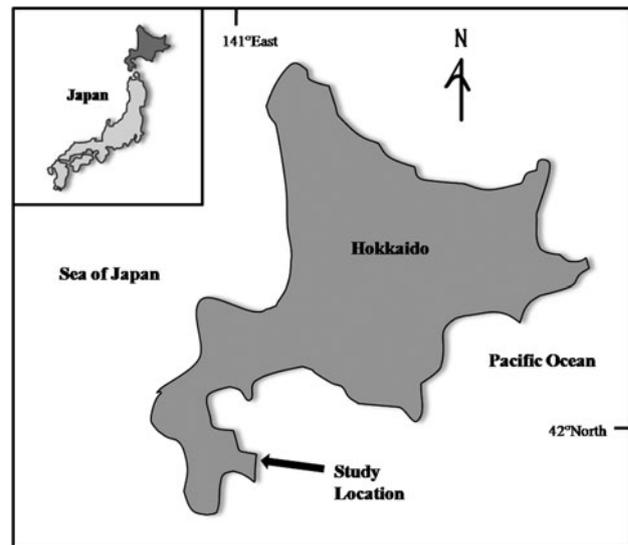

Fig. 1. Map of location of study plot. Inset (top left) shows location of Hokkaido within Japan; Hokkaido shown in dark grey. Black solid arrow indicates location of study plot on southern Hokkaido.

exposed location. Each summer, beginning in 2004 and continuing until 2007, an area 30 cm horizontally and 100 cm vertically was cleared of all surface organisms and plants in early July, by burning with gas torches and physical clearing with wire brushes during low tide. The plot was divided vertically into 5 tide level bands, each 20 cm in height and named tide level 1–5 starting with 1 in the upper intertidal (Figure 2).
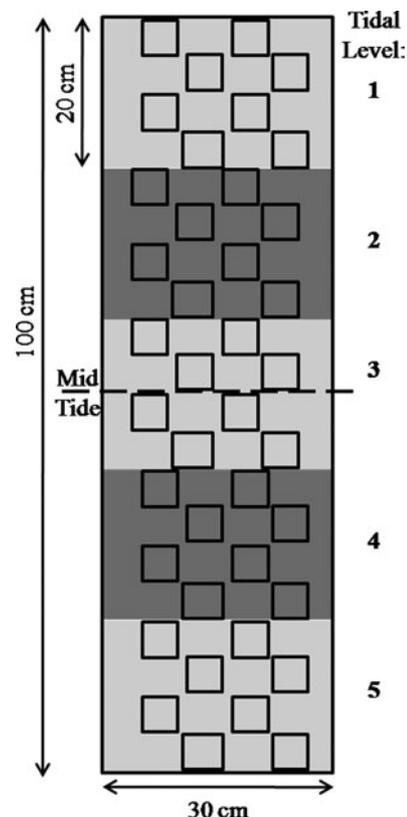

Fig. 2. Layout of rocky intertidal plot. Dotted black line marks mid-tide line, small black boxes show approximate location of photographs. Tidal level labelled on right of figure and shading corresponds to tidal level.

Detailed description of the study site and biogeographical features of the area can be found in Okuda *et al.* (2004) and Nakaoka *et al.* (2006).

After clearing each year, the plot was not disturbed further and natural recruitment of barnacles progressed. Photographs were taken after 134 days ($\pm$ 20 days SD) using a Canon IXY Digital 320 camera, macro setting and 180 dpi at a distance of 10 cm from the rock surface. A plastic quadrat grid was placed on the rock surface to frame each photograph within a 5 × 5 cm quadrat. Eight photographs were taken in each 20 cm vertical band to block for tidal height (8 photographs × 5 vertical bands = 40 photographs per year) (Figure 2). These photographs were used to map locations of barnacle recruits (using XYit Digitizer software, Geomatix Ltd. UK), measure average maximum barnacle diameter (using Adobe Photoshop CS3 Extended, Adobe Systems Incorporated 2008) and count number of recruits per quadrat. Maximum barnacle diameter in each photograph was estimated by measuring the maximum diameter (the length along the carina–rostrum axis) of approximately 20 (in low density photographs) to 55 (in high density photographs) random individuals. Calibrations for length were based on scale included in each photograph. Log transformed density and maximum barnacle diameter of recruits in each quadrat were compared over year and tidal level using two-way analysis of variance.

