

Testing scale variance in species–area and abundance–area relationships in a local assemblage: an example from a subtropical boulder shore

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Abstract Constancy or scale variance of species–area and abundance–area relationships has rarely been considered within relatively small spatial domains of a local assemblage. Patterns of species/abundance–area relationships were experimentally investigated in a stone-associated molluscan community on a subtropical boulder shore. In order to systematically examine the effects of variation in habitat area while maintaining other habitat characteristics constant through time, naturally occurring stones were selected and divided into different size classes according to surface area and used as habitat units for regular monitoring of a mobile molluscan community. Species richness and abundance (number of individuals and biomass) of molluscs scaled with stone area, but the power or double-logarithmic regression was not always the best description of the species–area relationship. Seasonal scale invariance was shown by the species–area relationship, whereas scale variance was clearly recognizable in the abundance–area relationships. The latter phenomenon was generated mainly by large stones contributing disproportionately to increases in molluscan abundance in particular. Furthermore, there was a negative effect of small habitat area whereby molluscan abundance was disproportionately reduced on small stones. Some temporal variation in the observed patterns was also recognizable, with higher species richness and abundance in spring than in winter, again with larger stones showing preponderant importance. This study thus demonstrates the significance of scale variance/invariance in species/abundance–area relationships, even within relatively small spatial scales of local habitat.

Keywords Species richness · Abundance · Biomass · Molluscs · Spatial scales · Habitat

Introduction

The relationship between the number of species and the area from which the species were recorded (the species–area relationship) constitutes one of the classic ecological patterns that has been the focus of concerted research effort in community ecology (Williams 1943; Rice and Kelting 1955; Simberloff 1976; Connor and McCoy 1979; McGuinness 1984a; Quinn and Harrison 1988; Douglas and Lake 1994; Rosenzweig 1995; Tokeshi 1999; Connor et al. 2000; Crawley and Harral 2001; Chittaro 2002). Much debate has been raised over its possible explanations, including the effect of area itself, passive sampling and the diversity of microhabitats present in a habitat (Williams 1943; MacArthur and Wilson 1967; McGuinness 2000; Triantis et al. 2003; Turner and Tjørve 2005; Drakare et al. 2006). Similarly, population abundance of terrestrial organisms, particularly insects, birds and mammals, were found to be positively related to area (Connor et al. 2000). There have been few attempts to examine such abundance–area patterns alongside species–area patterns for a set of biota. In particular, few aquatic assemblages have been subjected to a simultaneous analysis of species–area and abundance–area relationships. This may be related to the fact that species/abundance–area relationships can be constructed only for well-known assemblages and that the idea was closely linked to island biogeographical theory where terrestrial biota are of principal concern (MacArthur and Wilson 1967; Rosenzweig 1995).

On the other hand, studies on benthic assemblages in boulder-dominated habitats have been instrumental in the

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testing and development of theories in community ecology (Osman 1977; Sousa 1979a, b; McGuinness and Underwood 1986; Douglas and Lake 1994; Chapman and Underwood 1996; Townsend and Scarsbrook 1997; Barnes and Lehane 2001; Chapman 2002a, b). Whereas patterns of diversity in hard-bottom habitats including boulder shores have been investigated intensively from various angles (Osman 1977; Connell 1978; Sousa 1979a, b, 1984; Shanks and Wright 1986; Davies and Wilce 1987; Cusson and Bourget 1997; Smith and Otway 1997; Cruz Motta et al. 2003), few studies have closely examined the relationships between species/population abundance and area. Though not true islands, boulder habitats may technically be considered as island patches for some groups of benthic organisms and, therefore, investigation into the species–area and abundance–area relationships of these biota can potentially throw new light onto their community organization.

In the case of species–area relationships on large spatial scales, Rosenzweig (1995) drew attention to systematic variation in the slopes of species–area regressions among different categories of habitat, e.g., nested areas in a mainland, islands in an archipelago, and collections of separate islands. This relates to an important issue of “scaling” in ecological patterns (Schneider 1994) and raises a question as to the constancy or scale variance of species–area and abundance–area relations within small to medium spatial scales of a local habitat. The present study is aimed at elucidating the scale-associated patterns of species–area and abundance–area relationships in a mobile molluscan assemblage of a subtropical boulder shore in the western Pacific. A particular focus of this analysis is to examine scale variance/invariance in species–area and abundance–area relationships within a small spatial domain of a local assemblage. Scale variance would manifest itself as significant differences in parameter values when regression lines are fitted to data covering different spatial ranges from the same local assemblage. The rejection of this hypothesis is the acceptance of the alternative, i.e., scale invariance, of the relationships. In order to look into this issue, we first checked the regressions using different plotting schemes, as there is no inherently superior scheme of regression in this discipline. Second, we examined patterns of species/individual accumulation with two different ways of accumulating habitat areas, large to small areas versus small to large areas, in order to identify area-related variation in diversity and abundance. Third, we examined the scaling effect of a large area by applying regression analysis to two subsets of data encompassing partially different spatial domains. These analyses were applied to seasonal data so that seasonal variation in scale variance/invariance in this community may be identified. Consideration was given to the implications of scale variance with

respect to the maintenance of diversity in boulder-shore communities.

