RESEARCH NOTES

Species diversity, abundance and body size in rocky-shore Mollusca: a twist in Siemann, Tilman & Haarstad's parabola?

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May[1] first reported that species richness, abundance of individuals and body size in natural communities were interrelated. According to Morse *et al*[2], no unifying theory for these was possible without viewing their association as a three-dimensional surface. Siemann *et al*[3] provided evidence for grassland insects that species richness (S) and number of individuals (I) within body-size classes (B, calculated as 'biovolume') form a parabola when viewed in three-dimensions (Fig. 1). When projected onto the S-I plane a power-law emerges where $S = I^{0.5}$. Such richness-abundance relationships were shown to hold across numerous body types and a 100,000-fold range of body sizes in five different orders of insects. This finding points to an association between interspecific resource division, abundance and diversity in natural communities that is independent of body size. Moreover, their data suggests that within any taxonomic group, undescribed species are more likely to be of intermediate sizes. This has important implications regarding current

estimates of global diversity[4], and the causes for this diversity, provided that empirical evidence from other taxonomic groups should turn up similar relationships. To investigate if these results represent a general rule, we explored these relationships using mollusc datasets from rocky shore macrofaunal communities sampled along a biogeographical range along the southern Iberian Peninsula.

We sampled littoral faunas along continuous belt transects perpendicular to the water's edge[5,6] at 20 sites stretching from Vila Nova de Milfontes on the Atlantic coast of Portugal to La Manga del Mar Menor, on the Spanish Mediterranean coast (Fig. 2). All samples were taken from outward-facing, unobstructed rocky coasts, with a slope of between 30°–60° to the horizontal during the months of July-September 1993 at low water. At each site a prior generalised shore search was undertaken in order to select the most appropriate and representative location for the transect[7-10].
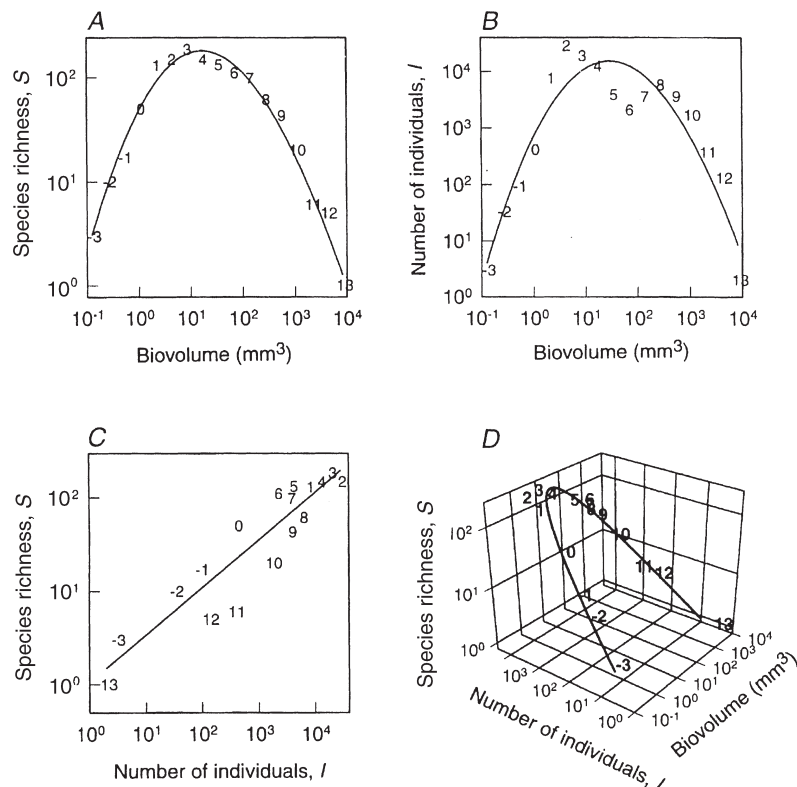
Figure 1. Results obtained by Siemann *et al.* (1996) for body size relationships in insects sampled from 48 grassland fields and savannahs.

A) Relation between species richness (S) per $\log_2$ biovolume class and biovolume (B).
B) Relation between number of individuals (I) per $\log_2$ biovolume class and biovolume (B).
C) Relation between species richness (S) and number of individuals (I) for each $\log_2$ biovolume class.
D) relation between species richness (S) and number of individuals (I) within $\log_2$ biovolume classes and biovolume (B) using fitted curves from A) and B).