To assess level of aggregation on small spatial scale (0–2 cm), grid co-ordinate locations of barnacles in each quadrat were used to calculate the Ripley's K function (Ripley, 1977), and neighbourhood density function (NDF or O-ring statistic) (Stoyan & Stoyan, 1994; Wiegand *et al.*, 1999) for each photograph. Ripley's K describes the number of other points within circles centred at each point in the pattern, and with progressively larger radii (Perry *et al.*, 2006). Neighbourhood density function is very close to Ripley's K, except that rings are used in place of circles (Perry *et al.*, 2006). Second order statistics such as these can characterize point patterns over a range of spatial scales and can reveal scales at which a pattern may switch from aggregation to dispersion for example (Wiegand & Moloney, 2004). Because these two analysis methods have different characteristics (Ripley's K is cumulative while NDF is not), it is
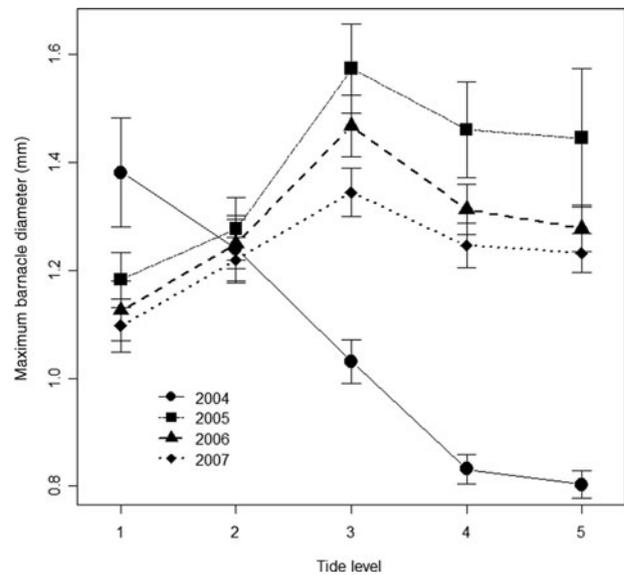

Fig. 3. Maximum barnacle diameter (mean and 95% CI) for each tidal level and year. For each point, N varies from 77 to 438 depending on the density of barnacles in the photograph.

appropriate to use them together to derive the most information from the pattern (Wiegand & Moloney, 2004; Perry *et al.*, 2006).

Null models for Ripley's K and NDF assuming heterogeneity were used (methods following Wiegand & Moloney, 2004). An important underlying assumption of Ripley's K and NDF is that the point process is homogeneous over the space in question (i.e. first-order stationary). Our pattern demonstrated first-order inhomogeneity and therefore moving windows with a radius of 3 mm were used to create heterogeneous Poisson null models (Wiegand & Moloney, 2004). This method compensates for small scale density inequalities (first-order clustering) and allows examination of second-order properties. Second-order analyses are not
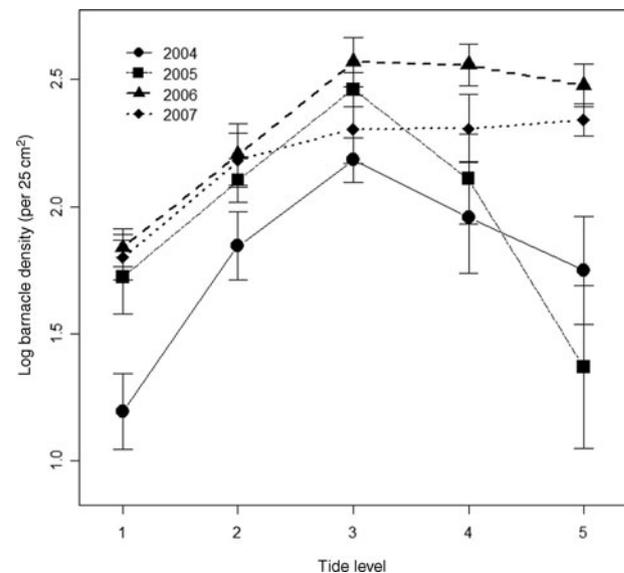
Table 1. Results of two-way ANOVA for barnacle maximum diameter by year and tide level.

Sources of variances	DF	MS	F	*P*-value
Year	3	20.57	109.8	<0.00001
Tidal level	4	6.65	35.5	<0.00001
Year × tidal level	12	3.97	21.2	<0.00001
Residuals	4849	0.19		

Table 2. Results of two-way ANOVA for log-transformed barnacle density by year and tidal level.

Sources of variances	DF	MS	F	*P*-value
Year	3	4.14	11.89	<0.00001
Tidal level	4	1.99	5.68	<0.001
Year × tidal level	12	0.58	1.66	0.080
Residuals	155	0.35		

Fig. 4. Log barnacle density (mean and 95% CI) for each tide level and year. N = 8 for each point.

limited to small spatial scales in the way that first-order analyses are and allow examination of spatial patterns over a range of distances (Perry *et al.*, 2006).

Second-order statistics were calculated for each photograph. Resulting statistics from the eight replicate photographs from each 20 cm tidal level band were combined following the methods of Diggle (2003). The above calculations of second-order statistics and combination of replicates were carried out in Programita (produced by T. Wiegand, Department of Ecological Modelling, UFZ Centre for Environmental Research Leipzig-Halle; procedures described in Wiegand & Moloney, 2004).

Quadrat density counts provided estimates of aggregation using Morisita's standardized index (described in Krebs, 1998) for scales of 20 cm, 30 cm and 50 cm. This index is popular because it is independent of sample size and density and can be easily applied (Myers, 1978). The results are easy to interpret because the results range from −1.0 to +1.0 and 95% confidence limits are at −0.5 and +0.5 (positive values indicate a clumped pattern and negative values an ordered pattern) (Krebs, 1998). Calculated values for Morisita's standardized index for each spatial scale were used for two-way analysis of variance without replication on the ranked values to test the influence of year and tidal level on degree of aggregation at 20 cm, 30 cm, and 50 cm. Interaction of year

and tide level was tested using Tukey's test for non-additivity in R statistical package 'agricolae' (Mendiburu, 2007; R Development Team, 2007).

