NOTE

Abundance-occupancy patterns in British estuarine macroinvertebrates

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ABSTRACT: Macroecology is essentially concerned with understanding the large-scale patterns in organisms' abundance and distribution, and determining how these patterns arise. Whilst macroecological studies abound in terrestrial and freshwater ecology, few comparable studies have ever been conducted using marine data. We examined the relationships between mean organismal abundance and the extent of site occupancy of 95 species of estuarine macroinvertebrates, censused over 143 grid squares of 1 km spread across the UK. A significant positive relationship between abundance and occupancy was revealed, with the slope of this relationship not differing significantly between taxonomic groups. Taxa with planktonic/lecithotrophic larvae showed no significant difference in abundance–occupancy slope compared to taxa with other reproductive/dispersal biologies. The patterns observed are consistent with those reported in many studies of terrestrial and freshwater taxa.

KEY WORDS: Macroecology · Abundance · Occupancy · Distribution · Estuaries · Marine dispersal · Reproductive strategy

INTRODUCTION

The study of marine systems has a great deal to contribute to the burgeoning field of macroecology, which seeks understanding of abundance and distribution at large spatial and temporal scales (Brown & Maurer 1989). Despite a long history of investigation into the patterns of organisms' distribution (e.g. Thorsen 1957, Sanders 1968, Pearson et al. 1986, Rex et al. 1993), and the elucidation of macroecological patterns through studies in other disciplines such as fisheries science (Swain & Sinclair 1994), marine ecologists have only recently (see Gaston 1996a) begun to apply data explicitly addressing questions in macroecology (Cornell & Karlson 1996, 2000, Brazeiro 1999, Fernandez et al. 2000, Roy et al. 2000, Findley & Findley 2001, Gaston & Spicer 2001, Gray 2001, Defeo & Cardoso 2002). A search of the term 'macroecology', within the titles, keywords and abstracts in the Science Citation Index of primary research literature produced 138 articles of which 53 had publication dates of 2002 or later; only 8 of these articles contained the term 'marine', of which 3 have been published since the start of 2002. Interest in marine macroecology is however gathering pace; the 'Workshop on Marine Macroecology and Conservation' held in Chile in 2000 (Wieters 2001), and the 2002 British Ecological Society symposium 'Macroecology: reconciling divergent perspectives on large-scale ecological processes' (see Blackburn & Gaston 2003) both highlighted the need for macroecological studies in marine systems.

Large-scale, multi-species approaches to ecology offer both a new way of predicting the responses of ecosystems to the challenges of climate change and environmental degradation, and also provide a 'top down' route to formulating hypotheses about the mechanisms underlying the distribution and abundance of organisms (Gaston & Blackburn 1999, Lawton 1999). Marine examples are important missing pieces of the macroecological jigsaw because the marine

environment imposes a contrasting set of constraints upon life history, physiology, energetics and behaviour to those in terrestrial and freshwater systems. Differences between patterns in marine and terrestrial systems may allow for development of new hypotheses to explain mechanisms underlying large-scale distribution patterns, whilst existing hypotheses developed from analyses of terrestrial datasets can be effectively tested using marine data.

One macroecological pattern from terrestrial examples that is well documented is the positive interspecific relationship between organisms' abundance and their degree of site occupancy or range size (Gaston 1996a,b, Holt et al. 1997, Gaston 1999, Gaston et al. 2000). Gaston (1996a) proposes that this pattern is so ubiquitous that it constitutes one of the broad statistical generalisations upon which the study of ecology should be founded. Despite this, such relationships between either species total population size or mean density within sites, and the extent of range size or proportion of potential sites occupied ('occupancy'), have rarely been explicitly documented in marine systems, however. Russel & Lindberg (1988) reported a significant positive relationship between abundance and extent of occurrence in a partial study of prosobranch molluscs of the eastern temperate Pacific, and Macpherson (1989) reported a weak positive relationship for benthic fish off the coast of Namibia.

