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Source: *Ecography*, Vol. 16, No. 3 (Jul. - Sep., 1993), pp. 269-277

Published by: Wiley on behalf of Nordic Society Oikos

Stable URL: <http://www.jstor.org/stable/3683002>

Accessed: 04-09-2017 14:47 UTC

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Temporal variation in species-area curves for invertebrates in clumps of an intertidal mussel

Anthony J. Peake and G. P. Quinn

Peake, A. J. and Quinn, G. P. 1993. Temporal variation in species-area curves for invertebrates in clumps of an intertidal mussel. – Ecography 16: 269–277.

We examined the temporal variation in the relationships between the number of invertebrate species, and of total individuals, inhabiting clumps of the intertidal mussel *Brachidontes rostratus* and the area of the clumps. We collected clumps in four seasons – autumn, winter, spring and summer – from a rocky shore in south-eastern Australia. Positive curvilinear relationships between species number and area were recorded for all seasons but fewer species for a given area were found in autumn and summer compared with winter and spring. These species-area relationships were different from those predicted from a passive sampling model (Random Placement Model). Positive relationships between number of individuals and area were also recorded but these did not vary between seasons. There was no short-term difference (i.e. between phases of tide and day) in species or individual number in clumps. Seasonal variation, and small-scale spatial unpredictability, in recruitment patterns are potentially important determinants of species numbers in this system. The seasonal differences we have recorded for mussel clumps suggest that future studies on island systems, particularly in marine habitats, should consider temporal variation in species-area relationships and that conclusions from previous comparisons of species-area curves based on one-off sampling must only be tentative.

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Introduction

The species-area relationship has had a long history of investigation and analysis. Although originally considered from a mathematical perspective (Arrhenius 1921, Gleason 1922), it was placed in a theoretical context as part of island biogeography theory for true oceanic islands (MacArthur and Wilson 1967) and positive relationships between species number and habitat area have been reported for many other types of “islands” or patches of habitat (see Connor and McCoy 1979, McGuinness 1984a). An essential first step in any study of species-area relationships is to test whether the number of species found in an area is simply a function of random colonization (McGuinness 1984b) and thus whether the observed species-area relationship simply

represents a trivial consequence of sampling, without any underlying ecological mechanism. McGuinness (1984b) has argued that fitting the Random Placement Model is an appropriate test for this phenomenon.

One difficulty in interpreting many species-area studies is that they have usually been conducted on limited, discrete time frames, implying that species-area relationships for a given community are temporally invariant. However, seasonal peaks in reproduction and recruitment are common amongst plants and invertebrates and many habitats experience large variations in environmental factors over even smaller temporal scales (e.g. floods in streams, tides on rocky shores). It is likely that species-area relationships could vary between sampling times in such habitats.

Rocky intertidal shores have provided ideal systems

Accepted 2 February 1993

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ISSN 0906-7590

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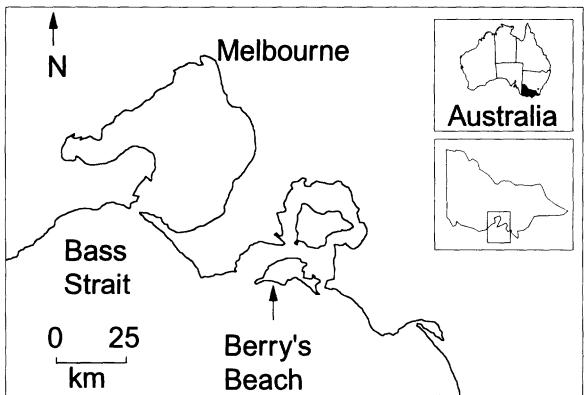


Fig. 1. Map showing location of study area.

for investigating the structure of plant and animal communities (Connell 1972, Underwood 1985), in part because considerable variation in environmental factors can occur on realistic and quantifiable spatial and temporal scales. The intertidal region experiences temporal variation on at least two scales. First, the effects of environmental changes with daily tidal events may be substantial. The risks of desiccation when exposed at low tide, and of predation and wave action when immersed at high tide, have been considered important (Connell 1972, Underwood 1979). Second, seasonal fluctuations in the dynamics of populations (e.g. Paine and Levin 1981, Quinn 1988) and interactions between species (e.g. Underwood 1984) may result in seasonal changes in community composition. An overriding factor in community structure may be the spatial and temporal unpredictability of larval settlement and subsequent recruitment in intertidal populations (Underwood and Denley 1984, Underwood and Fairweather 1989).