RESULTS

Barnacle size and density varied both by year and tide level. The results of two-way analysis of variance are shown in Table 1 (maximum barnacle diameter) and Table 2 (log barnacle density). The mean and 95% confidence interval of maximum barnacle diameter and log transformed density are shown in Figures 3 and 4 respectively. Barnacles tended to be largest in the middle and lower intertidal (tide level 3, 4, 5) in all years except 2004 when barnacles were largest in the upper intertidal and smallest in the lower intertidal. Year, tide level and the interaction of year and tidal level were significant factors ($P < 0.0001$ for all) influencing barnacle length (Table 1). Year and tidal level ($P < 0.0001$, $P < 0.001$ respectively) were significant factors influencing the density of barnacles (Table 2). Barnacle density was higher in middle and lower tide level (tide level 3, 4, 5) and also varied annually with 2006 showing the greatest density and 2004 showing the lowest. It should be noted that date of
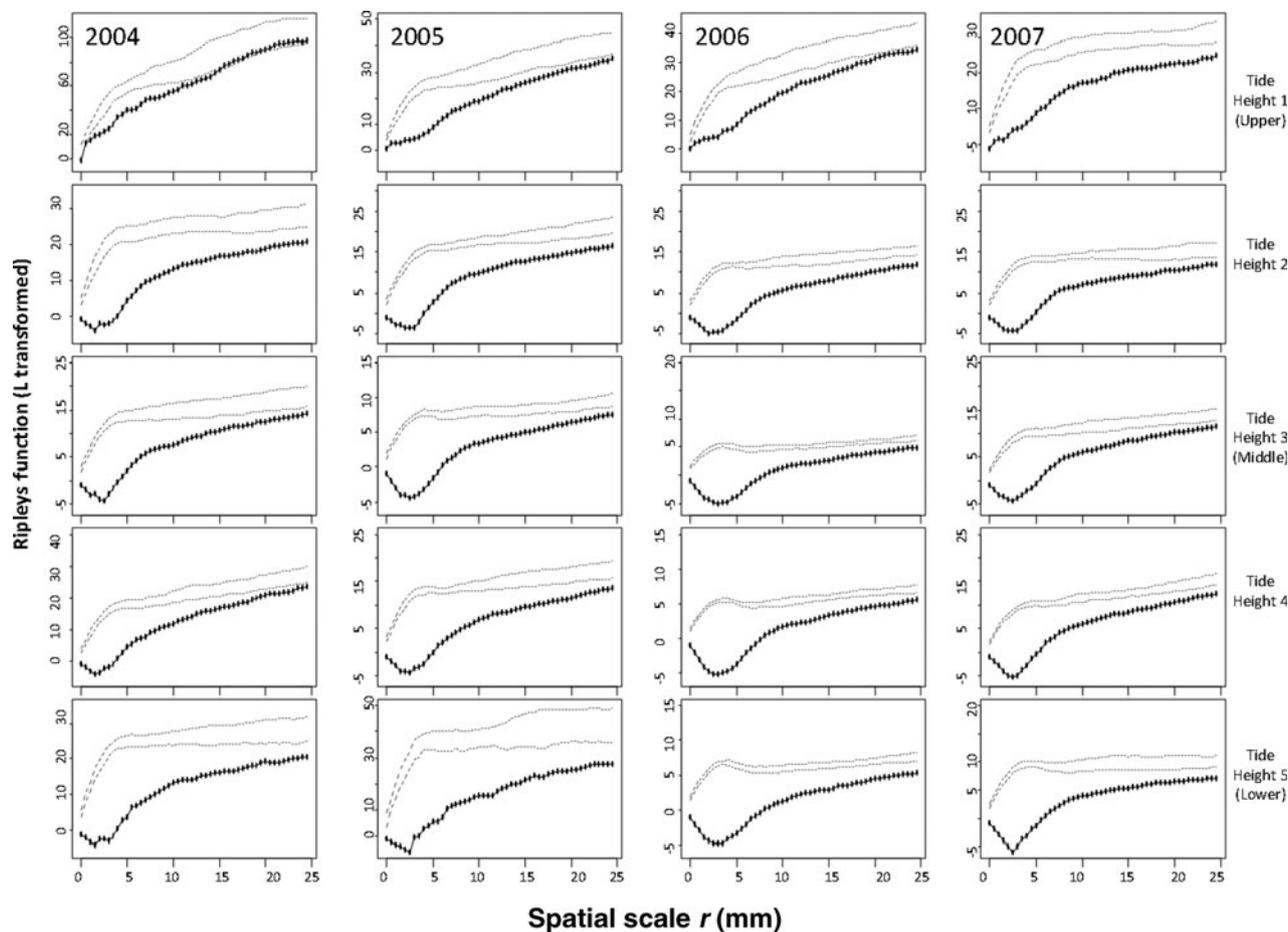