For all curves the labels refer to the power to which 2 needs to be raised to obtain the required size class (i.e. 2^{label} mm^3 size class—e.g. the 8 shows where organisms within the 2^8 mm^3, or 256 mm^3 size category, fell on the graph). Curves are fitted by an asymmetric peak function. Reprinted by permission from *Nature* (**380**, p.704) copyright (1996) Macmillan Magazines Ltd.
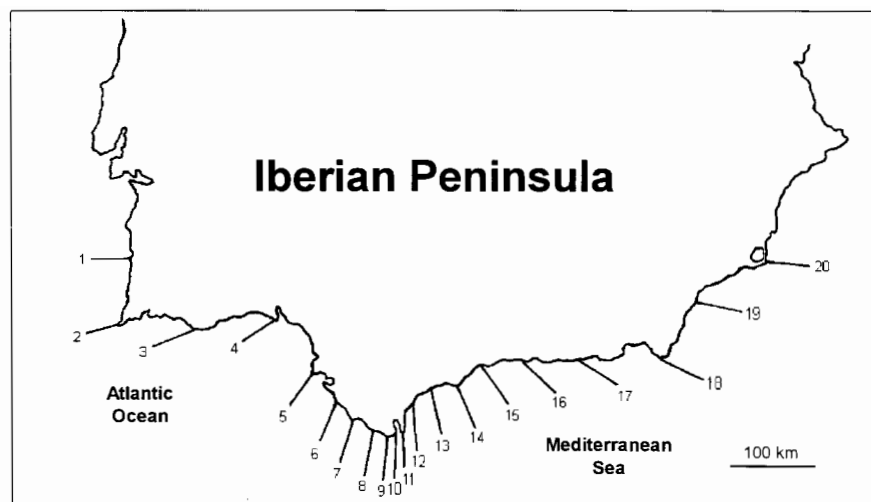
Figure 2. Map of the lower Iberian Peninsula showing the locations of the study sites. They cover a stretch of approximately 1500km of coastline.
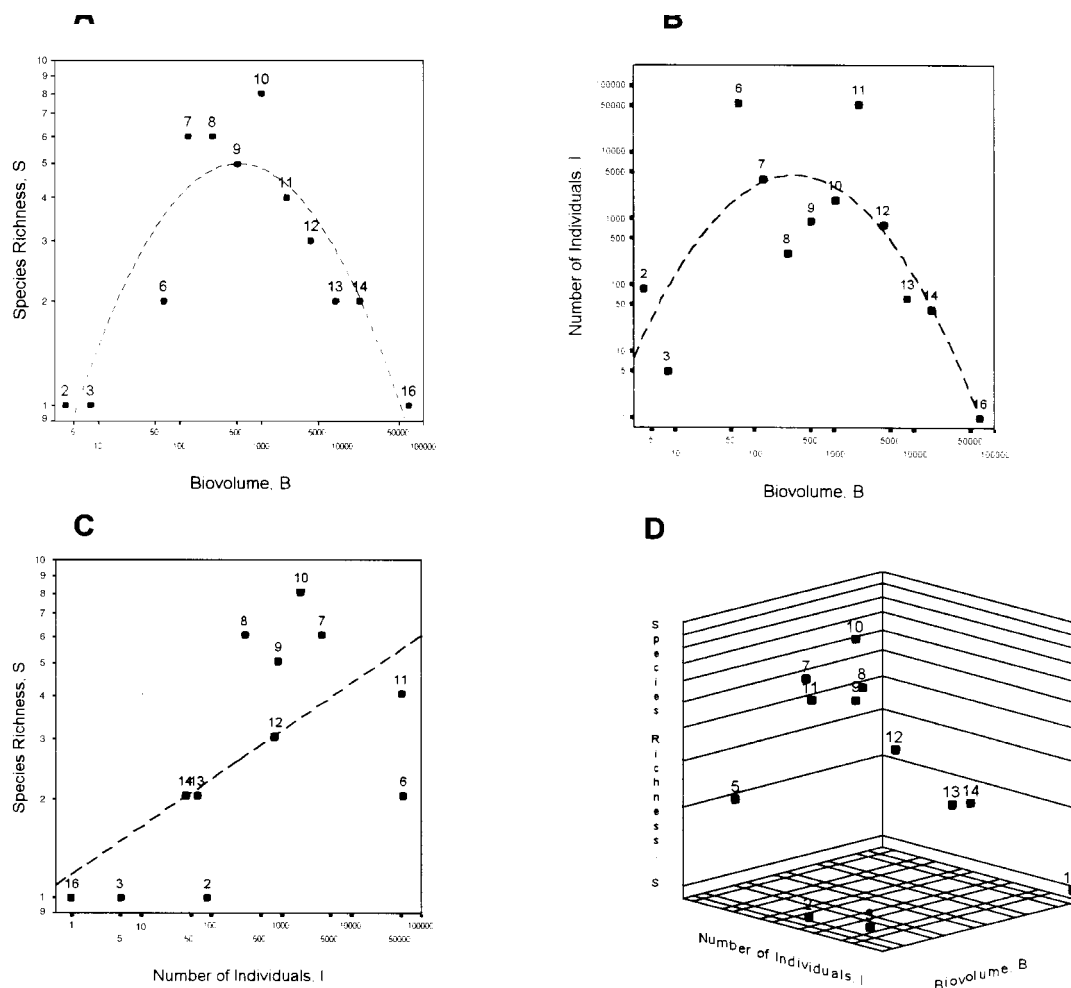