Intertidal mussels often occur in extensive beds which support a diverse invertebrate fauna (Hewatt 1935, Tsuchiya and Nishihira 1985, 1986). These beds can range from a complete cover of mussels to a mosaic of clumps, separated from each other by bare rock or other flora and fauna, and these clumps may act as islands for the mussel-associated fauna. This study examined whether a relationship existed between the areas of mussel clumps and the numbers of species and numbers of individuals of macroinvertebrates in these clumps and whether this relationship was consistent over two different temporal scales.

Methods

The field work for this study was conducted on an exposed rocky shore, west of Berry's Beach, on the southern coast of Phillip Island, Victoria, Australia (38°27'S, 145°15'E, Fig. 1). A flat section (vertical

height range 0.3 m) of the basalt platform, measuring 40 m by 30 m and situated at about mid-tide level, was used. Mussels *Brachidontes (Austromytilus) rostratus* Dunker were common on this platform, forming clumps varying in size from a single mussel to many square metres. Apart from this mussel bed, the majority of the platform was either bare rock or covered by a number of algal species (particularly *Hormosira banksii*).

Mussel clumps between 400 mm² and 30 000 mm² (the largest that could be practically sampled) were collected to examine seasonal differences in the relationship between species number and clump area. Only clumps that were on flat rock, out of standing water at low tide and physically distinct from any nearby clump were collected. Clumps were collected at low tides in 1989, during autumn (March-April: 20 clumps), during winter (June: 24 clumps), during spring (September: 25 clumps) and during summer (December: 25 clumps). Before each clump was collected, it was photographed and later digitized to determine its area. All mussels and other macro-invertebrates (>0.5 mm), as well as sand and debris, from each clump were collected. The clumps were preserved in 10% formalin in seawater and stored for later sorting. The macro-invertebrates were identified to the lowest possible taxonomic level, usually species.

As measures of clump structure, the number and total weight of mussels in all clumps from autumn and winter were measured. Mussels from each clump were counted, put in crucibles and placed in an oven at 60°C for 24 h, and then weighed to the nearest 0.1 g. As an indicator of clump age, the shell length of the largest mussel in each clump was also measured (at least two similarly-sized "largest" mussels were present in all

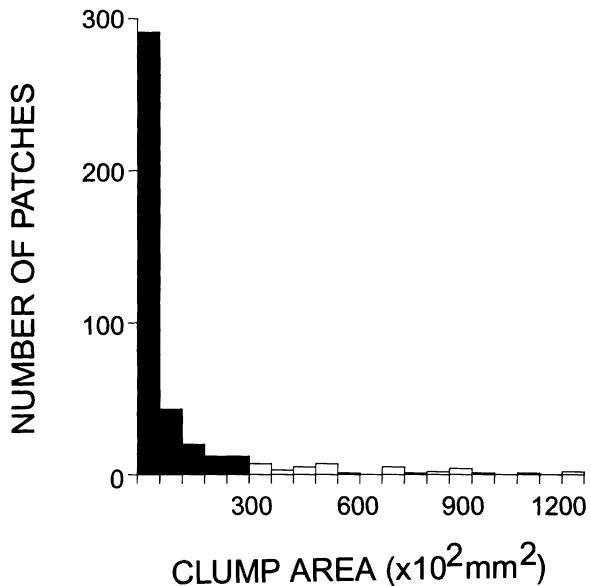


Fig. 2. Frequency distribution of clump areas of *B. rostratus* at the study site. The range of clumps sampled is shaded.

clumps, making it unlikely that these mussels could have washed in from other clumps). To examine how representative the clumps collected were of the whole site, a size-frequency distribution of clumps of *B. rostratus* was determined. Twenty haphazardly chosen 1 m² quadrats were photographed throughout the mussel bed. The area of all complete clumps in the photographs were measured by digitizing.

To examine if species composition of clumps changed diurnally and tidally, clumps of similar size were collected during a successive night low tide, day low tide and day high tide in August 1989. Night high tide samples were not possible. The high tide samples were collected by scraping the clumps into a 300 µm FBA pond net, only with an incoming wave so that all associated fauna was quickly washed into the net. Five clumps were collected at each time and their areas measured as above.

The Random Placement Model was fitted for all seasons: an expected species-area curve, and the variance around it, was generated based on the probability of finding a species in an area being proportional to the abundance of that species (McGuinness 1984b). Approximately two-thirds of the observed points should lie within the region bounded by the predicted number of species plus and minus the standard deviation of the predicted number of species if random placement holds (Coleman 1981, Coleman et al. 1982).