Fig. 5. Ripley's K function (L transformed for plotting) for 2004–2007. Plots arranged in columns by year (2004 on the left, 2007 on the right) and in rows by tide height (upper intertidal on top, lower intertidal on bottom). Dark solid line shows the combined Ripley's L function for 8 replicate maps (N = 8). Grey dashed lines indicate the upper and lower simulation envelope (the lowest and highest values of 19 simulations) based on heterogeneous Poisson null model. The null model used first order density of barnacles at a radius of 3 mm. Measured values below the simulation envelope indicate ordered pattern, within the envelope indicates random and above the envelope indicates aggregation.
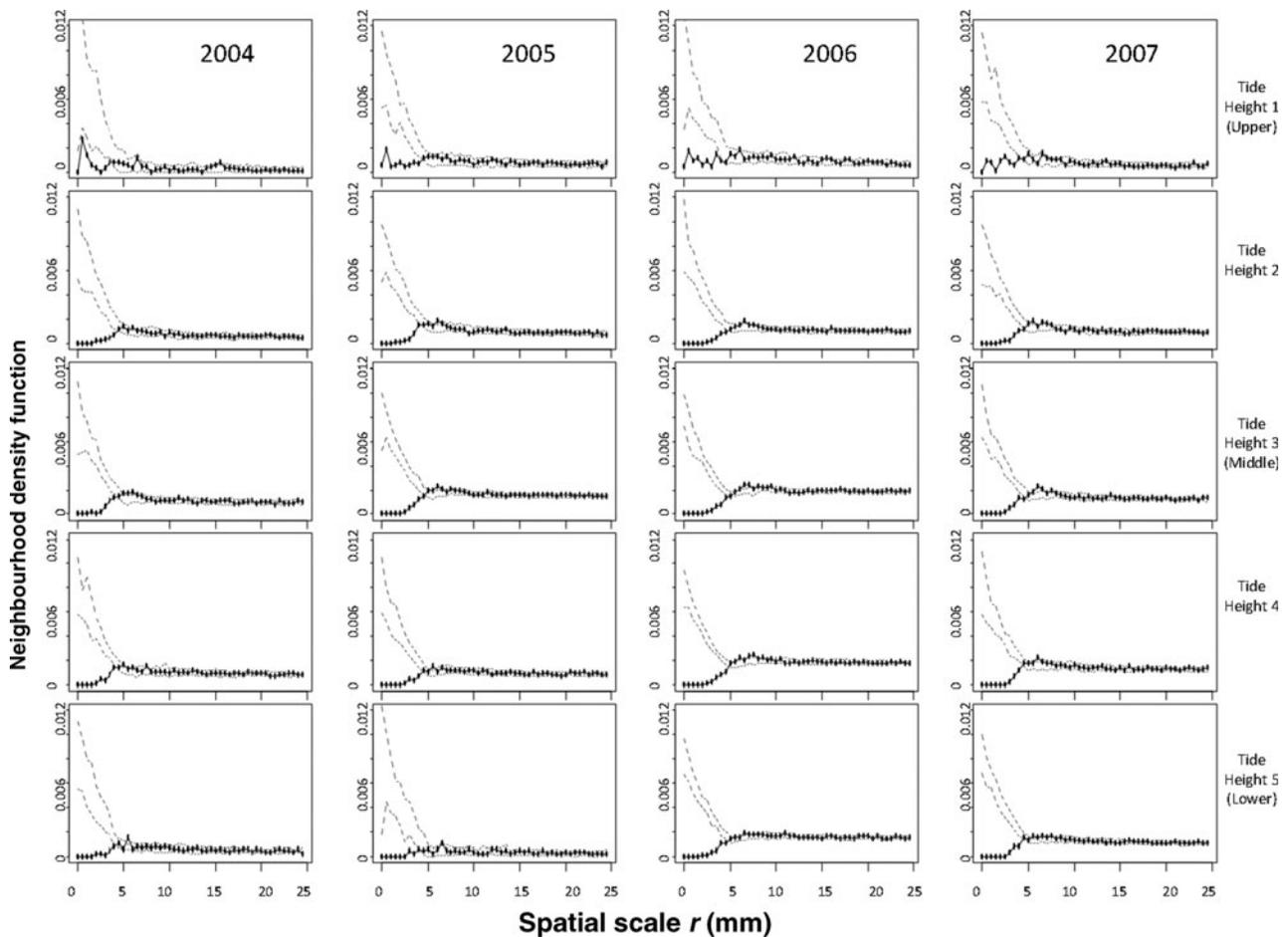
Fig. 6. Neighbourhood density function for 2004–2007. Plots arranged in columns by year (2004 on the left, 2007 on the right) and in rows by tide height (upper intertidal on top, lower intertidal on bottom). Dark solid line shows the combined neighbourhood density function for 8 replicate maps (N = 8). Grey dashed lines indicate the upper and lower simulation envelope (the lowest and highest values of 19 simulations) based on heterogeneous Poisson null model. The null model used first order density of barnacles at a radius of 3 mm. Measured values below the simulation envelope indicate ordered pattern, within the envelope indicates random and above the envelope indicates aggregation.

recruitment may have also varied among years and is likely to influence annual variation in both barnacle length and density.