Materials and methods

Study site

The study site was located in a relatively sheltered, gently sloping, intertidal boulder field on the Amakusa Shimosima Island, southwestern Japan (32°31′N, 130°02′E). The field extends for approximately 200 m along the shore and roughly 50 m toward the sea. The study site was bordered by rocky formations on both landward (high-tidal level) and seaward (low-tidal level) sides, forming a large, shallow pool during high tide, which remained unperturbed even during the typhoon season. Disturbance mainly occurred in the form of human activities during low tide when locals searched for different species of edible molluscs. The stony shore consisted of relatively small stones (10–20 cm in the longest dimension) resting on a coarse sand/gravel substrate. The stones were mostly of weathered chert/rhyolite and were oval and flat in shape. Some boulders in the low intertidal field were covered by macroscopic algae in winter, but most were bare and devoid of sessile organisms all year round. Stony shores in this area support rich assemblages of molluscs, gastropods in particular (Takada 1996, 1999; Takada and Kikuchi 1990; Tokeshi et al. 2000), which generally occur attached to stones rather than scattered in the substrate matrix underneath (Ota and Tokeshi 2000, 2002; Paruntu and Tokeshi 2003).

Experimental design

In order to assess the effect of variation in area while keeping variation in other factors of the habitat to a minimum, preselected stones of different sizes were used for experimental monitoring through time of the mobile molluscan community. Prior to the experiment, stones (of similar shapes and surface texture) were collected from above the upper tidal level, digitally photographed for area calculation (Scion Image 4.0.2), and labeled using small waterproof paper tags glued to the top surface. Sixty stones were sorted into six geometrical size classes (ten each class) according to top surface area (cm²): A 25–50, B 50–100, C 100–200, D 200–400, E 400–800, F 800–1,600. Although an attempt was made to collect stones of relatively similar sizes, the within-size class variation was relatively large (especially in the two largest size classes due to the scarcity of large stones); mean \pm standard deviation (SD) for each size class was: A 37.7 \pm 6.8, B 71.5 \pm 12.1, C 154.6 \pm 32.3, D 288.0 \pm 57.0, E 569.4 \pm 124.1, F 950.6 \pm 104.2 (cm²).

The 60 stones were randomly placed in the midintertidal zone of the study site (about 130 cm above mean chart datum) with a minimum distance between neighboring stones of 1.2 m in July 2002, 1 month before starting the observation. The space underneath the stones was naturally variable and to some extent depended on the stone size and the characteristics of local substrate matrix, but no manipulation of the substrate matrix was carried out to avoid extra disturbance to the habitat. Gastropod species in this habitat could move across substrates when immersed, but mobility apparently varied among species and between individuals of different sizes.

Data collection

The 60 individually marked stones were monitored at an interval of 28 days between August 2002 and July 2003. In order to guarantee a consistent sampling regime under temporally variable environmental conditions, 12 stones (two per class) were sampled daily at low tide (day or night); all sampling was completed in 5 days on each sampling occasion. The following steps were taken for sampling: (1) all visible molluscs on the top surface of a stone were picked up and kept in a plastic container; (2) a chain was placed along the bottom perimeter of the stone on the substrate and a large plastic tray placed beside the stone; (3) the stone was lifted from the substrate, placed on the tray, and all molluscs on the stone and the substrate were collected. The lifting was conducted as swiftly as possible to avoid the loss of snails from the bottom of the stone—the bail-out behavior (Wright and Shanks 1995); (4) molluscs were identified and measured in situ with digital calipers to the nearest 0.01 mm before being returned to the habitat; (5) the stone was replaced in its original position and orientation as demarked by the chain (cf. Chapman and Underwood 1996).

As the stones were not overturned before being placed on the tray, disturbance was minimal. Our observations suggest that the efficacy of this method was very high and the few snails that fell off the boulder were easily recovered in the plastic tray. For the current analysis, however, we combined the data of the three microhabitats (top, bottom, and underneath). Before the collection of organisms, the surface temperature of the top and bottom of each stone, as well as underneath each one, was recorded with an infrared thermometer (Horiba IT-540). Use of a headlight for nighttime sampling caused no more disturbance than approaching the stones at daytime, when some snails were seen to drop from the top surfaces of stones. With careful approach to the sampling site, however, the frequency of these incidents (referring almost exclusively to *Monodonta labio*) was kept low and did not affect overall data handling.

Our observations confirmed that the sampling interval of 28 days was more than sufficient to allow complete recovery of the mobile molluscan assemblages on the stones: comparison of nonsampled versus regularly sampled stones showed no difference in faunal composition and abundance. Indeed, our unpublished data suggest that these assemblages can recover in less than 2 weeks. Similarly swift recovery of mobile faunas on boulder shores was reported by Chapman and Underwood (1996) and McGuinness (1984b). Therefore, whereas we did not have detailed information on the mobility and abundance of each species in these assemblages, stones in the study site were considered to be equally exposed to rapid colonization by mobile molluscan species, as those species were capable of moving across gravel substrates.

