Population Abundance and Body Size in Animal Assemblages [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1994 **343**, 33-39
doi: 10.1098/rstb.1994.0005

Population abundance and body size in animal assemblages

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SUMMARY

Studies of the relationship between body mass and population abundance for terrestrial and aquatic animal species based on pooling data from many taxa and assemblages suggest that abundance scales with mass to the -0.75 power. Because metabolic rate scales with mass as (plus) 0.75, this result has been taken as evidence that all species in assemblages use equal amounts of energy. The evidence for 'energetic equivalence' is, however, equivocal, because within many individual assemblages the scaling of abundance on mass differs significantly from -0.75. Here, we present a summary of patterns of size and abundance in a number of different terrestrial, freshwater and marine animal assemblages, with the aim of discovering whether there is any generality in size–abundance patterns within assemblages, and whether any generality might hold across terrestrial, freshwater and marine environments.

1. INTRODUCTION

Early studies of the relationship between population density and body size (measured as mass) in terrestrial and aquatic animals yielded linear relationships on logarithmically transformed scales (Damuth 1981, 1987; Peters & Wassenberg 1983; Peters & Raelson 1984). The slopes of these relations approximated -0.75, using ordinary least squares (OLS) regression. Because body mass scales with metabolic rate to the 0.75 power (Kleiber 1962), the -0.75 exponent between size and abundance was taken as evidence that a species' abundance is limited by its energetic requirements, and that equal amounts of energy are available to each species in a community: the so-called 'energetic equivalence rule' (Damuth 1981, 1987, 1991; Nee *et al.* 1991). In principle, such arguments ought to apply with equal force to animals living in marine, freshwater, and terrestrial environments. This paper explores body size–abundance relationships for animal assemblages from all three environments, and summarizes patterns, processes and problems in their analysis. An excellent recent review can also be found in Cotgreave (1993).

The main criticism of the earlier studies listed above is that the data are not samples of whole communities, but tend to be compendia from the literature, which may have underestimated the number of rare species, and small-bodied, rare species in particular (Brown & Maurer 1987; Morse *et al.* 1988; Lawton 1989, 1991). Subsequent studies sampling whole assemblages of taxonomically similar animals (albeit over a smaller total size-range) revealed different, polygonal relationships between log body size and log abundance, with intermediate-sized species having peak abundance (Brown & Maurer 1987; Gaston 1988; Gaston & Lawton 1988; Morse *et al.* 1988). These polygons generally showed either no overall correlation between body size and population abundance (Morse *et al.* 1988) or a weak negative relationship of slope much less than -0.75 (Brown & Maurer 1987; Gaston & Lawton 1988; Pagel *et al.* 1991). However, sampling whole assemblages also has problems: for example, such samples may contain transient individuals from species not otherwise resident in the assemblage, inflating the number of apparently rare species observed (Gaston *et al.* 1993). Another criticism of the energetic equivalence rule is that it assumes energy to be equally available to species of all sizes (Lawton 1989). This assumption seems hard to justify, especially across the diversity of terrestrial, freshwater and marine ecosystems, and there is evidence that it is false (Maurer & Brown 1988; see also Pagel *et al.* 1991).

Most species in these assemblages are very unlikely to be energy limited anyway: many small species are no more abundant than many large species (Lawton 1989), even in samples from whole assemblages where the overall slope approximates to -0.75 (Nee *et al.* 1991). In at least one marine invertebrate assemblage which exhibits a clear negative relationship between log body mass and log abundance with a slope of -0.75, energy is known not to be limiting (Marquet *et al.* 1990). If important at all, energetic limitations may be relevant only to the most abundant species (those species adjacent to the negative upper bound slope of a size–abundance polygon) in an assemblage (Brown & Maurer 1987; Lawton 1989, 1991; Blackburn *et al.* 1992, 1993*a*).

A further problem is that the expected value for the slope of a plot of log body mass against log abundance

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Phil. Trans. R. Soc. Lond. B (1994) **343**, 33–39
Printed in Great Britain

for an energy limited population depends on whether reduced major axis (RMA) regression or OLS regression is used (LaBarbera 1987; McArdle 1988; Griffiths 1992). The RMA slope of log body mass against log metabolic rate is 0.8 (Griffiths 1992), so using RMA, abundance would have to scale with mass to the -0.8 power for the energetic equivalence rule to hold.