The heterogeneous Ripley's K function (L transformed) for each tidal height and each year are shown in Figure 5. This figure shows considerable consistency among tidal levels and years in small scale point pattern of barnacle recruits. All patterns indicate an ordered pattern, or maximum spacing between individuals (this is true when empirical values lie below the simulation envelope). At larger values of r, Ripley's K function follows the lower bound of the simulated random pattern and indicates an ordered pattern, although not as strongly as is seen at smaller scales.

The heterogeneous NDF for each tidal height and each year is shown in Figure 6. We again observe consistency in the patterns among tidal height and among years. The NDF also indicates an ordered pattern at smaller spatial scales, up to approximately 5 or 6 mm. The NDF indicates random spacing of individuals at distances larger than 6 mm, in contrast to the result of Ripley's K function. The likely explanation for this inconsistency is that Ripley's K uses a cumulative estimator, while NDF uses a localized estimator and therefore is more precise at larger scales (Wiegand & Moloney, 2004).

At larger spatial scales, all Morisita's standardized quadrat density index calculations indicated aggregation (Figure 7). Density estimates are a first-order character, unlike the second-order small scale tests used above. Two-way analysis of variance of ranked Morisita's standardized index values showed no significant effect of year, tide level or the interaction of year and tidal level at $\alpha = 0.05$ at any of the scales examined (Tables 3 & 4).

DISCUSSION

Current understanding of larval transport and recruitment dictates that annual variability in larval recruitment is large (Crisp, 1974). Annual differences in magnitude of larval recruitment are evident here (Table 2; Figure 4) and have been demonstrated for *Chthamallus challengeri* by Miyamoto *et al.* (1999) and may result from annual variation in fertilization success (Levitan, 1995), larval food availability (McEdward & Qian, 2001), successful return to suitable habitat (Gaines & Bertness, 1992; Pineda, 1994) and pre- and post-settlement predation (Thorson, 1946; Navarette & Wieters, 2000). Also evident are annual differences in maximum barnacle diameter (Table 1; Figure 3) which
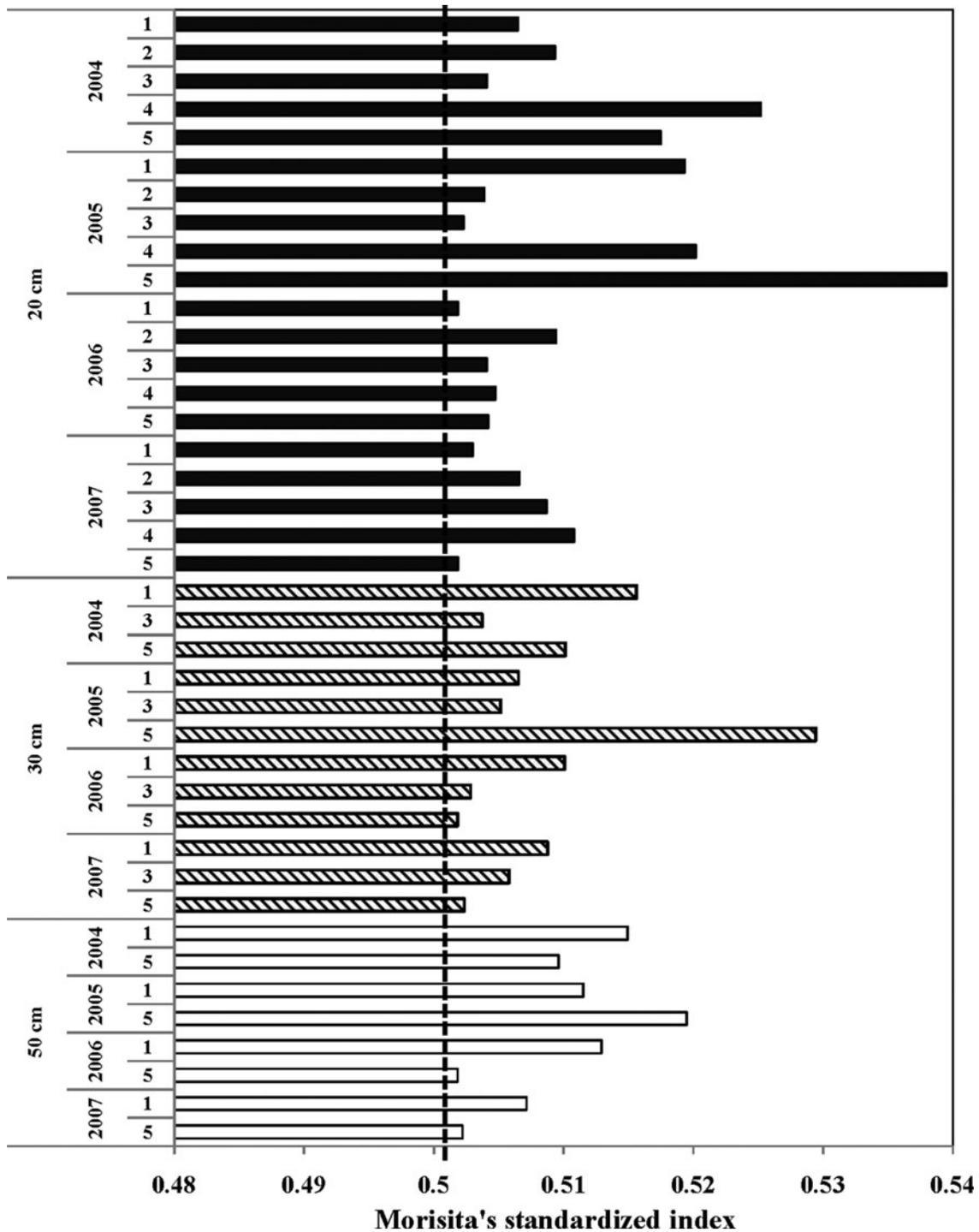
Fig. 7. Morisita's standardized index values for quadrat counts. Black bars represent values for 20 cm scale; hatched bars 30 cm scale; white bars 50 cm scale. Dotted black line marks the 0.5 value, all calculated values greater than 0.5 are considered significantly aggregated. Y axis labels separate scale, year and tidal level.