Biomass calculation

For most species, biomass was calculated using the size–weight information given in Tokeshi et al. (2000); for the species not reported therein (*Nipponacmea radula*, *Cellana nigrolineata*, *C. toreuma*, *Siphonaria japonica*, *Muricodrupa fusca*, *Clipeomorus bifasciata*, and *Omphalius rusticus*), extra collections were made, and Tokeshi et al.'s (2000) method was followed to estimate biomass. For three species (*Acanthopleura japonica*, *Monodonta neritoides*, and *Telasco velatus*) that were not abundant enough to determine a length–weight relationship, the equations for species with similar shapes were used for biomass estimation.

Data analysis

Traditionally, data subjected to the analysis of species–area relationships often had a nested structure whereby smaller areas were subsets of larger ones. This was inevitable in the case of data spanning over large spatial scales; for example, an island is nested within an archipelago that in turn is nested within a geographical region (Rosenzweig 1995). Data on relatively small spatial scales can be either nested or random (e.g., Crawley and Hurrell 2001). As the present study was focused on analyzing the relationships within relatively small spatial scales of stone habitats, the data were amenable to both nested and nonnested structures, and these were both considered in the analyses. Nested structure was generated by cumulative enumeration of abundance values and stone areas such that smaller areas were progressively nested within larger ones, whereas nonnested structure lacked such a treatment. For examining the species–area relationships in the molluscan community, the number of species (Y) was regressed against area (X) in four different forms: arithmetic X – arithmetic Y , logarithmic X – logarithmic Y , arithmetic X – logarithmic Y , and logarithmic X – arithmetic Y . As measures of species

richness, annual mean number of species and annual total number of species were calculated for each stone and subsequently used either cumulatively or noncumulatively for regressions. Area refers to the sum of three layers, i.e., top and bottom surfaces of the stone plus the area underneath it, which is equivalent to the projected surface area for the predominantly flat stones occurring in the study site and used for the experiment.

For examining area-related variance, two analytical procedures were applied to seasonal data. In the first procedure, the pattern of habitat fragmentation was assessed by arranging the stones in (1) increasing (from small to large) and (2) decreasing (from large to small) order, and the values of species richness and abundance as well as stone surface area were cumulatively enumerated and plotted following Quinn and Harrison's (1988) approach. The second procedure was more specifically aimed at investigating the possibly preponderant effect of larger stones on community patterns. For this, regression analysis was performed with two different groupings of stones, the first including the largest size class but excluding the sublargest classes (D and E), i.e., A – C + F (line 1 or "L1"), and the second including the sublargest but not the largest class, i.e., A – E (line 2 or "L2"). In other words, L1 encompassed a wider range of spatial scale than L2 did, whereas the two shared the same data toward the lower range of values. Therefore, if scale invariance prevails particularly toward higher values, the two lines would have the same regression. In this case, the values (area, species richness, abundance, and biomass) were enumerated either cumulatively or noncumulatively for small to large stones within each size class and a regression line was fitted to each grouping. The homogeneity of the slopes model and the analysis of covariance test were applied to assess differences between regression lines.

Note that we employed regression analysis despite the fact that our data were statistically not independent due to unavoidable spatiotemporal autocorrelation, which was expected from the nature of the sampling and analytical procedures adopted. In fact, this problem is inherent in the analyses of all species–area data with nested structure. The net consequence of this is that, due to partial dependency or autocorrelation in our data, detection of scale variance or a real difference between regression lines that may be present in the data would become more difficult. In other words, given the null hypothesis of no difference in the slope value (scale invariance), our approach would increase the risk of type II error while reducing that of type I error. However, in the context of the present study, this situation is more desirable than the opposite case of increased type I error that would lead to a false indication of scale variance where none, in reality, exists. It is therefore more instructive to search for variability despite the dependent structure