Figure 3. Graphs illustrating the relationships between species richness (S) and abundance (I) within each $\log_2$ biovolume class, and biovolume (B) for the combined datasets for 20 littoral sites from the Atlantic to the Mediterranean. For all curves, labels refer to the power to which 2 needs to be raised to obtain the required size class.

A) Relation between S and B (quadratic regression fit: $R^2=0.826$, F=21.349, $P<0.0005$);
B) Relation between I and B (quadratic regression fit: R2=0.5815, F=6.254, P<0.05);
C) Relation between S and I (linear regression fit: $R^2=0.392$, F=6.440, $P<0.05$);
D) Relation between between S, I and B in three dimensions.

A minimum sampling area of 0.25m^2 per sampling point was determined using Pielou's pooled quadrat method[11], and a rectangular (1m × 0.25m) quadrat, placed vertically against the substrate and parallel to the air-water interface was used to sample the macrofaunal assemblages because the small tidal amplitudes encountered (particularly in the Mediterranean) meant that the recognised littoral zones showed extreme vertical compression. At each transect, all individuals of species found in 12 sampling points from mean low water to the supralittoral were counted, giving a total area coverage of 3m^2 at each site[10]. It should be noted that the methodology was devised to allow an investigation of littoral community structure and diversity, and therefore would not provide an exhaustive species inventory.

As systematic under-sampling of small organisms has been identified as a possible reason for the low numbers of small organisms reported in many studies[4,12], a minimum sampling time of fifteen minutes per quadrat was established. Even following intensified sampling at small sizes no significant increase in numbers occurred. All specimens were identified[13-18] to species or morphospecies (11.9% of total dataset) within known genera. The total fauna for all 20 sites were 41 species in 8 orders totalling 112,985 individuals.

Although not as precise as biomass, biovolume is a relatively

Table 1. Taxonomic information, number of Individuals (*I*) and calculated biovolumes (*B*) for each of the mollusc species used in the analysis. Species within each order are listed in order of increasing biovolume.