In sum, the expected relationship between population abundance and body size is not clear. We suspect there is a tendency to draw attention to log abundance–log body size plots that have OLS slopes close to -0.75, because these are consistent with a simple energetic explanation based on per capita energy demands. But as shown above, this theoretical expectation rests on some tenuous assumptions. Here, we present a summary of patterns of size and abundance in a number of different terrestrial, freshwater and marine animal assemblages, with the aim of discovering whether there is any generality in size–abundance patterns within assemblages, and whether any generality might hold across terrestrial, freshwater and marine environments.

2. METHODS

Data on body size–abundance relationships from 19 natural animal assemblages including 17 terrestrial, one freshwater and one marine assemblage, were collated from the literature (see table 1 legend for sources). Species abundances in these assemblages are the number of individuals of the species in a given sampling area. Most of these studies report only the slope of the OLS regression line of log abundance on log body mass for the assemblages studied, but for 15 assemblages the raw data were available to us, allowing calculation of the negative upper bound slope (NUBS) of the log body size–log abundance relationship. It is species near to this slope that are most likely to be energy limited (Lawton 1989). The NUBS was calculated using the method developed by Blackburn *et al.* (1992), and both OLS and RMA regression. If species near the upper boundary of log mass–log abundance plots are energy limited, this slope should approximate to -0.75 (OLS) or -0.8 (RMA).

We also collated data on body size–abundance relationships for eight species compendia (see table 2 legend for sources). Note that the species data in these compendia are compiled from a number of different literature sources, and these relationships cannot be considered as representative of natural assemblages (see Introduction).

In addition, we also report the relationship between body size and abundance in a deep marine demersal fish assemblage (N. R. Merrett, unpublished data; Blackburn & Merrett, in preparation) from the Porcupine Seabight area, in the eastern North Atlantic ocean (49–52°N,11–15°W). Full details of the area and sampling methods are given by Merrett *et al.* (1991*a*,*b*), and a discussion of sampling problems by Merrett & Blackburn (in preparation). We limit ourselves here to a brief summary of these methods. Merrett *et al.* (1991*a*,*b*) reported the demersal ichthyofauna of the continental slope and abyssal plain of the Porcupine Seabight, sampled using three different types of ocean bed trawls. Our analysis is limited to demersal fish from 119 samples collected by one of those nets, the semi-balloon otter trawl, from a sounding range (depth of the ocean bed) of 247–4787 m. Species were not considered part of the deep demersal fish assemblage and were excluded from the analysis if they were only caught at soundings above 500 m, or if they were known to be predominantly pelagic. This left a total of 39 179 individuals of 114 species. Species abundance was taken as the number of individuals of each species summed over all samples.

We used maximum recorded body mass as the measure of body size in the analysis (data supplied by N. R. Merrett). Maximum mass data were available for 58 of the 114 species. Maximum masses for a further 50 species were estimated using data on maximum snout-vent length. Log body mass was regressed on log snout-vent length for those species for which both measures were available. The regression equation was then used to calculate an estimated maximum mass from the snout-vent length of those species for which we had no maximum mass data.

3. RESULTS

Relationships between log body size and log population abundance for species in 20 natural animal assemblages, from 17 terrestrial, one freshwater and two marine ecosystems, together with OLS and RMA regression model estimates of the slopes of the regression lines through these data and OLS and RMA NUBS estimates for 15 of the assemblages, are summarized in table 1. Most, but not all, of these assemblage slopes are negative (table 1), but 12 of the 17 OLS regression slopes reported differ significantly from -0.75. (In addition, Basset & Kitching (1991) found no significant linear negative relationship between body size and abundance in a sample of 759 species of arboreal arthropods associated with an Australian rain forest tree, although they do not report any regression statistics.) In contrast, only two out of 16 OLS NUBS differ significantly from -0.75, although NUBS estimates have very broad confidence intervals (Blackburn *et al.* 1993*a*).

Figure 1 shows the data for the only one of these assemblages that has not previously been published, namely that for the deep demersal fish assemblage from the Porcupine Seabight area. The relationship is negative, but body mass explains only 1% of the variance in abundance (table 1). The OLS NUBS is more steeply negative than that of any other assemblage measured, although there are two assemblages with steeper RMA NUBS.