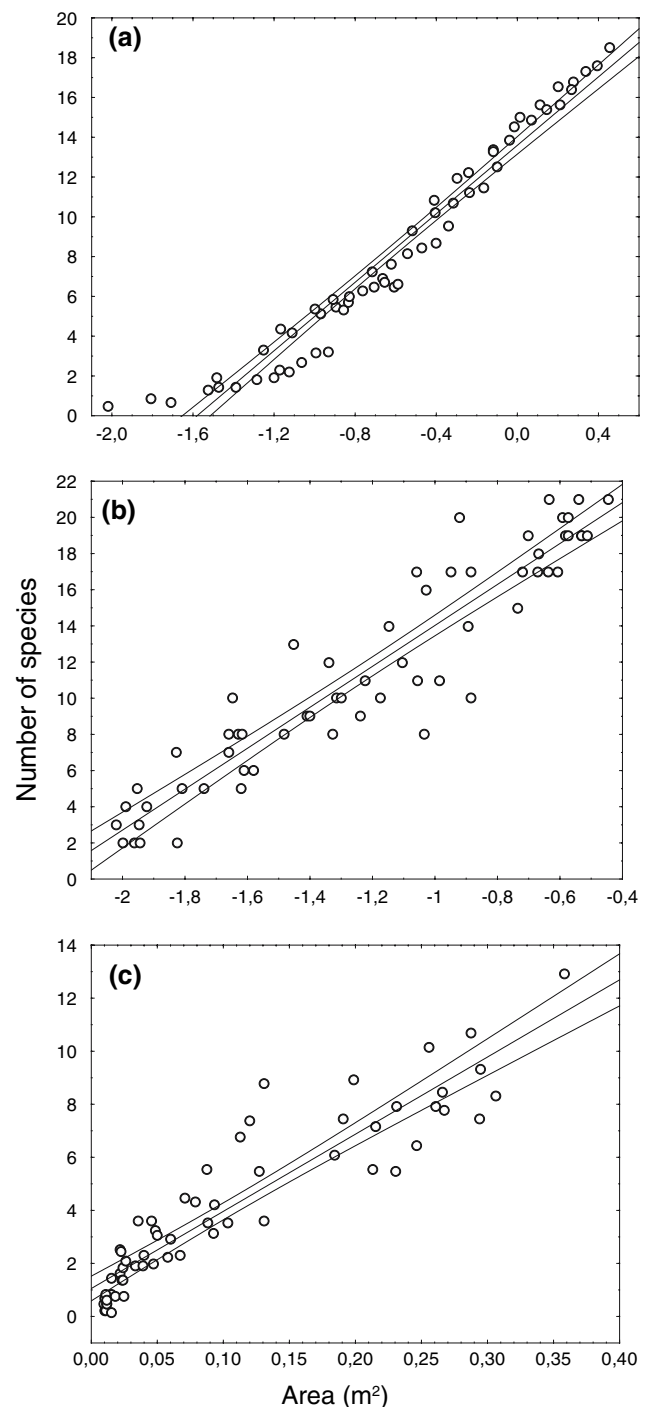


Fig. 1 Relationship between the number of species and stone area. **a** Cumulative annual mean number of species plotted against (log) cumulative area. **b** Annual total number of species plotted against (log) noncumulative area. **c** Annual mean number of species plotted against noncumulative area

in the data that would tend to homogenize parameter values.

For seasonal comparisons, critical values were adjusted by the Bonferroni correction. All analyses were performed with Statistica 6.0 (StatSoft Inc.).

Results

As expected, species richness positively scaled with habitat (stone) area (Fig. 1). In terms of the coefficient of determination (r^2), the semilogarithmic form (log X – arithmetic Y) was a slightly better descriptor when the annual cumulative mean number of species and the annual total number of different species were regressed against stone area (Fig. 1a, b). On the other hand, a double arithmetic form (arithmetic X – arithmetic Y) was a marginally better descriptor for the regression of the annual mean number of species versus stone area (Fig. 1c) than logarithmic forms (i.e., log X – arithmetic Y and log X – log Y , Table 1). Nevertheless, differences in the explanatory power of the regressions were small, as all these forms could explain well over 80% of the variation in species richness measures.

The cumulative species–area plots (Fig. 2a) showed variable patterns through time. In autumn and spring, the large to small line clearly increased faster and remained above the small to large line. In neither situation did a group of smaller stones, equal in area to a larger one, harbor more species. A slightly different pattern was seen in winter and summer where the initially faster rise of the large to small line was overtaken in the middle range by the small to large line, ending with the latter above the former.

The pattern for individual numbers (abundance) was temporally more consistent, with the large to small line always rising faster and remaining above the small to large line (Fig. 2b). The difference between the two lines was larger in spring and summer than in autumn and winter. It is interesting to note the difference between the species and the individuals’ lines (Fig. 2a–b), the former demonstrating an asymptotically increasing pattern and the latter a linear one.

Figure 3 shows the plotting of mean cumulative values (from small to large within a size class) of the number of

species, individuals, and biomass versus cumulative area in different seasons. The two lines (L1 and L2) for species richness showed similar patterns of increase, i.e., there were no significant differences between these two lines. However, those for the number of individuals and biomass demonstrated marked differences (Table 2), with L1 being consistently steeper than L2. The magnitude of difference varied with time, with the spring data showing the largest difference, followed by summer, winter, and autumn.

Area-related variation was also demonstrated by the plots of abundance measures against noncumulative stone area for each season (Fig. 4). Note that overall species richness remained at the same level through time (i.e., the maximum number of species was around 12 for the largest stones), whereas the number of individuals and biomass varied seasonally, with higher values recorded in spring and summer. Marked nonlinearity indicative of scale variance was observed for the number of individuals and biomass, whereas the pattern for species richness was somewhat equivocal and variable among seasons. The observed nonlinearity was caused by low values of molluscan abundance on relatively small stones coupled with high values associated with the largest stone size class that had large within-size class variation in abundance measures.

Discussion

The present study demonstrated consistent patterns of species/abundance–area relationships despite some temporal variation. Whereas species–area relationships have been treated only indirectly in most previous studies on boulder/stone-dominated ecosystems, McGuinness (1984b) [see also Douglas and Lake (1994) for a freshwater