Loehle (1990) has pointed out the problem of comparing species-area curves when the data are transformed to different scales to improve linearity. In the present study, we compared linear ($S = C + z^*A$), exponential ($S = C + z^*\log(A)$) and power ($S = CA^z$) functions by least squares nonlinear modelling (SYSTAT NONLIN, Wilkinson 1990) on untransformed data. Once the best model was chosen on the basis of residual analyses and highest R^2 (which always agreed), an appropriate transformation was used to linearise the relationships and improve variance homogeneity. The equality of the seasonal linear regression slopes was then tested with analysis of covariance (ANCOVA). If the slopes were homogeneous, the ANCOVAs were used to compare adjusted means. Exact probabilities (p) are provided for statistical tests of null hypotheses except when <0.001 ; p values <0.05 were considered statistically significant.

Results

There were significant positive correlations between clump area, clump weight and number of mussels in each clump, pooling autumn and winter samples ($0.929 < r < 0.968$, $p < 0.001$ in all cases). Additionally, the length of the largest mussel in each clump for autumn and winter (as an indication of the clump age) was significantly correlated with clump area for all samples

($r = 0.535$, $p < 0.001$). The size frequency distribution of clumps throughout the mussel bed showed that the majority were below 30 000 mm² (Fig. 2), the largest clump size sampled.

A total of 56 macro-invertebrate species, from 8 phyla, were described for the clumps collected in all seasons (Table 1). These were mostly molluscs (43% of species), polychaetes (21%) and crustaceans (17%). The community was dominated by a few very abundant species: the bivalves *Lasaea australis* and *Xenostrobus pulex*, the barnacle *Chthamalus antennatus*, and the gastropod *Nodilittorina unifasciata*.

Positive species-area relationships occurred for the autumn, winter, spring and summer samples (Fig. 3); a nonlinear power model was overall a slightly better fit than an exponential and both were considerably better than a linear model for three out of four seasons. The power function was therefore used to examine the seasonal curves: larger C values were associated with smaller z values and the number of species increased more rapidly with area in spring, followed by winter and summer, with autumn the having the flattest curve (Fig. 3). Although there appeared to be some undersampling of large clumps in autumn (Fig. 3), the largest clump in that season was not statistically significant as an outlier or as an influential point. A formal test of differences between seasonal species-area relationships was done using analysis of covariance (ANCOVA). Graphical analysis of residuals showed that the species-area relationships were best linearized by log transformations of both number of species and area, which also improved variance homogeneity. The ANCOVA showed no significant difference between slopes of these linear regressions but there were significant differences between adjusted mean log number of species (Table 2a). A conditional Ryan's multiple comparison test (Day and Quinn 1989) on adjusted mean log species number showed there were significantly more species per area (c. 10 more species) in winter and spring than in autumn and summer. Although the ANCOVA did not reject the null hypothesis of parallel slopes of the log species-log area lines, these lines must by definition converge at the origin and the comparison of the linear regressions will be least accurate at small clump sizes. Given this constraint, the increased number of species in winter and spring probably represents a difference in asymptotic species richness.

Fitting the Random Placement model showed that the observed species-area curves were significantly below the predicted Random Placement curve in autumn (only 55% of observed points inside ± 1 standard deviation), winter (52%), spring (48%) and summer (24%), indicating the observed increasing species richness with area was not simply a passive sampling phenomenon.

Positive relationships between total number of individuals and clump area occurred for all four seasons (Fig. 4); a linear model was as good a fit as the nonlinear power and exponential functions except in spring.

Table 1. The numbers of individuals of each species recorded in this study. Clumps within each sampling period are pooled and + indicates present but not counted.