Systematic deviations of assemblage slopes from predicted values can also be taken as evidence against energetic equivalence. We tested both OLS and RMA slopes for such deviations, using two-tailed binomial tests. Of the 16 assemblages for which the magnitude of the slope was given in the original reference, 13 had OLS slopes shallower (less negative) than predicted by an energetic equivalence rule (binomial $p = 0.02$), and 13

Table 1. *Regression slope and negative upper-bound slope (NUBS) estimates for the relationship between log size and log abundance in 16 natural animal assemblages*

(These assemblages consist of South African dung beetles (Hluhluwe, Mkuze; Blackburn *et al.* 1993*a*), oak canopy beetles from Richmond Park (Richmond; Blackburn *et al.* 1993*a*), rainforest canopy beetles from Brunei (Brunei; Morse *et al.* 1988), bugs from early (early bug), mid (mid bug) and late (late bug) successional plots at Silwood Park (Blackburn *et al.* 1993*a*), British moths (moths; Gaston 1988), auchenorrhyncha from montane rainforest in Vietnam (auchenorrhyncha; Novotny 1992), hoverflies from an English suburban garden (Syrphidae; Owen & Gilbert 1989), British birds from Common Bird Census farmland (CBC farm) and woodland (CBC wood) census plots (Blackburn *et al.* 1993*a*), British (Nee GB) and Swedish (Nee S) breeding birds (Nee *et al.* 1991), British (British winter) and Irish (Irish winter) wintering birds (Blackburn, *et al.* 1994), North American birds (U.S. birds; Brown & Maurer 1987), invertebrates from a pond in York, England (York pond; Blackburn *et al.* 1993*a*), intertidal animals from rocky shore assemblages in central Chile (intertidal; Marquet *et al.* 1990), and deep demersal fish from the Porcupine Seabight area of the North Atlantic ocean (deep demersal; N. R. Merrett unpublished data, Blackburn & Merrett, in preparation). Measure is the original body size measure in the data; sizes for those assemblages for which body length was the original size measure were converted to masses using appropriate length–mass regressions (see footnote). r^2 is the amount of variance in population abundance explained by the correlation with body size across all species in each assemblage. R is the regression slope through all species in the assemblage, calculated using either OLS or RMA regression; NUBS is the same for the negative upper bound slope. N_R is the sample size for r^2, R_{OLS} and R_{RMA}. *OLS slope significantly different from -0.75, tested using partial F-tests (Draper & Smith 1981). Missing values are not provided in, and cannot be calculated from the original references.)

data set	measure	N_R	r^2	R_{OLS}	R_{RMA}	$\mathrm{NUBS}_{\mathrm{OLS}}$	$\mathrm{NUBS}_{\mathrm{RMA}}$
terrestrial							
arthropods							
Hluhluwe	mass	150	0.068	−0.36*	−1.40	−0.91	−1.00
Mkuze	mass	120	0.044	−0.29*	−1.37	−0.47	−0.74
Richmond	length[a]	144	0.042	0.22*	1.09	−1.34	−2.83
Brunei	length[b]	856	0.0004	0.02*	0.80	−1.75*	−1.84
early bugs	length[c]	24	0.001	−0.03*	−1.01	−0.76	−2.61
mid bugs	length[c]	24	0.003	−0.07*	−1.21	−0.04	−1.19
late bugs	length[d]	38	0.047	−0.25*	−1.13	−1.17	−1.70
moths	wing span	263	0.010	negative			
auchenorrhyncha	length	223	0.004	negative			
Syrphidae	head width	33	0.005	negative			
vertebrates							
CBC farm	mass	112	0.125	−0.48*	−1.34	−1.54	−1.85
CBC wood	mass	97	0.149	−0.49*	−1.26	−1.03	−1.16
Nee, GB	mass	147	0.139	−0.75	−2.01	−1.51	−1.71
Nee, S	mass	206	0.179	−0.77	−1.82	−1.04	−1.11
British winter	mass	175	0.080	−0.57	−2.02	−1.60	−1.85
Irish winter	mass	149	0.106	−0.74	−2.27	−1.81*	−1.99
U.S. birds	mass	380	0.019	−0.09*	−0.65	−0.89	−0.92
freshwater							
York pond	mass	45	0.038	−0.26*	−1.33	−1.10	−1.36
marine							
intertidal	mass	47	0.530	−0.77	−1.06		
deep demersal	mass	108	0.011	−0.16*	−1.51	−2.23*	−2.42