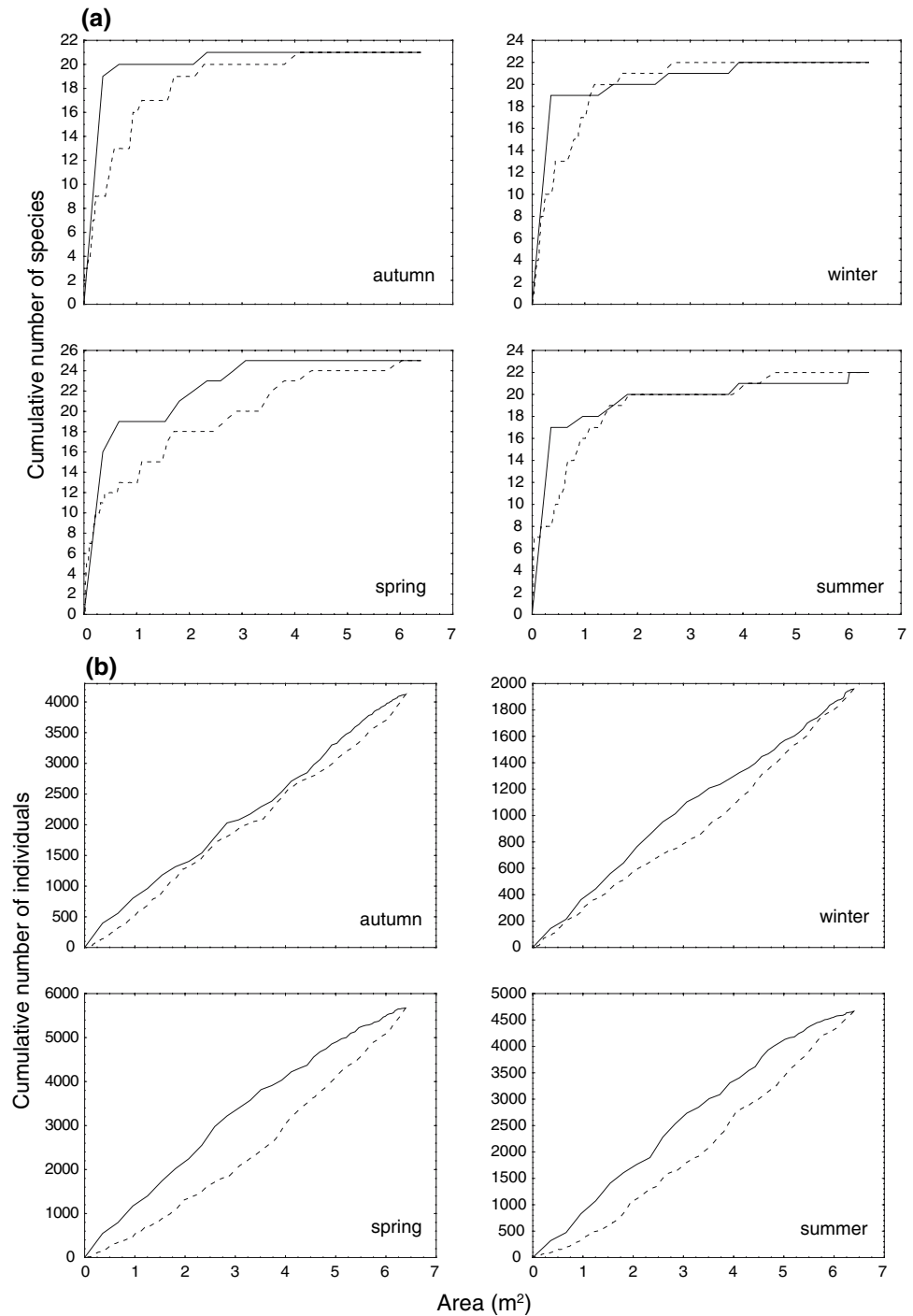
Table 1 Different forms of regression with coefficient of determination (r^2) exceeding 0.8 for the relationships between measures of species richness (Y) and habitat area (X), $Y = a + bX$

Variables		Regression form	Parameters		
X	Y		a	b	r^2
AC	SAMC	Log X – arith Y	13.59	8.604	0.950
		Log X – log Y	1.172	0.6214	0.919
AN	STA	Log X – arith Y	25.34	11.32	0.886
		Log X – log Y	1.629	0.5298	0.821
AN	SAM	Arith X – arith Y	1.054	29.09	0.852
		Log X – log Y	1.477	0.8568	0.843
		Log X – arith Y	11.26	5.854	0.836

All regressions were statistically significant at $P < 0.001$

AC cumulative area, AN noncumulative area, SAMC annual mean number of species (cumulative values), STA annual total number species for each stone, SAM annual mean number of species

Fig. 2 Cumulative number of **a** species and **b** individuals on stones arranged from largest to smallest (*solid line*) and from smallest to largest (*dashed line*) for seasonal data



example] reported highly variable and unpredictable patterns in a boulder-shore system, though parameters for the observed relationships were not given. Amongst different regression schemes, the exponential (semilog) form was a better fit for the annual cumulative mean number of species and the annual total number of different species; the annual mean number of species versus area relationship was better fitted by a simple arithmetic form. It is interesting to note that in neither case was one form markedly superior to

another (Table 1). The power law, which has been used more widely than other models to describe species–area relationships in different assemblages, was not appreciably better than other forms. Clearly, our analyses concur with the view that the log–log regression is neither the only nor the best fit to most species–area data (Connor and McCoy 1979; McGuinness 1984a). In fact, small-scale patterns are often better fitted by the semilog (species vs. log area) plotting (Williams 1943; Rosenzweig 1995).