could be a reflection of greater time since settlement and greater influence of post-settlement mortality. A trend of larger barnacles in the middle and lower intertidal was evident in all years except 2004. That year was also the year of lowest density and a possible explanation of the unusual size pattern observed is that there may have been a failure of early recruitment (thus larger size-classes at the time of observation) to middle and lower tide levels. Although barnacle size and density varied by year, small scale (ordered) and large scale (aggregated) spatial patterns did not vary. Our

failure to observe changes in recruitment spatial patterns related to changes in density and barnacle size may mean that recruitment patterns are unrelated to these factors. Alternatively, the variability in density and barnacle size observed over the four years of this study may have been inadequate to observe a response in spatial pattern.

Intertidal rocky shore communities are characterized by vertical changes in community due to strong environmental and biological gradients and recruitment of *Chthamallus challengeri* has likewise been shown to be significantly related to

Table 3. Results of two-way ANOVA without replication test on ranked values of Morisita's standardized index for year and tidal level (scales from 20 cm to 50 cm).

Sources of variances	DF	MS	F	P-value
20 cm scale				
Year	3	36.60	1.136	0.37
Tidal level	4	42.13	1.307	0.32
Residuals	12	32.23		
30 cm scale				
Year	3	11.67	0.979	0.46
Tidal level	2	18.25	1.531	0.29
Residuals	6	11.92		
50 cm scale				
Year	3	6.67	1.143	0.46
Tidal level	1	4.50	0.771	0.44
Residuals	3	5.83		

tidal level (Table 2; Figure 4, and previously by Miyamoto *et al.*, 1999). In the upper intertidal desiccation stress dominates while in the lower intertidal biological interactions such as predation and competition have the largest influence (Connell, 1972). In our study, many of the biological factors were eliminated at the beginning of the experiment (except mobile predators that could access the plot from neighbouring refuge areas), however, desiccation stress remained. Our results showed that there was very little change in spatial patterns among tidal levels indicating that at this location desiccation stress and post-settlement predation did not appear to influence small scale spatial pattern of recruitment and again density-dependant changes in spatial patterns was not evident. The consistency of our results indicate that desiccation stress and intraspecific density may have limited influence on variation in small scale spatial patterns of barnacle recruitment and that site specific characteristics and interspecific interactions may play a larger role.

Previous research using these spatial pattern analysis methods used a heterogeneous model to test spatial patterns (Wiegand *et al.*, 2007). In that study, the nature of associations between points (in their case trees) allowed authors to identify and separately test small scale aggregation due to individual interactions with larger scale environmental variation. In the case of rocky intertidal recruitment, variation of environment (surface roughness and cracks) and species interactions both occur on small spatial scales (LeTourneux & Bourget, 1988) and therefore cannot be separated in the same manner. Interestingly, once first order variation (small scale aggregation)

Table 4. Results of Tukey's test for non-additivity testing for interaction of year and tide level on ranked values of Morisita's standardized index (scales from 20 cm to 50 cm).

Sources of variances	DF	MS	F	P-value
20 cm scale				
Non-additivity	1	19.09	0.571	0.466
Residuals	2	33.42		
30 cm scale				
Non-additivity	1	0.397	0.028	0.874
Residuals	5	14.221		
50 cm scale				
Non-additivity	1	5.00	0.800	0.466
Residuals	2	6.25		

is accounted for in the model (heterogeneous model), the remaining pattern of larval recruitment is maximally spaced or random. This may be the result of known barnacle association with cracks in the rock surface causing first order aggregation (Wethey, 1984) in concert with competition avoidance behaviour causing maximum separation. Manipulative experimentation is required to separate this definitively.