	Autumn	Winter	Spring	Summer	Low day	Low night	High day
Phylum Mollusca							
Class Bivalvia							
<i>Xenostrobus pulex</i>	278	407	830	759	236	206	245
<i>Lasaea australis</i>	4953	7217	8251	9207	1284	1385	1121
Class Gastropoda							
S. Cl. Prosobranchia							
<i>Nodilittorina unifasciata</i>	740	156	104	291	25	20	6
<i>Bembicium nanum</i>	15	23	31	39	7	5	2
<i>Nerita atramentosa</i>	42	28	32	52	11	3	6
<i>Lepsiella vinoso</i>	25	50	33	51	8	21	6
<i>Thais orbita</i>	3	30	13	6	0	0	1
<i>Dicathais baileyan</i>	0	0	1	4	0	0	0
<i>Clypidina rugosa</i>	4	2	1	2	0	0	1
<i>Cellana tramoserica</i>	0	30	13	18	3	4	2
<i>Patelloida alticostata</i>	0	0	1	1	0	0	0
<i>Patelloida insignis</i>	0	2	2	0	0	0	0
<i>Patelloida latistrigata</i>	17	15	21	8	3	2	0
<i>Notoacmea alta</i>	194	274	307	426	31	36	56
<i>Notoacmea flammea</i>	0	1	6	9	0	2	1
<i>Collisella mixta</i>	0	0	15	31	0	1	0
<i>Austrocochlea constricta</i>	50	118	77	54	8	5	2
<i>Phasianella australis</i>	1	1	1	0	1	0	0
<i>Phasianella ventricosa</i>	0	1	0	0	0	0	0
Prosobranch spp. 1	10	0	0	0	0	0	0
Prosobranch spp. 2	1	0	0	0	0	0	0
Prosobranch spp. 3	0	1	0	0	0	0	0
S. Cl. Pulmonata							
<i>Siphonaria diemenensis</i>	5	3	3	22	1	0	1
<i>Onchidella patelloides</i>	0	0	0	1	0	0	0
Class Polyplacophora							
Chiton spp. 1	0	0	3	1	0	0	0
Phylum Chelicerata							
Class Acarina							
Acarina spp. 1	0	1	0	0	0	0	0
<i>Desis marinae</i>	0	0	1	0	0	0	0
Class Pycnogonida							
Pycnogonida spp. 1	0	0	1	1	0	1	0
Phylum Crustacea							
Class Cirripedia							
<i>Chthamalus antennatus</i>	331	565	345	853	255	98	135
<i>Catomerus polymerus</i>	1	0	1	3	0	0	1
<i>Ibla quadrivalvis</i>	0	0	0	1	0	0	0
Class Malacostraca							
Order Decapoda							
<i>Cyclograpus audouinii</i>	2	19	28	17	1	4	4
<i>Pinnotheres hickmani</i>	0	1	5	2	0	0	0
Order Amphipoda							
<i>Allorchestes compressa</i>	32	779	814	688	115	108	145
<i>Jaera</i> spp. 1	0	9	26	1	0	13	9
Order Isopoda							
<i>Zuzara venosa</i>	0	24	6	1	4	4	6
Order Tanaidacea							
Tanaid spp. 1	0	0	1	0	0	0	0
Class Copepoda							
Harpacticoid spp. 1	0	607	972	9	12	47	78
Phylum Annelida							
Class Polychaeta							
Family Cirratulidae							
Cirratulid spp. 1	0	0	1	1	0	0	0
Family Polynoidae							
Polynoid spp. 1	0	1	0	0	0	0	0

(cont.)

Table 1.
(Cont'd).

	Autumn	Winter	Spring	Summer	Low day	Low night	High day
Family Nereidae							
<i>Perinereis</i> spp. 1	54	107	127	225	28	17	15
Nereid spp. 1	0	0	5	1	0	0	0
Nereid spp. 2	0	0	6	3	0	0	0
Family Syllidae							
<i>Odontosyllis polycera</i>	0	1	6	15	0	1	1
<i>Typosyllis</i> spp. 1	7	22	52	59	8	22	19
<i>Typosyllis</i> spp. 2	12	1	9	19	0	3	0
Family Spionidae							
<i>Boccardia proboscidea</i>	0	12	12	31	0	0	0
Family Spirorbidae							
Spirorbid spp. 1	+	+	+	+	0	0	0
Family Serpulidae							
<i>Galeolaria hystrix</i>	+	+	+	+	+	+	+
Family Terebellidae							
Terebellidae spp. 1	0	0	1	0	0	0	0
Phylum Nemertea							
Nemertine spp. 1	0	2	10	6	0	1	1
Nemertine spp. 2	0	0	0	0	0	2	1
Phylum Platyhelminthes							
Class Turbellaria							
Polyclad spp. 1	1	19	23	8	0	8	4
Phylum Cnidaria							
Class Anthozoa							
Order Actinaria							
<i>Actinia tenebrosa</i>	1	2	2	0	0	0	3
<i>Oulactis muscosa</i>	0	2	2	3	0	0	0
Class Hydrozoa							
Hydroid spp. 1	0	6	56	0	0	10	1
Phylum Sipuncula							
Sipunculid spp. 1	0	1	1	0	0	0	0

Graphical analysis of residuals showed that linearity and variance homogeneity of these relationships were improved by log transformations of both number of individuals and area and a subsequent ANCOVA showed no significant difference between slopes or adjusted mean log number of individuals between seasons (Table 2b).

The areas of clumps sampled at each phase of the tide were not significantly different (ANOVA, $F_{2,10} = 0.19$, $p = 0.824$; 2 areas missing due to inadequate photographs). There was no significant difference in log transformed numbers of species between times (ANOVA, $F_{2,12} = 3.65$, $p = 0.058$; Fig. 5) nor in the log-transformed total number of individuals between times (ANOVA, $F_{2,12} = 0.01$, $p = 0.992$; Fig. 5).