Body lengths were converted to body masses using length–mass regressions calculated from: [a] Coleoptera from Australian forests (Gowing & Recher 1984); [b] Coleoptera from tropical wet forest (Schoener 1980); [c] Homoptera and Hemiptera from shrub-steppe habitat (Rogers *et al.* 1977); and [d] Hemiptera from temperate forest (Schoener 1980).

had RMA slopes steeper (more negative) than energetics predict (binomial $p=0.02$). In addition, of the 13 assemblages for which the NUBS could be calculated, 11 (binomial $p=0.03$) had OLS NUBS and 12 (binomial $p=0.006$) had RMA NUBS steeper (more negative) than predicted by energetic equivalence. Body size generally explained very little of the variance in abundance within an assemblage: less than 5% in ten assemblages, and more than 20% in only one assemblage.

In contrast to the natural assemblages, body size explains much more of the variance in abundance in the eight species compendia (table 2). In addition, the slopes of these relationships are all negative, and fall randomly around the -0.75 slope predicted by the energetic equivalence rule (OLS slopes, binomial $p=0.72$; RMA slopes, binomial $p=0.08$; although all but one of the RMA slopes is steeper than predicted).

4. DISCUSSION

Most of the data currently available on body size and abundance in natural animal assemblages comes from

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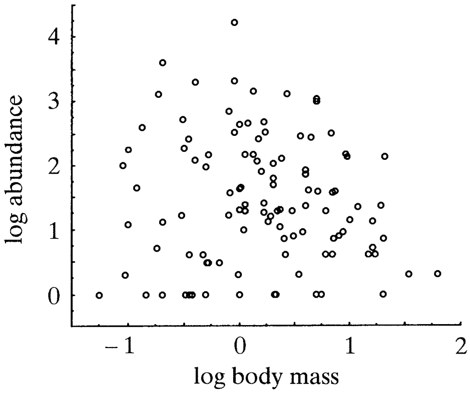

Figure 1. The relationship between log body mass (kg) and log abundance (number of individuals) for deep demersal fish in the porcupine seabight area of the North Atlantic (see also table 1).

terrestrial ecosystems, albeit for a wide variety of taxa. Freshwater and marine data are limited. Nevertheless, on the bases of these limited samples, we currently see no difference in the basic patterns (or lack of them!) observed in assemblages from all three ecosystems, nor any appreciable differences between taxa. The relationship between body size and population abundance in natural animal assemblages is normally negative, with larger species tending to live at lower abundances. However, there is little evidence for an 'energetic equivalence rule'. In most natural assemblages, the slope of the size–abundance relationship is significantly greater (less negative) than −0.75 using OLS regression, implying that large species control a greater proportion of available resources (Brown & Maurer 1987; Maurer & Brown 1988; Pagel *et al.* 1991). However, the slope is less than −0.8 more often than expected by chance when using RMA regression, implying that small species control a greater proportion of available resources (Griffiths 1992). Evidence for whether OLS or RMA is the more appropriate method for describing biological relationships is equivocal: plausible arguments have been presented in favour of each (Harvey & Mace 1982; McArdle 1988; Griffiths 1992). RMA regression supports Harvey & Lawton's (1986) argument that the greater number of small species in assemblages more than compensates for lower energy use per species at small sizes, so that small species, in total, control a greater proportion of assemblage resources. Conversely, OLS regression supports the argument that large species control a greater proportion of available resources. The discrepancy highlights the attention that ecologists need to pay to the assumptions of different regression, and the need for a simple unbiased method.

Even when the assemblage regression slope does not differ significantly from the predicted value, there is so much variation in species abundance at a given body size that it seems implausible to claim that all species in the assemblage get equivalent amounts of the resources available to the whole assemblage. Further, in the intertidal marine assemblage, which exhibits a −0.75 OLS regression slope of log abundance on log body mass, it is space, rather than energy, that is known to be limiting (Marquet *et al.* 1990).