Barnacles are uniquely constrained by two opposing traits; a sessile body form that is permanently attached to the rock surface, and sexual reproduction requiring physical copulation (Anderson, 1994). This means that proximity to other barnacles, and thus its reproductive potential, is determined long before sexual maturity during larval settlement and metamorphosis. Because of their sessile lifestyle, barnacles are in direct competition with neighbours for resources, yet paradoxically need to be close to neighbours for reproduction (copulation distance is limited by penis length; penis length has been reported to be around 5 cm (Barnes & Crisp, 1965)). Results of this study show that at small spatial scales (<6 mm), barnacle recruits repeatedly show a pattern of maximum spacing and at intermediate scales (6 mm–25 mm) random spacing, which is consistent with competition avoidance at spatial scales less than those constrained by penis length. On larger scales (>5 cm), barnacles show aggregation which is consistent with needs related to mate proximity.

Small scale ordered patterns can be the result of body size of the individuals under examination if the scale of the ordered pattern reflects that of body size. In this case, diameter of individuals was approximately 1.25 mm (± 0.01 95% CI), smaller than the scale of the ordered pattern measured (up to 6 mm). Further, this species has been shown to reach maturity in this region at 2 mm diameter (Nomura Hirotaka, Marine Ecology Research Institute, Chiba, Japan, personal communication), again smaller than the scale of the ordered pattern. This suggests that barnacle recruits are spacing with greater room between individuals than is necessary to accommodate their current body size and also greater than that necessary to accommodate future mature adult body size.

This small scale spacing was also observed by Crisp (1961) and was then termed 'territorial behaviour'. In contrast however, Crisp observed spacing between individuals on smaller scale than was observed here (2 mm), in species with larger adult body size (*Balanus balanoides* and *B. crenatus*). Crisp also noted a density dependant decrease in territorial spacing that we failed to detect in this study. López Gappa *et al.* (1997) conducted repeated observations of spatial patterns of an intertidal barnacle population to determine temporal changes in spatial patterns of individuals. In that study, they observed a trend towards ordered distribution of individuals at scales 1 cm and less and aggregation at larger spatial scales. The authors attribute this small scale ordered pattern to the body size of individual barnacles but also note that the uniform distribution observed is unexpected. Our study and Crisp's (1961) also shows a small scale uniform distribution of individuals that cannot be attributed to body size of individuals. Therefore it is possible that the pattern observed by López Gappa *et al.* (1997) and here result from small scale ordered recruitment patterns established by barnacles long before adult body size is reached.

Berntsson *et al.* (2004) suggest that substrata rejection drives aggregation in *Balanus improvisus* based on field and

laboratory experiments. Their tests used adjacent experimental panels 60 × 60 mm and they showed that barnacle recruits rejected unsuitable substratum on this spatial scale. This result indicates that substratum rejection may account for the scale of aggregation we observed here (>20 cm) if substratum heterogeneity varies on this same scale (unmeasured here). Likewise, substratum rejection on the scale of 0–6 mm based on presence of conspecifics could lead to the observed scale of ordered spacing measured here.

CONCLUSIONS

Small scale spatial patterns indicate that *Chthamalus challengeri* shows first-order aggregation and second-order maximum spacing. This pattern may be the result of aggregation due to rock surface microtopography while maximal spacing between individuals attempts to minimize competition with neighbours. Larger scale aggregation in barnacles may be the result of necessity of physical copulation between attached individuals and therefore a strategy for increasing reproductive success. These suggestions are supported by the observations made here but explicit experimental testing is necessary to separate these fully.

Barnacle recruits exhibit ordered spacing up to a distance of approximately 6 mm; from 6 mm to 2 cm recruits are spaced randomly or ordered; at scales from 20–50 cm they arrange in an aggregated manner. This pattern remains consistent among years with different recruitment densities and among tidal levels, indicating site-specific characteristics and interspecific interactions may have a larger influence than desiccation stress or density dependence on spacing of recruits.

ACKNOWLEDGEMENTS

REFERENCES

Anderson D.T. (1994) *Barnacles: structure, function, development and evolution.* London: Chapman & Hall.

Barnes H. and Crisp D.J. (1956) Evidence of self-fertilization in certain species of barnacles. *Journal of the Marine Biological Association of the United Kingdom* 35, 631–639.

Beasley C.L., Cotter D.R. and Everall I.P. (2002) Density and distribution of white matter neurons in schizophrenia, bipolar disorder and major depressive disorder: no evidence for abnormalities of neuronal migration. *Molecular Psychology* 7, 564–570.

Berntsson K.M., Jonsson P.R., Larsson A.I. and Holdt S. (2004) Rejection of unsuitable substrata as a potential driver of aggregated settlement in the barnacle *Balanus improvisus. Marine Ecology Progress Series* 275, 199–210.

Connell J.H. (1972) Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* 3, 169–192.

Cornulier T. and Bretagnolle V. (2006) Assessing the influence of environmental heterogeneity on bird spacing patterns: a case study with two raptors. *Ecography* 29, 240–250.

Crisp D.J. (1961) Territorial behaviour in barnacle settlement. *Journal of Experimental Biology* 38, 429–446.