Discussion

The positive curvilinear relationships between the number of species of macroinvertebrates inhabiting clumps of *Brachidontes rostratus* and the area of the clump are

similar to those found in many other species-area studies (Connor and McCoy 1979, McGuinness 1984a, Loehle 1990). In marine habitats, positive species-area relationships have been reported for decapods on coral heads (Abele and Patton 1976), for intrasponge macrofauna (Westinga and Hoetjes 1981), for sessile organisms on settlement plates (Schoener and Schoener 1981), for macroinvertebrates inhabiting specimens of an intertidal alga (Gunnill 1982, Stoner 1985), and for invertebrates within clumps of the mussel *Mytilus edulis* (Tsuchiya and Nishihira 1985). McGuinness (1984b) also described positive species-area relationships for macroflora and fauna on intertidal boulders but he found considerable spatial variation in the numbers of species.

For all seasons, there was a lower asymptotic levelling of the species-area curves than predicted by the Random Placement Model, indicating that there were fewer species per area for this community than would be predicted by a passive sampling explanation. McGuinness (1984b) argued that this pattern implies that some factor must consistently increase diversity on larger clumps (or decrease it on smaller clumps), given that the predicted

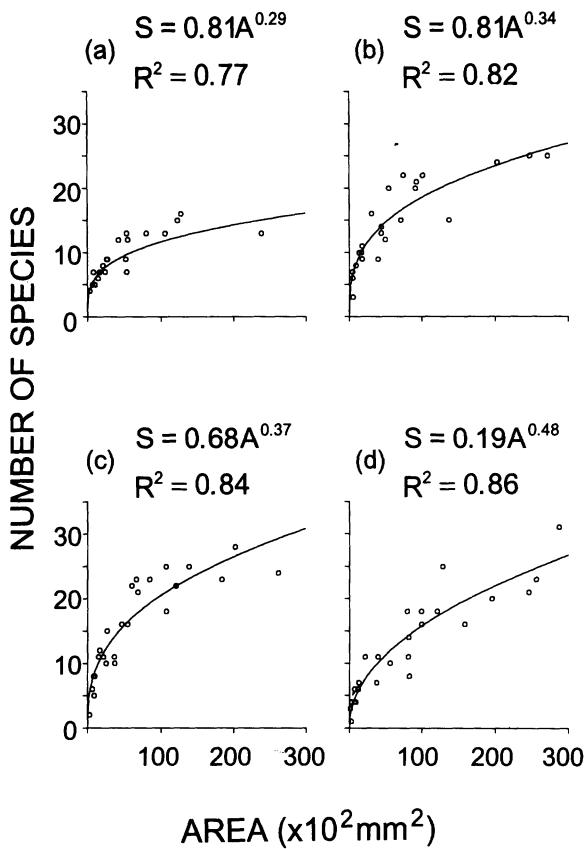


Fig. 3. Relationships between the number of species and clump area for (a) autumn, (b) winter, (c) spring and (d) summer. Fitted curves and equations are power functions, where S is species number and A is clump area (mm^2).

and the observed curves must converge at the asymptote. Although we could not identify the underlying ecological mechanism in this study, larger clumps of mussels were comprised of more mussels, which may have increased habitat diversity (Tsuchiya and Nishihira 1986), and appeared to be older (based on largest mussel size), which would allow more time for species colonization of clumps. In contrast, Abele and Patton (1976) demonstrated that the Random Placement Model could explain decapod diversity on coral heads and McGuinness (1984b) found the same result for some, but not all, of his boulder communities. Although random sampling effects have been proposed as causes for increasing species number with area in marine "islands" (e.g. Stoner 1985), the Random Placement Model has not been tested in other marine species-area studies.

The curvilinear species-area relationships in this study were best modelled by the power function although it was only a slight improvement over the exponential. Opinions vary over the biological significance of parameters from mathematical descriptions of spe-

cies-area relationships (Connor and McCoy 1979, Gould 1979, Martin 1981, Sugihara 1981, McGuinness 1984a, Lomolino 1989, Loehle 1990). Although the values of z from the power functions in the present study were significantly >0.25 (Gould 1979) in all seasons except autumn (using 95% confidence levels around z from nonlinear regression – see Loehle 1990), the large seasonal differences in the values of both C and z are of much greater significance. This seasonal variation clearly makes comparisons of these parameter estimates difficult to interpret and also makes the value of mathematical descriptions of species-area curves based on single-time sampling questionable.

Few previous studies of species-area relationships have considered the importance of temporal variation. Stoner (1985) recorded no significant difference between wet and dry seasons for log species – log plant weight relationships of macrocrustaceans on algal plants in the tropics, despite higher abundances in the wet season. In contrast, Schoener (1974), Osman (1977), Kay and Keough (1981) and Keough and Butler (1983) have all found considerable seasonality in colonization curves for marine epifaunal communities; in at least one

Table 2. (a) Linear log species number – log area regressions and ANCOVA comparing slopes and adjusted means. (b) Linear log individual number – log area regressions and ANCOVA comparing slopes and adjusted means.