Evidence for a metabolic explanation for the abundances of the commonest species in each assemblage (NUBS; Blackburn *et al.* 1992) is more equivocal. There are significantly more NUBS more steeply negative than predicted by an energetic equivalence argument. However, taken individually, most of the slopes are not significantly different from metabolic predictions (table 1; Blackburn *et al.* 1993*a*). Significance tests on NUBS have fewer degrees of freedom than on simple regression slopes, because of smaller sample sizes, and so will be less likely to reject a null hypothesis of no significant difference between observed and expected values. However, the upper boundary of the relationship between size and abundance is where energy is most likely to be limiting (Brown & Maurer 1987; Lawton 1989, 1991; Blackburn *et al.* 1992), and an energetic equivalence rule cannot be ruled out for the NUBS (but see below).

The above generalizations apply to natural animal assemblages from terrestrial, freshwater and marine habitats. While the majority of data available are from terrestrial assemblages, statistics for aquatic assemblages (with one exception) fall well within the range found in terrestrial assemblages, and evidence

Table 2. *Regression slopes for the relationship between body mass and abundance in animals, calculated from eight different compendia of data from literature sources*

(r^2 is the amount of variance in population abundance explained by the correlation with body mass across all species in each compendium. R is the regression slope through all species in the assemblage, calculated using either OLS or RMA regression. N is the number of species.)

data set	N	r^2	R_{OLS}	R_{RMA}	source
mammals	467	0.647	−0.78	−1.19	Damuth (1981)
mammals	175	0.624	−0.86	−1.09	Peters & Raelson (1984)
mammals	57	0.570	−0.77	−1.02	Peters & Wassenberg (1983)
neotropical mammals	103	0.449	−0.61	−0.91	Robinson & Redford (1986)
birds	564	0.180	−0.49	−1.15	Juanes (1986)
birds	60	0.030	−0.19	−1.10	Peters & Wassenberg (1983)
poikilothermic invertebrates	10	0.420	−0.77	−1.19	Peters & Wassenberg (1983)
invertebrates	62	0.550	−0.54	−0.73	Peters & Wassenberg (1983)

for metabolic limits to abundances is equally lacking. The one exception is the OLS NUBS of the deep demersal fish assemblage, but while this slope is steeper than all other NUBS, it is not dramatically so, and two assemblages have steeper RMA NUBS.

In contrast to natural animal assemblages, species compendia data (table 2) generally show strong negative relationships between size and abundance, with OLS regression slopes generally approximating more closely to −0.75. As discussed in § 1, species compendia have been criticized as unrepresentative of natural assemblages, because they are unlikely to include the rarest species (Brown & Maurer 1987; Morse *et al.* 1988; Lawton 1989, 1991). Because rare species should be most often included in the assemblage data, under-represented in the compendia, and irrelevant to NUBS estimates, it is interesting that the slopes of the size–abundance relationships steepen in this same order (table 1 and 2): compendia slopes are broadly intermediate between assemblage and NUBS slopes.

Given that a metabolic argument seems inadequate to explain the relationship between body size and abundance, in natural assemblages at least, what other explanations might there be for the form of this relationship, irrespective of the type of habitat under investigation? Two alternatives have been suggested: first, that the relationship is an artefact of statistical sampling effects (Blackburn *et al.* 1990; Currie 1993), and second, that it is a consequence of the frequency distributions of body size and abundance within assemblages (Lawton 1989; Blackburn *et al.* 1993*b*).

There are, in fact, two statistical arguments to explain observed assemblage size–abundance relationships. The first arises from the observation that small species in assemblages generally show lower maximum abundances than medium-sized species (Lawton 1989, 1991; Blackburn *et al.* 1990). If there are fewer small species in total than medium-sized species (which is generally the case), small species will appear to reach high densities less often than medium-sized species (Blackburn *et al.* 1990). Alternatively, small species may be consistently less efficiently collected by virtue of their size, creating a consistent sampling artefact.