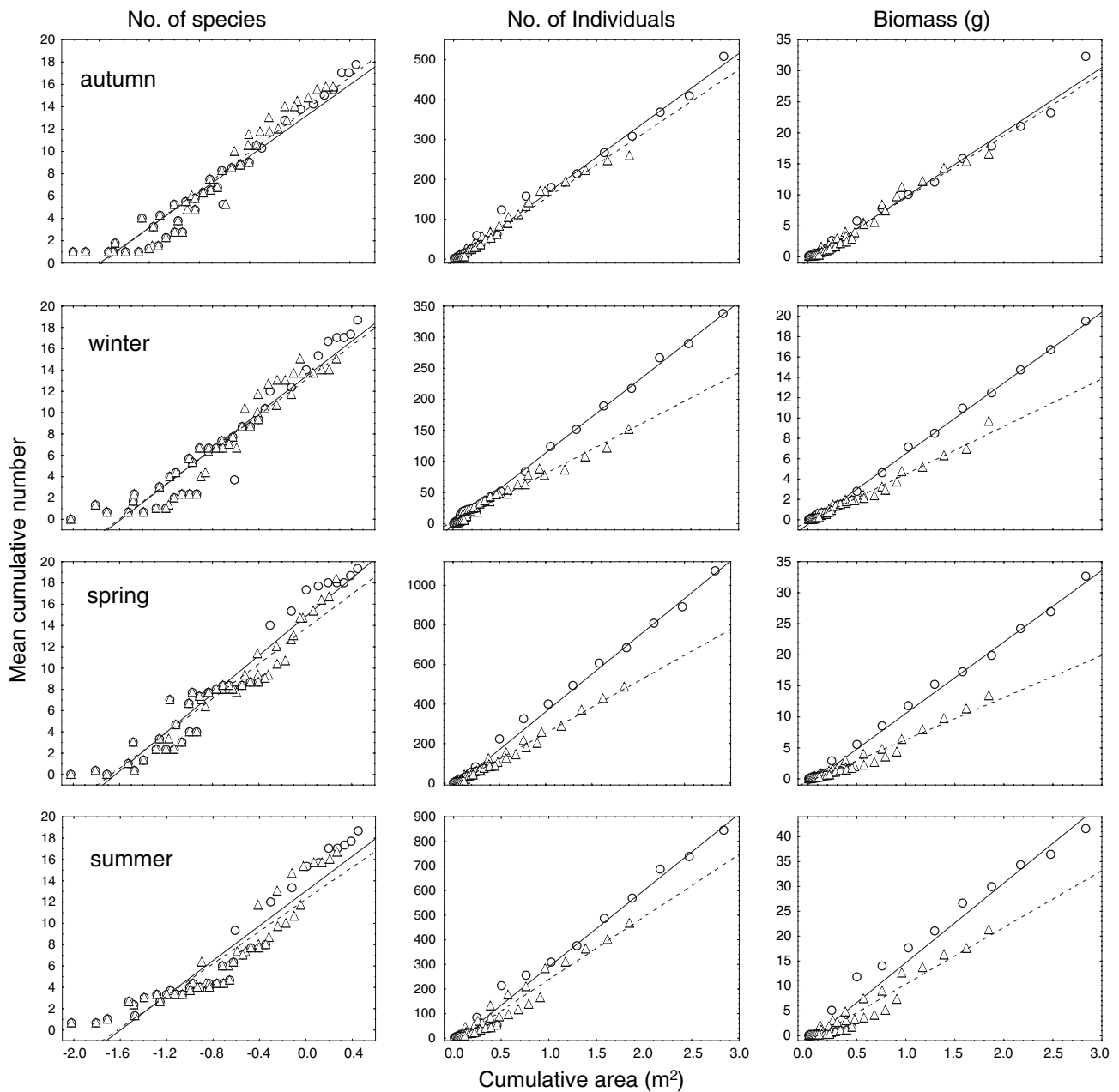


Fig. 3 Cumulative mean number of species (*left*), individuals (*centre*), and biomass (*right*) versus cumulative area of stones (log scale for species only) for seasonal data. L1 circles with *solid line*; L2 triangles with *broken line*

The slope of the species–area regression for the boulder-shore molluscan community was well within the range of values reported for different communities (Connor and McCoy 1979). This suggests that the rate of species increase in this habitat resembles that of others and lends credence to the view that the species–area relationship is considered as one of few authentic laws of community ecology (Schoener 1976). On the other hand, the scattering of data points with noncumulative values indicates variation independent of area. It is possible that similar-sized stones differ in the number and types of microhabitats

(e.g., pits, cracks, under-stone space, etc.) available for colonisation; this trend in the species–area curves (area-independent variation) at small spatial scales has been described as “the small island effect” (Lomolino 2000; Lomolino and Weiser 2001).

Our data demonstrated the negative effect of small habitat size whereby a collection of small stones had a more impoverished community than did a large stone of similar area (Fig. 2). This phenomenon was more marked in autumn and spring than in winter and summer, indicating temporal variation in community pattern. This seasonal

Table 2 Comparison of two regression lines (L1 and L2) encompassing partially different spatial ranges (see text) for cumulative mean number of species, individuals, and biomass versus cumulative stone area