(a)

Season	Slope	Adjusted mean		
Autumn	0.331 ± 0.062	2.239 ± 0.096		
Winter	0.392 ± 0.069	2.549 ± 0.088		
Spring	0.490 ± 0.072	2.590 ± 0.087		
Summer	0.469 ± 0.072	2.271 ± 0.087		
Source of variation	df	MS	F	p
Slopes	3	0.161	2.514	0.064
Residual	86	0.064		
Adjusted means	3	0.774	11.479	<0.001
Residual	89	0.067		

(b)

Season	Slope	Adjusted mean		
Autumn	0.627 ± 0.251	5.580 ± 0.249		
Winter	0.876 ± 0.120	5.574 ± 0.225		
Spring	0.880 ± 0.135	5.734 ± 0.221		
Summer	0.982 ± 0.228	5.398 ± 0.221		
Source of variation	df	MS	F	p
Slopes	3	0.701	1.740	0.165
Residual	86	0.403		
Adjusted means	3	0.469	1.136	0.339
Residual	89	0.413		

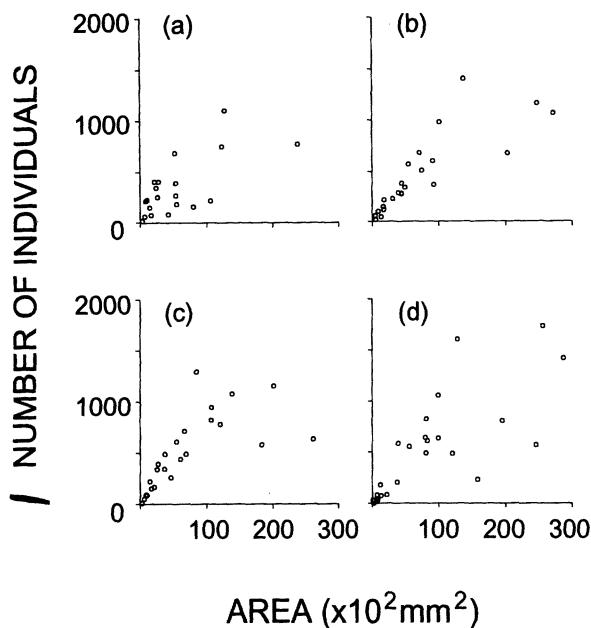


Fig. 4. Relationships between the total number of individuals and clump area for (a) autumn, (b) winter, (c) spring and (d) summer.

case, this has produced seasonal differences in species-area relationships in this habitat (Schoener and Schoener 1981). The results obtained in the present study demonstrate that seasonal variation in species composition and species-area relationships can potentially confound comparisons between communities based on single-time sampling and future studies on island systems should attempt to account for seasonal variation.

The reduced number of species per area in autumn, and to a lesser extent in summer, compared with winter and spring may be due to physical stress on local shores in summer and autumn when high temperatures often coincide with extremely low tides in the middle of the day. Parry (1982) and Quinn (1988) have shown for a nearby shore (10 km east of Berry's Beach) that limpets can suffer intense seasonal mortality as a result of food shortage, and seasonal movements of intertidal gastropods in response to physical stress are also common (Underwood 1979). The seasonal differences appeared not to be simply a result of short-term variation as there was no significant difference in species number between day low tide, day high tide and night low tide. The fewest species were, however, recorded at day low tide, suggesting again that physical factors at low tide may restrict the abundance of some species.

Underwood and Fairweather (1989) have pointed out the stochastic nature of marine populations and communities, emphasising the considerable temporal and spatial variation in recruitment of species with planktonic larval stages as a major cause. Spawning (Underwood

1974, Starr et al. 1990), larval abundance and recruitment for many species of marine invertebrates show strong seasonal peaks (e.g. intertidal barnacles in N.S.W., Caffey 1985). Although we know little of the biology of some of the rarer species found in these mussel clumps (e.g. mites, pycnogonids), the majority of species recorded have a planktonic stage in their life cycle and should show seasonality in recruitment patterns. Schoener (1974) and Osman (1977) have both argued that seasonal variation in colonization curves on marine hard substrata is determined primarily by seasonality in larval abundance. It is also likely that many of the species in the mussel clumps would show high variability in recruitment at the scale separating the clumps we sampled (i.e. <1 m); considerable settlement variability at this spatial scale has been demonstrated for barnacles (Caffey 1985, Raimondi 1990). Therefore, a combination of seasonal recruitment and mortality patterns may explain the seasonal difference in number of species and the high turnover of species between seasons may be due to the spatial unpredictability in recruitment patterns of most species.