Order	Species	Authority	Number of Individuals per species	Calculated Biovolume, *B* (mm^3)
Archaeogastropoda	*Jujubinus sp. A*	Monterosato, 1884	6	150.2
	Diodora gibberula	(Lamarck, 1822)	24	252.5
	Copulabyssia corrugata	(Jeffreys, 1883)	10	324.1
	Patella intermedia	Knapp in Murray, 1857	224	386.9
	Diodora apertura	(Montagu, 1803)	27	514.3
	Gibbula pennanti	(Phillipi, 1846)	75	780.0
	Monodonta articulata	Lamarck, 1822	7	1180.0
	Diodora italica	(Defrance, 1820)	22	1440.6
	Gibbula divaricata	(Linné, 1758)	8	1458.8
	Gibbula umbilicalis	(Da Costa, 1778)	52	1680.3
	Patella caerulea	Linné, 1758	1610	1885.7
	Gibbula richardii	(Payraudeau, 1826)	1	2722.5
	Patella rustica	Linné, 1758	572	4430.0
	Monodonta turbinata	(Von Born, 1778)	47	4847.2
	Patella ulyssiponensis	(Gmelin, 1791)	168	5481.9
	Patella nigra	(Da Costa, 1771)	48	8551.0
	Patella ferruginea	Gmelin, 1791	1	17904.8
Neogastropoda	*Pollia dorbignyi*	(Payraudeau, 1826)	86	7.5
	Ocinebrina edwardsi	(Payraudeau, 1826)	5	267.5
	Nassarius incrassatus	(Stroem, 1768)	5	270.6
	Pisania striata	(Gmelin, 1791)	33	500.6
	Columbella rustica	(Linné, 1758)	2	675.4
	Nucella lapillus	(Linné, 1758)	24	2390.6
	Stramonita haemastoma	(Linné, 1767)	41	20244.0
Mesogastropoda	*Rissoa sp. A*	Freminville in Desmarest, 1814	5	9.1
	Littorina neritoides	(Linné, 1758)	53893	34.8
	Littorina punctata	(Gmelin, 1791)	3469	165.9
	Littorina saxatilis	(Olivi, 1792)	116	173.3
	Trivia monacha	(Da Costa, 1778)	1	973.3
	Littorina littorea	(Linné, 1758)	51	1049.8
Mytiloida	*Mytilaster minimus*	(Poli, 1795)	9	223.1
	Cardita calyculata	(Linné, 1758)	16	453.7
	Chlamys multistrata	(Poli, 1795)	1	1850.6
	Lithophaga lithophaga	(Linné, 1758)	44	2104.1
	Mytilus galloprovincialis	Lamarck, 1819	51196	2758.8
	Crassostrea angulata	(Thunberg, 1793)	14	11026.7
Chitonida	*Chiton cf. olivaceus*	Spengler, 1797	130	136.7
	Acanthochitona fascicularis	(Linné, 1767)	103	1741.7
Gymnomorpha	*Onchidella celtica*	(Cuvier, 1817)	60	60.0
Basommatophora	*Siphonaria pectinata*	(Linné, 1758)	778	515.0
Anaspidea	Aplysia punctata	(Cuvier, 1803)	1	209650.4

accurate measure of space occupied by an organism[19] and is of particular relevance to the primarily space-structured littoral. Biovolume for each species was ascertained by approximating general body shape to the closest geometric form[20]; for example, the equation for a cone was used to calculate the biovolume of patellids. If no simple geometric shape provided a good fit then length, height and breadth were multiplied. Biovolumes calculated in this way were found to agree well ($0.730 \leq \varrho_s \geq 0.978$; n~50; $P < 0.001$, where ϱ_s = Spearman's correlation coefficient) with biovolumes measured by immersing organisms in distilled water at 20°C and measuring the displacement. Between 10 and 100 individuals of each species were used to calculate mean biovolume (B) per species. As sizes were calculated from regional samples, this method does assume that sizes are generally constant across the biogeographic area studied. Although intra-specific size variations were found both within and between sites, with variations in body size spanning five orders of magnitude and the buffering effect of aggregating species into logarithmic size classes, it was felt that variations due to locality would not be large enough to effect any significant displacement between size classes. Table 1 summarizes the results obtained.

The relations between S, I and B were studied for $\log_2$ biovolume classes (*sensu* Siemann et al.). The emergent pattern for all species combined (Fig. 3) is very similar to that obtained for grassland insects although with greater scatter, attributed to the relatively smaller size of the littoral mollusc dataset. Nonetheless, despite the fact that the datasets under comparison stem from widely differing evolutionary pathways, peak species richness and maximum number of individuals occur at intermediate body sizes, and the parabolic pattern persists in the *S-I-B* plot (Fig. 3D). The main difference is that modal biovolumes for molluscs are consistently one order of magnitude greater than those for insects. These patterns also persist when data were analysed at the level of individual sites, although these results fall outside the scope of this initial report.