The absence of a body of literature supporting the presence of patterns for marine organisms could be due to a lack of focus upon such issues amongst marine ecologists, but it could also be due to a general lack of such patterns. De Troch et al. (2002) presented results of studies of harpacticoid copepods in tropical seagrass beds that indicate a possible difference between marine and terrestrial systems with respect to the distribution of range sizes. Such differences are also indicated by studies of rocky intertidal assemblages in which narrow ranges were uncommon in contrast with the situation in terrestrial systems (Rivadeneira et al. 2002). If limits to the extent of occupancy in marine systems are different to those in the terrestrial environment, a strong abundance–occupancy pattern may not be apparent. However, other reported studies fail to support the case for a marine/terrestrial difference; studies of sandy beaches have found patterns that are in accordance with those from terrestrial habitats, with species of greater abundance occupying a greater number of sandy beach sites (Wieters 2001). There is clearly a need for further studies of marine assemblages to determine whether the 'general laws' (Lawton 1999) that are tentatively being applied to terrestrial and freshwater systems can be extended to marine habitats.

Here, we examine an extensive dataset describing the in- and epi-macrofaunal assemblages of estuaries across the mainland of Great Britain, for patterns linking both total population size and mean abundance in sites to the extent of occupancy of the organisms represented by the proportion of sites occupied by the species. Estuaries have long been regarded as classic examples of 'closed' ecosystems with limited dispersal potential for many of the taxa (Bilton et al. 2002). Such a scenario presents an interesting opportunity to test the generality of abundance–occupancy patterns, and in particular, mechanisms based upon population dynamics of the organisms. Many of the estuarine organisms in the UK fall broadly into 2 categories in terms of reproductive strategy: those with low inherent dispersal including brood developers (peracarid crustaceans) and frequent asexual reproducers (oligochaetes), and those with greater inherent dispersal characteristics, particularly lecithotrophic/planktonic dispersal (many decapods, most polychaetes and bivalves). Within-site population dynamics (e.g. relative importance of larval retention vs. immigration/ emigration of dispersive stages) are likely to differ in these 2 groups (Woolf 1973, Bilton et al. 2002). We therefore also seek similarities and differences in the nature of the abundance–occupancy relationship between taxonomic groups with different reproductive/dispersal biologies, in order to investigate the role that these parameters might have in determining any patterns.

MATERIALS AND METHODS

Data are derived from the Marine Nature Conservation Review (MNCR) of the UK (Macdonald & Mills 1996); the methodologies employed whilst undertaking this review are described in detail by Hiscock (1996). Over 250 of the sites surveyed in this review include quantitative sampling of estuarine macroinfauna and epifauna. We selected data from sites that met a set of arbitrary *a priori* criteria; they had variable salinity in the range of 18 to 40 ppt, with sediment comprising a minimum of 40% mud/clay fraction, and a maximum of 10% of large sediment fraction. These prescriptions ensured that sites included were subjectively classified as 'estuaries' and precluded sites designated as 'muddy beaches'. All the sites were sampled with multiple-sediment cores across the full tidal range of the estuary and samples were sieved through a 0.5 mm mesh. We calculated the mean abundance (organisms m^{-2}) of each species across all samples from the site. We then allocated sites to 1 km grid squares based on the British Ordnance Survey system, and eliminated any 1 km squares that contained fewer than 3 sampled sites. We reviewed the species list for the sites for synonymy, and any taxonomically intractable
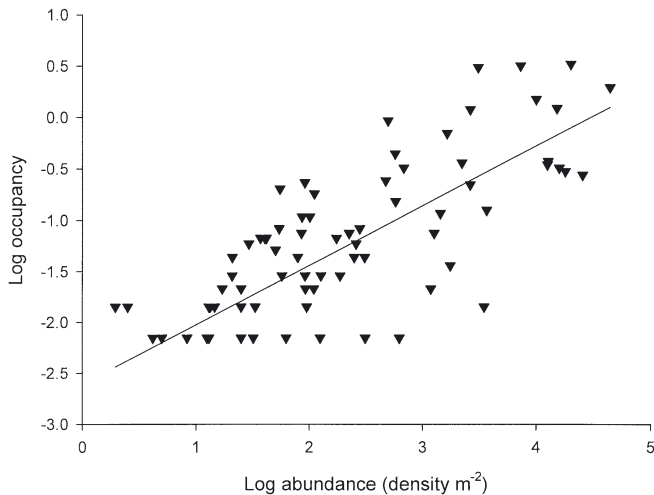
Fig. 1. Linear regression of log occupancy (see 'Materials and methods' for details) against log abundance (mean density per m^2 in occupied sites) for 95 estuarine taxa sampled across 143, 1-km grid squares distributed throughout the UK

species complexes or sister taxa were lumped together. We finally used the mean density of organisms in each site to calculate mean abundance for each species in each 1 km grid square.