Neither island biogeography theory nor the explanations for positive species-area relationships predict how abundances should be related to area. Previous studies in marine habitats have shown increasing abundance

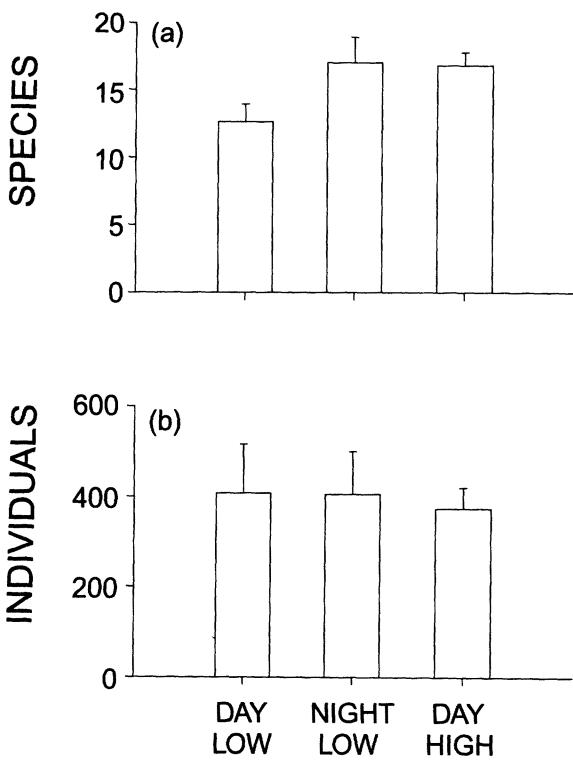


Fig. 5. The mean number (\pm SE) of (a) species and (b) individuals recorded from clumps collected at daytime low tide, night low tide and daytime high tide.

with island area (Westinga and Hoetjes 1981, Gunnill 1982, Stoner 1985, Tsuchiya and Nishihira 1985), as shown here for mussel clumps. Compared to the species-area relationships, however, the fits of the various models for the relationships between total numbers of individuals and area were worse (due to markedly increased variance in numbers of individuals with area) and more variable between seasons, the relationships were less obviously curvilinear, and there was no significant seasonal difference in the number of individuals for a given area. It may be that the total numbers of individuals a clump of a given size can support is relatively fixed by availability of resources (e.g. surface area, microalgae or detritus) and the priority of arrival of recruits determines which species occur (Stoner 1985). Turnover of these species would thus be high and species number could vary between seasons, based on differential recruitment times of potentially dominant species, whereas total numbers of individuals would stay relatively constant. This argument implies that competition is the dominant structuring agent in this community, although the importance of predation or physical disturbances at this small spatial scale is difficult to assess.

In summary, the positive species-area relationships found in this study were not simply a sampling phenomenon, although the underlying mechanisms were not identified. Significant seasonal variations in the shape (and parameter estimates) of the species-area curves were found and studies on species-area relationships must consider seasonal variation and small-scale unpredictability, particularly in marine habitats.

Acknowledgements – We would like to thank P. Fairweather and S. Lake for helpful criticism of the manuscript, K. Nicholls for assistance in sorting samples, G. Poore of the National Museum of Victoria for expert identification of many invertebrates and the Zool. Dept at the Univ. of Melbourne for use of their field station at Rhyll. Particular thanks to the numerous people who assisted in the field.