Whether there are consistent sampling artefacts across such a wide range of assemblages, taxa and sampling methods is unknown, and perhaps unlikely. However, most methods of sampling whole assemblages are not without problems. For example, the composition of the deep demersal fish assemblage is affected by the type of ocean bed trawl used for sampling (Merrett *et al.* 1991*a*,*b*), whereas the slope of the size–abundance relationship in birds wintering in Britain and Ireland depends on whether or not abundance estimates are corrected for species conspicuousness (Blackburn *et al.* 1994). However, in at least one assemblage, excluding species known to be transient has little effect on the form of the size–abundance relationship (Gaston *et al.* 1993).

The second statistical argument suggests that patterns of size and abundance within natural assemblages are simply limited sub-samples of the overall negative relationship shown by compendium data (Currie 1993). Currie (1993) shows that sampling a limited range of body sizes from a broad negative size–abundance relationship produces simulated assemblage relationships very similar to those observed in nature (e.g. those in table 1). The implication is that assemblage patterns will not reveal the true size–abundance relationship because of problems inherent in sampling real assemblages. We do not disagree with Currie's argument. However, whether this argument is true or not, it does not alter the fact that a broad comparison is not very helpful for an understanding of the composition and structure of local assemblages of animals. Global comparisons of the relationship between size and abundance (Damuth 1981, 1987; Peters & Wassenberg 1983; Peters & Raelson 1984) are almost certain to show a strong negative relationship (Nee *et al.* 1992). For example, most species of shrews will live at higher population densities than elephants. Despite the fact that compilations of data such as Damuth's (1987) may overestimate minimum abundances by omitting rare or very rare species (Lawton 1989, 1991), there is still a large range of variation (about four orders-of-magnitude in mammal assemblages) in abundances at a given size, or sizes at a given abundance. The counter argument (Currie 1993), that the negative size–abundance relationship is missed or underestimated in local assemblages because of the more restricted size range in such data, misses this point. It is at least as interesting to understand the mechanisms which generate and maintain order-of-magnitude differences between abundances of species of similar taxonomy and size in a local assemblage as it is to discover that on a scale from shrews to elephants, large species are on average rarer than small species.

Over and above statistical arguments, an alternative to metabolic arguments is that observed body-size–abundance patterns can result purely from underlying log-normal frequency distributions of species of different body sizes and population abundances (Lawton 1989; Blackburn *et al.* 1993*b*). There is an extensive body of theory on the frequency distributions of body size and abundance (see in Blackburn *et al.* 1993*b*). Blackburn *et al.* (1993*b*) show that simple models based on the concatenation of realistic frequency distributions of size and abundance produce predictions for the NUBS of animal assemblages which are much more in line with real NUBS than are either statistical or metabolic hypotheses. Patterns of size and abundance in assemblages may therefore not require explanations independent of those for their constituent frequency distributions.

In sum, on present evidence we see no reason to distinguish between marine, freshwater or terrestrial ecosystems in seeking simple, general rules and explanations that determine population abundances within local animal assemblages, as a function of animal body sizes. Here, at least, the phenomena that ecologists seek to explain are the same, be they fowls, fish or fleas.

We thank Nigel Merrett for allowing us to use his unpublished data.

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Discussion

R. J. H. Beverton (*Emeritus Professor of Fisheries Ecology in the University of Wales College of Cardiff, U.K.*). Professor Lawton emphasizes that body mass is a poor predictor of abundance. Could it be that abundance is a poor statistic to predict anyway? I have in mind the enormous changes – perhaps six orders of magnitude – in numbers and habitat space of a year-class of fish through their life history, or the highly fluctuating density of strongly aggregating animals such as locusts. Could it be that some of the large vertical scatter in his plots is due to variability in the definition and measurement of 'abundance'?

J. H. Lawton. Yes. Some of the problems in discussing abundances in work of this kind are outlined in Lawton (1989). Difficulties posed by large changes in abundance during development in organisms such as fish are discussed briefly by Gaston & Lawton (1990). *Journal of Fish Biology* 37 (Supplement A) 97.

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K. R. Clarke (*Plymouth Marine Laboratory, Plymouth, U.K.*). I have noted a similar lack of dependence in abundance versus body-mass plots for soft-sediment marine macrobenthic assemblages, using primary and literature data provided by R. Warwick and colleagues at Plymouth Marine Laboratory. the exception appears to be for 'spot' samples for polluted or disturbed assemblages, where a significant negative slope for abundance on body mass is apparent.