Of particular interest, however, is the presence of a distinct dip at modal biovolume in the graph of I against B (Fig. 3B). Here, modal biovolumes are seen to fall into two size groups: 10–100m[3], and 1000–10000mm[3], with a reduction in numbers in the intervening (100–1000mm[3]) size interval. Siemann et al's graph (Fig. 1B) shows the same dip at the same size category, although this went unreported. Such a similarity suggests that this may in fact be an important empirical effect within taxonomic groups and not just merely a sampling artefact.

Following the sequential increase in body size categories, values in the *S-I* plot (Fig. 3C) are seen to increase proportionally, loop back on themselves at the upper right hand of the graph because of the dip in abundance, and subsequently drop. This is also evident in Siemann et al.'s Fig. 1C. Thus, it would then appear that the original parabola now folds back on itself close to the apex, generating a unimodal distribution for *S* against *B* but a bimodal one for *I* against *B* (Fig. 4).

Further investigation of these relationships within orders indicates that a shared phylogeny and/or morphology confines organisms to similar size ranges (Fig. 5), and that the distributions obtained are due to the close superimposition of a number of unimodal distributions centred around maximal abundance biovolumes. The degree of overlap is higher for the *S-B* distributions hence only a single maxima was obtained for the aggregated data, in contrast with the *I-B* distributions which clustered around 10–100mm[3] and 1000–10000mm[3], creating the 'dip' at 100–1000mm[3]. This is true for the entire group except for the neogastropods where no distinct peak in numbers occurred at any particular biovolume. An explanation for this deviation may be found in the predatory habits of this gastropod order. Although the modal biovolume for this order fell within the 100–1000mm[3] size interval, the relative invariance in numbers across a thousandfold range of biovolumes could be linked to the trophic structure of the community inhabited. Unlike the other orders, which are sessile grazers or filter feeders, the neogastropods found in the study area are important predators in intertidal ecosystems[20] and their numbers may be determined by the trophic structure of the underlying community and not by other factors.

The breakdown of the correlation between species richness and number of individuals at modal biovolumes may be explained in terms of resource partitioning and of carrying capacity of the habitat. Unused resources (defined as allocations which improve an organism's fitness and hence involves food and habitat selection) allow concurrent co-existence of a variety of species, but if we assume that a certain body size is more physiologically or ecologically efficient and, consequently, more speciose, a point is reached beyond which the environment can not support more than a certain amount of exploitation due to resource limitation. It is known that rates of all biological structures and processes are affected by body size[22-24]. Because the observed dip in our study is consistent in different taxa (similar results were also obtained for intertidal arthropods[10]), as in Siemman et al.'s insect example, it is possible that some form of density-dependent compensation is or has been operating at what may somehow be a 'best' body size for the taxon. It is clear that more detailed and extensive studies in this and other groups are still required, but our results provide preliminary supporting evidence that the relationships reported by Siemann et al. have a wider taxonomic application, as does the observed twist in the parabola. If other studies continue to provide supporting evidence for these patterns, it would suggest that a small subset of rules determines diversity, abundance and body sizes across taxa, which would provide fundamental insights into the origins of the diversity of life on earth.
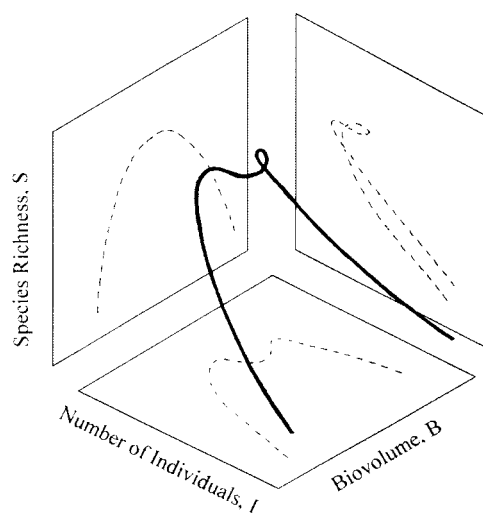
Figure 4. Three-dimensional idealised representation of the proposed relationship between *S*, *I* and *B* based on the dip in abundances observed at modal bivolumes. Siemann et al.'s parabola is now twisted at the apex and folded back on itself, this generating a unimodal *S-B* distribution, but a bimodal I-B distribution. The graph for *S-I* is unaffected by this transformation and remains linear. These are illustrated by projections for each of the *S-I*, *I-B* and *S-B* distributions (dashed lines) onto each plane and are obtained by linking the data points sequentially by size classes, rather than fitting a statistical model. Note that the amount of folding is exaggerated for illustration purposes.