Measure	Season	L1		L2		L1 versus L2 <i>F</i>
		<i>b</i>	<i>r</i> ²	<i>b</i>	<i>r</i> ²	
Species	Autumn	7.992	0.925	8.422	0.907	0.644 ^{NS}
	Winter	8.402	0.918	8.131	0.906	0.239 ^{NS}
	Spring	9.054	0.930	8.172	0.920	2.774 ^{NS}
	Summer	8.155	0.892	7.545	0.857	0.917 ^{NS}
Individuals	Autumn	173.8	0.992	159.4	0.982	12.40*
	Winter	119.6	0.998	79.72	0.971	352.7*
	Spring	382.0	0.993	263.0	0.989	274.2*
	Summer	311.1	0.987	254.5	0.954	31.36*
Biomass	Autumn	10.39	0.988	10.01	0.979	1.640 ^{NS}
	Winter	6.954	0.997	4.677	0.981	390.3*
	Spring	11.51	0.989	6.798	0.960	251.5*
	Summer	16.01	0.974	11.42	0.938	51.40*

Log area was used for the regression of mean number of species

NS $P > 0.05$

* $P < 0.001$ (significance was adjusted with the Bonferroni correction)

variation may be partially related to the milder/harsher environmental conditions in different seasons, which would affect vertical migration in some species (Takada 1996).

The observed crossing of curves in summer and winter (Fig. 2a) was caused by the appearance of three rare species—the limpet *C. toreuma* and the whelk *M. fusca* (in winter) and the whelk *Ergalatax contractus* (in summer)—on the smallest stones of the largest and second-largest size classes (*C. toreuma* and *M. fusca*) and on the second-smallest stones of class C (*E. contractus*). In general, the species present on small stones were just a subset of the species on larger stones: a collection of small stones harbors a lower number of species than a single stone of the same area.

It has been argued that large habitat area is important, as it can accommodate a larger number of individuals of a population, consequently reducing the risk of extinction (MacArthur and Wilson 1967). In contrast, populations in small habitats are considered to be more prone to local extinction. In the present study, the negative effect of small habitat sizes for individual numbers was consistently observed, with the “small stones first” curve being always below the “large stones first” one in all seasons (Fig. 2b). To our knowledge, this is the first time that the pattern was demonstrated for marine benthos. This means that a combination of small stones equaling the area of a single large one will not support the level of population abundance associated with the latter. This, in turn, suggests that the distribution of stone sizes in the intertidal zone would have an important implication for population abundance and maintenance of molluscan assemblages.

Our results agree with those of Douglas and Lake (1994), in which large to small cumulative data for natural and artificial stream stones showed higher diversity than did small to large cumulative data. It is interesting to note, however, that at larger spatial scales, this pattern was reversed (Quinn and Harrison 1988), indicating perhaps an opposite trend in fragmentation processes at different spatial scales. Large portions of landscape are supposed to have more types of habitat that in turn would accommodate more species. However, a subdivision of large area into smaller but still large enough pieces (true islands or continental patches) of landscape would allow the persistence of species populations that may otherwise be competitively eliminated.

Situations at smaller scales in stone-dominated habitats might be very different. Small stones tend to be more uniform in surface structure and habitable space underneath than do large stones. Thus, a set of small stones having the same area as a large one would, on average, have fewer microhabitats and hence a smaller number of species. Indeed, there was a tendency that an increase in species number with area was minimal for small stones, as indicated by the leftward displacement of data points with small *X* from regression lines for species number (Fig. 3) compared with patterns for individuals and biomass.

Scale variance/invariance in species/abundance–area relations

The present study demonstrates that even within small spatial scales, the effects of area on species richness and