Hanski & Gyllenberg (1997) model the interspecific abundance–occupancy relationship at macroecological scales as:

$$\log[\rho/(1 - \rho)] \; = \; \alpha + \beta \log \mu' \qquad (1)$$

where ρ is proportion of occupied sites, μ' is mean density of a species across all occupied sites, and α and β are the regression constant and coefficient, respectively. This form has proven more rigorous than other ways of representing the relationship, so we applied the following log-log regression to our data. First we regressed the log of occupancy against log of mean abundance at 1 km resolution for the entire dataset. We then tested for the abundance–occupancy relationship separately in the 4 main taxonomic groups present: oligochaetes, polychaetes, bivalves and crustaceans. Two species of decapods were excluded from the analysis of the pattern in Crustacea as they are known to disperse planktonically, and 4 species of polychaetes in the families Cirratulidae and Spionidae were similarly excluded as they are known to demonstrate either epitoky or asexual reproduction (Barnes 1994).

We routinely tested both our data and the residuals of each regression for normality using Kolmogorov-Smirnov (K-S) tests. We then tested for a significant interaction between the taxonomic group and log abundance in determining occupancy using an analysis of covariance in the ANOVA/MANOVA module of

STATISTICA version 5.5 (StatSoft), and used the 'parallelism test' in the same module to test the assumption of homogeneity of the slopes of the regressions for the 4 taxonomic groups.

RESULTS

The database yielded data for 143, 1-km grid squares over 30 estuary systems; 95 reliably identified taxa were included in analyses, of these 85 were members of the 4 most dominant taxonomic groups. All regressions tested (Figs. 1 & 2) gave significant relationships between log abundance and log occupancy (Table 1); all data and regression residuals were normally distributed (K-S tests $D_{max} < 0.11$, $p > 0.05$ in all cases). ANCOVA indicated that the slopes of the regression lines for the 4 groups did not violate the assumption of parallelism, and that there were no significant differences between occupancy levels in the 4 groups (Table 2).

DISCUSSION

Macroecological approaches rely on taking 'a sufficiently distant view that idiosyncratic details disappear, and only the important generalities remain' (Gaston & Blackburn 2000), an approach first advocated by MacArthur (1972). This approach can be criticised,
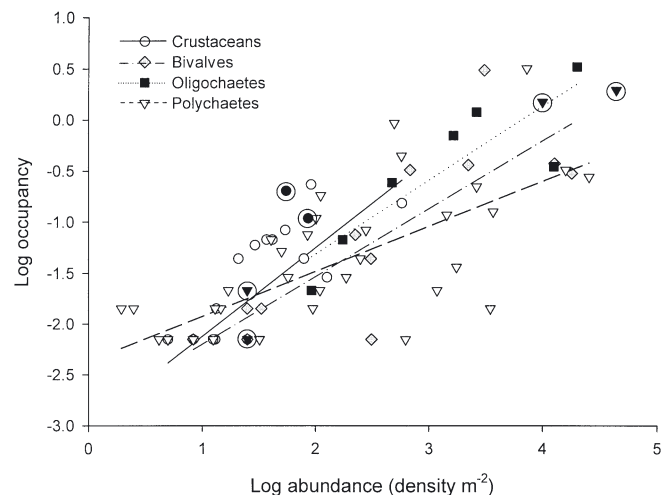

Fig. 2. Separate linear regressions of log occupancy (see 'Materials and methods' for details and Table 1 for regression coefficients) against log abundance (mean density per m^2 in occupied sites) for 4 major taxonomic groups of estuarine macroinvertebrates sampled across 143, 1-km grid squares distributed throughout the UK (crustaceans and polychaetes with atypical reproductive-dispersal traits excluded from the models and represented by encircled, closed symbols)

Table 1. Results of linear regressions of log occupancy against log abundance

	n	r^2	Slope	p-level
All taxa	95	0.638	0.583	<0.001
Crustaceans	22	0.548	0.869	<0.001
Bivalves	12	0.687	0.664	<0.001
Polychaetes	38	0.586	0.441	<0.001
Oligochaetes	7	0.750	0.724	0.012