A)

B)
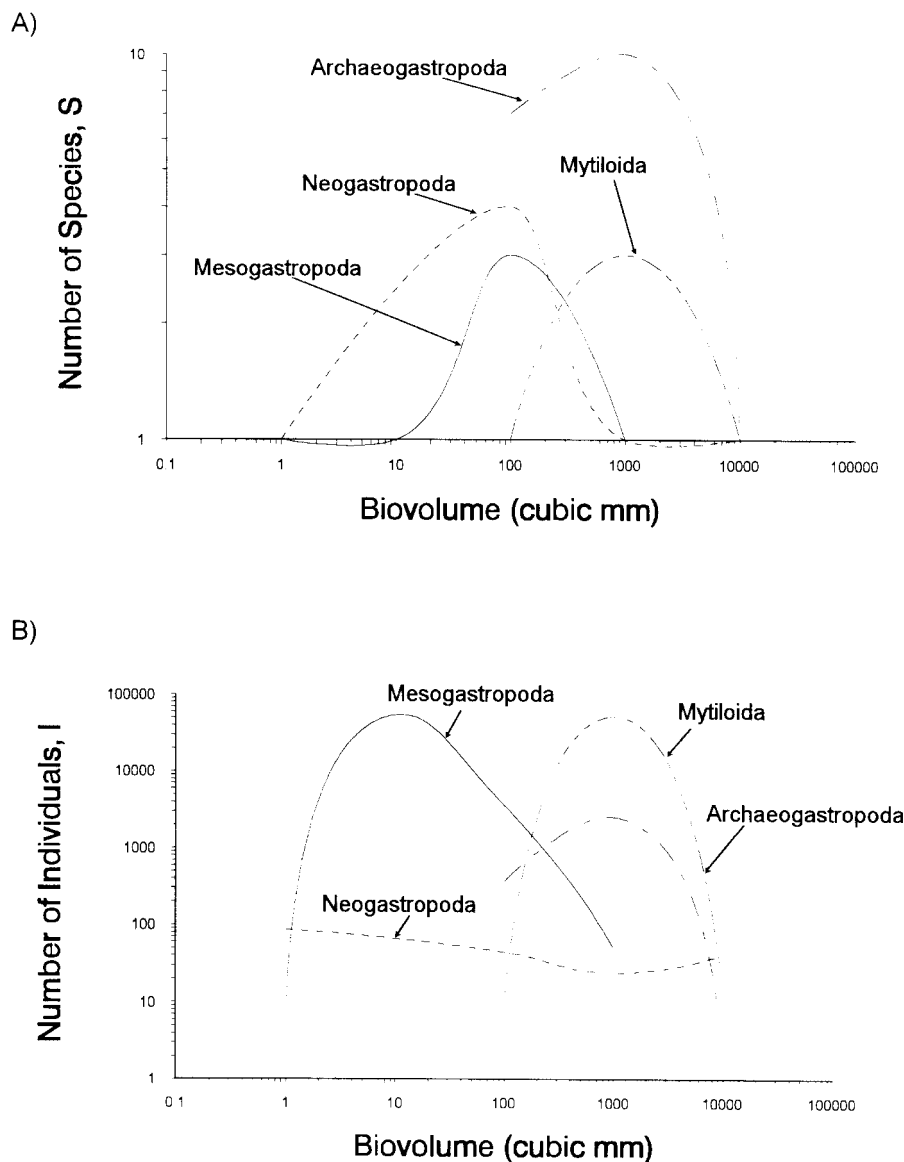
Figure 5. For the four most abundant molluscan orders:

A) Relationship between S per $\log_{10}$ biovolume class and B;

B) Relationship between I per $\log_{10}$ biovolume class and B.

Note how separate unimodal distributions concatenate to form the uni- and bimodal curves evident in Figs. 1 and 3. It then appears that taxonomy plays an important role in generating the multimodal distributions observed.

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