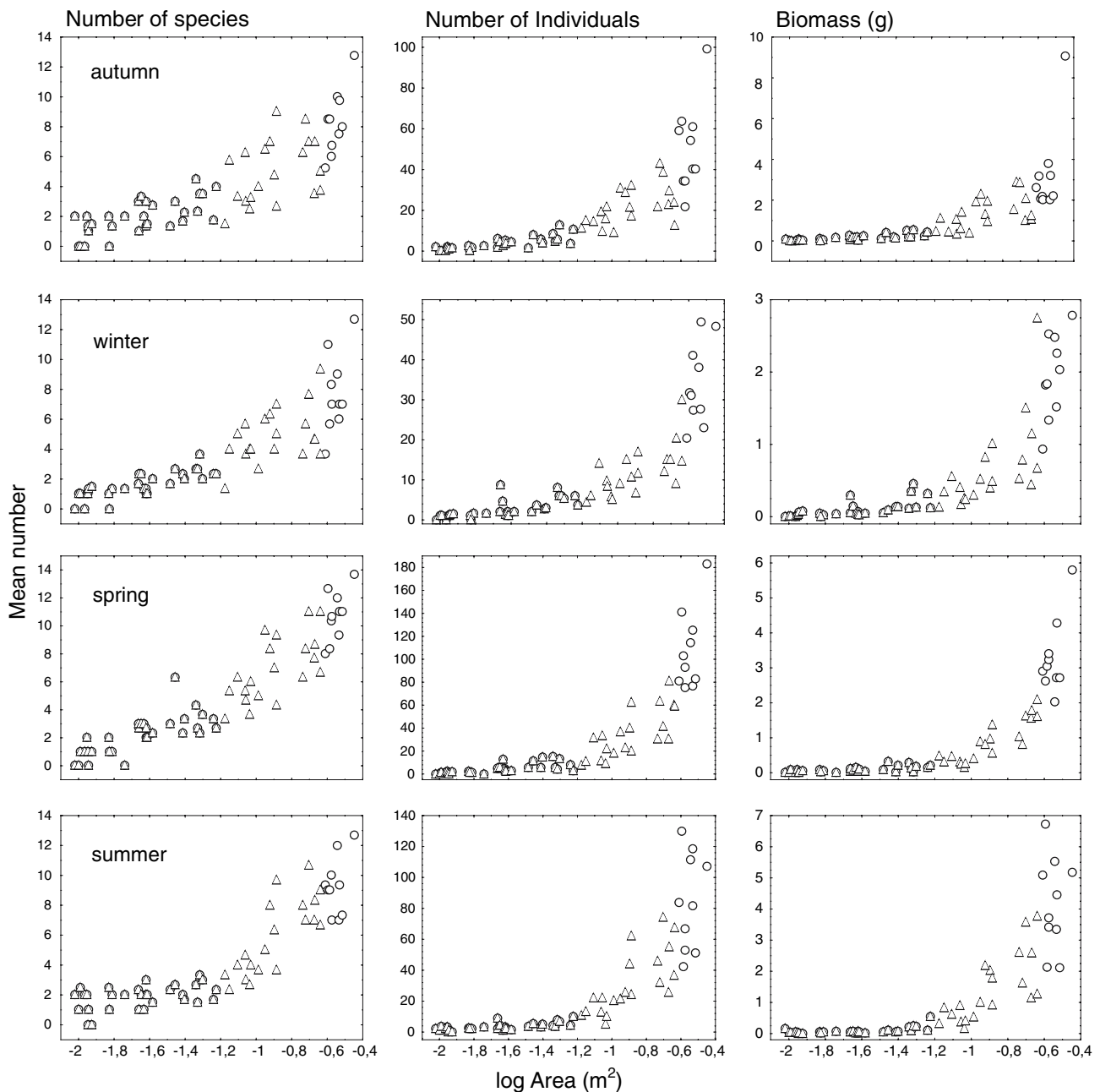


Fig. 4 Mean number of species (*left*), individuals (*center*), and biomass (*right*) versus stone area for seasonal data. L1 circles, L2 triangles

abundance patterns are variable and can be scale dependent. There is a dearth of information on the scaling effects of area on community patterns (richness and abundance) involving small spatial scales, such as within local habitats, despite the fact that spatial and temporal scaling is considered an important issue in population and community ecology (Schneider 1994). Most previous studies on boulder-shore assemblages simply document a general pattern of more species/individuals associated with larger stones without looking into variability in such a pattern.

In many studies, species–area curves have generally been fitted with a single line across the spatial scales sampled. However, Rosenzweig (1995) demonstrated variation in the slope of species–area regression depending on the range of spatial scales considered, and other studies noted the sigmoidal shape of species–area relations (Lomolino 2000; Lomolino and Weiser 2001). In the present study, although the species–area data were adequately described by linear relationships, there was a tendency for data points with small area values to depart from linearity, as stated above,

whereas the abundance–area data demonstrated more complex, scale-dependent patterns (Fig. 3).

Scale variance in abundance–area relationships was evident in the slope discrepancies of two regression lines (L1 and L2, Fig. 3) and strong curvilinearity in noncumulative data (Fig. 4). Although the number of individuals may not necessarily correlate with biomass (i.e., many small individuals may have less biomass than few large ones of the same species), similar patterns that emerged between number and biomass measures were striking. Nonsignificant difference between the two biomass lines in autumn was due to slightly smaller individuals on the largest stones (size class F) compared with other size classes, leading to similar slope values. This was also linked to the fact that the difference between the lines for individual numbers was significant but much smaller than in other seasons.

The nonlinear pattern shows an accelerated increase in molluscan abundance with stone area above a certain size ($\sim 0.25 \text{ m}^2$ in the present study). This was basically generated by the largest (and, to a lesser extent, the second largest) size class of stones, which suggests that larger stones (islands) have disproportionate importance in providing habitats to molluscan species. This, in turn, indicates that patchiness in distribution of boulder-shore organisms (e.g., Chapman 2002a) is influenced by the occurrence (i.e., frequency and distribution) of relatively large stones on a shore. Heavier, larger stones are less likely to be overturned by waves (Sousa 1979b), buried by sand, or disturbed by human activity and hence are more likely to lead to higher diversity and abundance.

It has been shown that habitat complexity enhances diversity in different aquatic assemblages (McGuinness and Underwood 1986; Takada 1999; Taniguchi et al. 2003; Taniguchi and Tokeshi 2004). In the case of the present study, however, it is unclear to what extent habitat complexity associated with larger stones contributed to increased diversity and abundance. As stated above, habitat stability (reduced physical disturbance) may be an overriding factor here.

In sum, the present study revealed the nature of variability in the species/abundance–area relationships within small spatial scales of a local community of mobile molluscs. The size of stones as habitat islands is important in a boulder-shore system, affecting the diversity and abundance of associated fauna. This, in turn, implies that the planning of protection areas on boulder shores requires careful consideration: not only the most common small stones are needed, but large ones are of particular importance in maintaining the diversity and abundance of local benthic assemblages. The results obtained here have clearly shown that rocks above a certain size harbor a richer community that may withstand the adverse effects of

catastrophic events, such as typhoons, and serve as sources for community recovery.

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