Table 2. Results of ANCOVA tests of parallelism of regression slopes for the 4 taxonomic groups, and effects of taxonomic group upon occupancy levels

	df	SS	MS	F	p-level
Parallelism					
Taxonomic group	3	0.857	0.286	1.459	0.233
Error	71	13.888	0.196		
Difference					
Taxonomic group	3	0.517	0.172	0.865	0.463
Error	74	14.745	0.199		

however, and all of the commonly levelled criticisms may apply to our study (see Blackburn & Gaston 1998). 'Noise' in the data derived, for example, from differences in the way staff performed individual sampling exercises, and the problems of the using Model I regression where there is error variance in the *X* variable, are unlikely to pose significant problems for the analyses presented. Missing species which occur at the limit of the sampled size range, or at extremely low abundances where they could have been overlooked, are likely to exist. However, these will be particularly those fragile organisms that are lost in the separation of organisms from the sediment. We believe that the influence of such taxa is unlikely to significantly change the broad patterns elucidated. Patterns of spatial distribution of the fauna may also produce artefactual abundance–occupancy relationships (Blackburn & Gaston 1998); however, we examined our data for significant spatial autocorrelation and found no evidence of such effects.

The results of our analyses indicate that abundance–occupancy relationships in the UK estuarine macrofauna are of comparable strength and the fit of the data to the estimated regression lines are broadly similar to published results for terrestrial and freshwater organisms.

Gaston (1996a) provides a summary of these relationships for over 90 studies, of which 14 had no significant slope, and only 4 had negative slope. The significant relationships in Gaston's table have r^2 values ranging from 0.075 to 0.756, with the numbers of taxa involved ranging from 12 to 461; the values we report here are at the high end of this scale, notwithstanding the influence of sample size upon the statistic. There is also no indication from this that the spread of abundance or occurrence in the UK estuarine macrofauna differs from that in other systems such as those described by Gaston (1996a), as suggested by other studies (De Troch et al. 2001). Moreover our analysis indicates consistent patterns of abundance–occupancy amongst a variety of phylogenetic groups with differing reproductive and/or dispersal strategies.

Gaston & Blackburn (2000) propose 9 potential mechanisms underlying the positive relationship between species abundance and range size (see Gaston & Blackburn 2000 for a review). Amongst these metapopulation dynamics and aspects of species' physiological and ecological traits such as reproductive and dispersive modes appear to receive little support from our data. The fact that groups with fundamentally different reproductive/dispersal strategies differ only slightly in the strength of the abundance–occupancy relationship indicates that such variables might only moderate, rather than generate, the abundance–occupancy relationship amongst the estuarine macrofauna.

The remaining hypotheses explaining the positive abundance–occupancy relationship relate to the fundamental biology of the organisms such as their niche breadth, resource utilization and availability (Brown 1984, Gaston & Spicer 2001), and to their population dynamics (Hanski et al. 1993) and vital rates (Holt et al. 1997). Resource availability is unlikely to be of significance in the estuarine macrofauna; Barnes (1994) states that most experimental studies in brackish waters failed to find much evidence of competition for resources, either within or between species. Niche breadth estimation for many of the species involved, meanwhile, is not possible, as there are too few data available to perform the calculations for many of the species. However, factors which are likely to be important in determining the suitability of sites for colonisation such as the salinity range of the sites (Attrill 2002) and particle size characteristics of the sites (e.g. Alexander et al. 1993) might warrant further investigation.

There are several important implications of the positive abundance–occupancy relationships we have demonstrated. Gaston (1999) has reviewed these, and highlights 4 main areas in which the generality of these patterns might be significant. These comprise (1) the potential use of presence-absence patterns as a surrogate for species abundance in biodiversity studies, (2) their use in predicting the implications of harvesting for long-term survival of species' local populations, (3) the use of the strength of the abun-

dance–occupancy relationship in predicting the effectiveness of maintaining locally high abundances of species in conservation, and (4) prediction of the spread of invasive species depending upon the extent of their sites of invasion, or their densities at invaded sites. Further studies of patterns of abundance and occupancy, and revisitation of existing data with the explicit intent of investigating these patterns, are required.

Our data show consistent, comparatively strong abundance–occupancy relationships across 4 taxonomic groups in 3 different phyla; such scope is rare in previous macroecological studies. The comparison of groups we have attempted here provides both evidence for the generality of the patterns, and a suggestion that the population biology of the taxa may play a role only in moderating the strength of the relationship. More rigorous testing of this tentative hypothesis is necessary however, along with further studies to corroborate or refute our findings and to further progress in marine macroecology in general.

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