References

- Abele, L. G. and Patton, W. K. 1976. The size of coral heads and the community biology of associated decapod crustaceans. – *J. Biogeog.* 3: 35–47.
- Arrhenius, O. 1921. Species and area. – *J. Ecol.* 9: 95–99.
- Caffey, H. M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. – *Ecol. Monogr.* 55: 313–332.
- Coleman, B. D. 1981. On random placement and species-area relationship. – *Math. Biosc.* 54: 191–215.
- , Mares, M. A., Willig, M. R. and Hsieh, Y. H. 1982. Randomness, area and species richness. – *Ecology* 63: 1121–1133.
- Connell, J. H. 1972. Community interactions on marine rocky intertidal shores. – *Ann. Rev. Ecol. Syst.* 3: 169–192.
- Connor, E. P. and McCoy, E. D. 1979. The statistics and biology of the species-area relationship. – *Am. Nat.* 113: 791–833.
- Day, R. W. and Quinn, G. P. 1989. Comparisons of treatments after an analysis of variance in ecology. – *Ecol. Monogr.* 59: 433–463.
- Gleason, A. H. 1922. On the relationship between species and area. – *Ecology* 3: 158–162.
- Gould, S. J. 1979. An allometric interpretation of species-area curves: the meaning of the coefficient. – *Am. Nat.* 114: 335–343.
- Gunnill, F. C. 1982. Effects of plant size and distribution on the numbers of invertebrate species and individuals inhabiting the brown alga *Pelvetia fastigata*. – *Mar. Biol.* 69: 263–280.
- Hewatt, W. G. 1935. Ecological succession in the *Mytilus californianus* community as observed in Monterey Bay, California. – *Ecology* 16: 244–251.
- Kay, A. M. and Keough, M. J. 1981. Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Perna bicolor* at Edithburgh, South Australia. – *Oecologia (Berl.)* 48: 123–130.
- Keough, M. J. and Butler, A. J. 1983. Temporal changes in species number in an assemblage of sessile marine invertebrates. – *J. Biogeog.* 10: 317–330.
- Loehle, C. 1990. Proper statistical treatment of species-area data. – *Oikos* 57: 143–145.
- Lomolino, M. V. 1989. Interpretations and comparisons of constants in the species-area relationship: an additional caution. – *Am. Nat.* 133: 277–280.
- MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press, Princeton.
- Martin, T. E. 1981. Species-area slopes and coefficients: a caution on their interpretation. – *Am. Nat.* 118: 823–837.
- McGuinness, K. A. 1984a. Equations and explanations in the study of species-area curves. – *Biol. Rev.* 59: 423–440.
- 1984b. Species-area relations of communities on intertidal boulders: testing the null hypothesis. – *J. Biogeog.* 11: 439–456.
- Osman, R. W. 1977. The establishment and development of a marine epifaunal community. – *Ecol. Monogr.* 47: 37–63.
- Paine, R. T. and Levin, S. A. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. – *Ecol. Monogr.* 51: 145–178.
- Parry, G. D. 1982. The evolution of the life histories of four species of intertidal limpets. – *Ecol. Monogr.* 52: 65–91.
- Quinn, G. P. 1988. Ecology of the intertidal pulmonate limpet *Siphonaria diemenensis* Quoy et Gaimard. I. Population dynamics and availability of food. – *J. Exp. Mar. Biol. Ecol.* 117: 115–136.
- Raimondi, P. T. 1990. Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. – *Ecol. Monogr.* 60: 283–309.
- Schoener, A. 1974. Colonization curves for planar marine islands. – *Ecology* 55: 818–827.
- and Schoener, T. W. 1981. The dynamics of the species-area relation in marine fouling systems: I. Biological correlates of changes in the species-area slope. – *Am. Nat.* 118: 339–360.
- Starr, M., Himmelman, J. H. and Therriault, J. 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. – *Science* 247: 1071–1074.
- Stoner, A. W. 1985. *Penicillus capitatus*: an algal island for macrocrustaceans. – *Mar. Ecol. Progr. Ser.* 26: 279–285.
- Sugihara, G. 1981. $S = CA^z$, $z = 1/4$: A reply to Connor and McCoy. – *Am. Nat.* 117: 790–793.
- Tsuchiya, M. and Nishihira, M. 1985. Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of island size on community structure. – *Mar. Ecol. Progr. Ser.* 25: 71–81.
- and Nishihira, M. 1986. Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. – *Mar. Ecol. Progr. Ser.* 31: 171–178.
- Underwood, A. J. 1974. The reproductive cycles and geographical distribution of some common eastern Australian

- prosobranchs (Mollusca: Gastropoda). – Aust. J. Mar. Freshwat. Res. 25: 63–88.
- 1979. The ecology of intertidal gastropods. – Adv. Mar. Biol. 16: 111–210.
 - 1984. Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. – Oecologia (Berl.) 64: 211–222.
 - 1985. Physical factors and biological interactions: the necessity and nature of ecological experiments. – In: Moore, P. G. and Seed, R. (eds), The ecology of rocky coasts. Hodder and Stoughton, London, pp. 372–390.
 - and Denley, E. J. 1984. Paradigms, explanations and generalizations in models for the structure of intertidal communities on rocky shores. – In: Strong, D. R., Simberloff, D., Abele, L. G. and Thistle, A. B. (eds), Ecological communities. Princeton Univ. Press, Princeton, pp. 151–180.
 - and Fairweather, P. G. 1989. Supply-side ecology and benthic marine assemblages. – Trends Ecol. Evol. 4: 16–20.
 - Westinga, E. and Hoetjes, P. C. 1981. The intrasponge fauna of *Spheciospongia vesparia* (Porifera, Demospongidae) at Curacao and Bonaire. – Mar. Biol. 62: 139–150.
 - Wilkinson, L. 1990. SYSTAT: The System for Statistics. – SYSTAT, Inc., Evanston.