Crisp D.J. (1974) Factors influencing the settlement of marine invertebrate larvae. In Grant P.T. and Mackie A.M. (eds) *Chemoreception in marine organisms.* London: Academic Press, pp. 177–265.

Diggle P.J. (2003) *Statistical analysis of point patterns.* Second edition. London: Arnold.

Gaines S.D. and Bertness M.D. (1992) Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360, 579–580.

López Gappa J., Calcagno J.A. and Tablado A. (1997) Spatial pattern in a low-density population of the barnacle *Balanus amphitrite* Darwin. *Hydrobiologia* 357, 129–137.

Hayashi R. and Tsuji K. (2008) Spatial distribution of turtle barnacles on the green sea turtle, *Chelonia mydas. Ecological Research* 23, 121–125.

Hills J.M. and Thomason J.C. (1996) A multi-scale analysis of settlement density and pattern dynamics of the barnacle *Semibalanus balanoides. Marine Ecology Progress Series* 138, 103–115.

Kent A., Hawkins S.J. and Doncaster C.P. (2003) Population consequences of mutual attraction between settling and adult barnacles. *Journal of Animal Ecology* 72, 941–952.

Krebs C.J. (1998) *Ecological methodology.* Second edition. Menlo Park, CA: Benjamin Cummings.

Le Tourneux F. and Bourget E. (1988) Importance of physical and biological settlement cues used at different spatial scales by the larvae of *Semibalanus balanoides. Marine Biology* 97, 57–66.

Levitan D.R. (1995) The ecology of fertilization in free-spawning invertebrates. In McEdward L. (ed.) *Ecology of marine invertebrate larvae.* Boca Raton, FL: CRC Press Inc., pp. 123–156.

McEdward L.R. and Qian P.Y. (2001) Effects of the duration and timing of starvation during larval life on the metamorphosis and initial juvenile size of the polychaete *Hydroides elegans* (Haswell). *Journal of Experimental Marine Biology and Ecology* 261, 185–197.

Mendiburu F. (2007) *Agricolae: Statistical Procedures for Agricultural Research.* R package version 1.0-4. http://tarwi.lamolina.edu.pe/~fmendiburu

Miyamoto Y., Noda T. and Nakao S. (1999) Zonation of two barnacle species not determined by competition. *Journal of the Marine Biological Association of the United Kingdom* 79, 621–628.

Myers J.H. (1978) Selecting a measure of dispersion. *Environmental Entomology* 7, 619–621.

Nakaoka M., Ito N., Yamamoto T., Okuda T. and Noda T. (2006) Similarity of rocky intertidal assemblages along the Pacific coast of Japan: effects of spatial scales and geographic distance. *Ecological Research* 21, 425–435.

Navarette S.A. and Wieters E.A. (2000) Variation in barnacle recruitment over small scales: larval predation by adults and maintenance of community pattern. *Journal of Experimental Marine Biology and Ecology* 253, 131–148.

Okuda T., Noda T., Yamamoto T., Ito N. and Nakaoka M. (2004) Latitudinal gradient of species diversity: multi-scale variability in rocky intertidal sessile assemblages along the Northwestern Pacific coast. *Population Ecology* 46, 159–170.

Perry G.L.W., Miller B.P. and Enright N.J. (2006) A comparison of methods for the statistical analysis of spatial point patterns in plant ecology. *Plant Ecology* 187, 59–82.

Pineda J. (1994) Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Marine Ecology Progress Series* 107, 125–138.

R Development Core Team (2007) *R: A language and environment for statistical computing.* Vienna: R Foundation for Statistical Computing. ISBN 3-900051-07-0, URL http://www.R-project.org.

Ripley B.D. (1977) Modelling spatial patterns. *Journal of the Royal Statistical Society* B41, 368–374.

Satchell E.R. and Farrell T.M. (1993) Effects of settlement density on spatial arrangement in four intertidal barnacles. *Marine Biology* 116, 241–245.

Stoyan D. and Stoyan H. (1994) *Fractals, random shapes and point fields: methods of geometrical statistics.* Chichester,UK: John Wiley and Sons.

Thorson G. (1946) *Reproduction and larval development in Danish marine bottom invertebrates.* Bianco, Lunos, Bogtrykkeri A/S Københaven: C.A.Reitzels Forlag.

Wethey D.S. (1984) Spatial pattern in barnacle settlement: day to day changes during the settlement season. *Journal of the Marine Biological Association of the United Kingdom* 64, 687–698.

Wiegand T., Moloney K.A., Naves J. and Knauer F. (1999) Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *American Naturalist* 154, 605–627.

Wiegand T. and Moloney K.A. (2004) Rings, circles and null-models for point pattern analysis in ecology. *Oikos* 104, 209–229.

and

Wiegand T., Gunatilleke S. and Gunatilleke S. (2007) Species associations in a heterogeneous Sri Lankan dipterocarp forest. *American Naturalist* 170, E77–E95.

Correspondence should be addressed to:
D.M. Munroe
Faculty of Environmental Science
Hokkaido University N10 W5, Kita-ku, Sapporo
Hokkaido, 060-0810, Japan
email: munroe@ees.hokudai.ac.jp