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COMMENT

Benthic species diversity and sediment composition: Comment on Compton et al. (2008)

J. J. Beukema*, **R. Dekker**

Royal Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands

ABSTRACT: Compton et al. (2008; Mar Ecol Prog Ser 373:25–35) presented data on the number of bivalve species encountered in small core samples (0.02 m^2) taken in various tidal flat areas, and they used these numbers to draw conclusions on relationships between sediment type and local species richness. We argue that their samples were too small, when used on their own, to yield realistic estimates of macrozoobenthic diversity. Small samples represent merely those few species that usually occur in high numerical densities. Only 2 of the ~10 bivalve species commonly found on European tidal flats belong to this group.

KEY WORDS: Species richness · Sample area · Sediment coarseness · Bivalves

INTRODUCTION

The study by Compton et al. (2008) suggests that bivalve diversity on tidal flats is (1) not associated with sediment heterogeneity and (2) maximal in fine-grained sediments. These conclusions are based on benthic samples taken at 9 temperate and tropical tidal flat systems. The numbers of samples taken was high, but the individual samples were small (0.02 m^2), and the samples were not aggregated to estimate species numbers for larger areas sampled, limiting the assessment to 'point diversity' ('diversity within a sample point', α diversity). This method is inadequate for studies of diversity in macrozoobenthic animals.

DATA FROM LONG-TERM MONITORING

To confirm this hypothesis, we used data obtained during a 40 yr monitoring program on the macrozoobenthos on Balgzand, a tidal flat of 50 km^2 in the westernmost part of the Wadden Sea (cf. Beukema 1988, Beukema & Cadée 1997, Beukema & Dekker 2011). This yielded annual species numbers in samples of 0.1 and 1 m^2 at 15 sites having widely different sediment compositions. Species numbers at the 15 fixed sites are comparable and can be accumulated over the entire 40 yr period, since (1) the methods were consistent, and (2) the distribution of the sediment types changed little over the observation period, by comparison with the map of Ente (1969).

As a consequence of the small sample areas used by Compton et al. (2008), their diversity estimates may be based almost exclusively on the limited group of species that occur at high numerical densities. If a species is distributed randomly, the chance of encountering it in any single sample of 0.02 m^2 is 86% at a density of 100 ind. m^{-2}, 63% at 50 ind. m^{-2}, 18% at 10 ind. m^{-2}, and 2% at 1 ind. m^{-2} (according to Poisson distributions at the appropriate means: 1.0 minus the zero-term). The distribution of macrozoobenthic species over tidal flats is generally more aggregative than random (Beukema et al. 1983), and encounter probabilities will be lower. Most macro-

*Email: jan.beukema@nioz.nl

zoobenthic species in marine habitats have low encounter probabilities in small samples, because only few species occur at high densities on tidal flats (Fig. 1b; Dankers & Beukema 1983, Bocher et al. 2007) as well as in other marine areas (Gray 2002, Ellingsen et al. 2007).

In accordance with the low numbers of species that have high densities frequently, the mean diversity values for bivalves reported by Compton et al. (2008, their Fig. 4) amount to only 0 to 2 species per 0.02 m^2 sample. The numbers of bivalve species actually present at the sampling sites is significantly larger (on Balgzand, we found on average around 5 bivalve species within 1 m^2) and amount to about 10 when

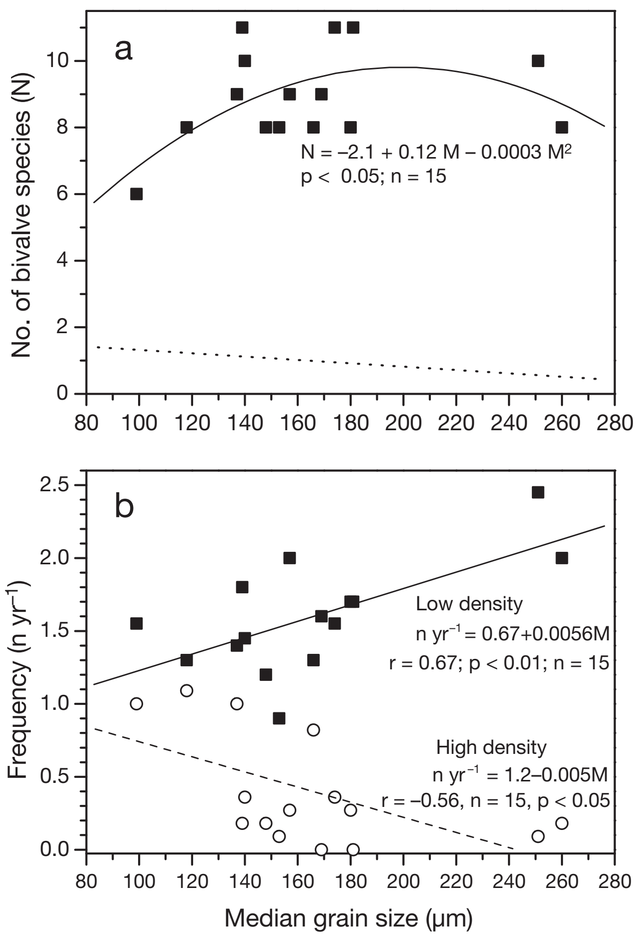

Fig. 1. Bivalve populations at 15 monitoring sites on Balgzand tidal flat. Relationships between sediment composition (median grain size, M in µm) and (a) numbers of bivalve species (N) found at least once during 1970 to 2009 (solid symbols, curvilinear fit; linear fit was not significant), and numbers of bivalve species found in samples of 0.02 m^2 (dotted line); redrawn after parts of Fig. 4 in Compton et al. (2008). (b) Frequency of occurrence (n yr^{-1}) of bivalve populations of any species having high or low density: (○) dense populations (of >100 ind. m^{-2}) and (■) thin populations (of <10 ind. m^{-2}), during 1998 to 2008

data are accumulated over several years (Fig. 1a; Beukema & Dekker 2011). Thus, the low diversity estimates reported in Compton et al. (2008) may be largely determined by the presence/absence of a special minority of the actual species assemblage. In other words: a high estimate at a site means little more than the local presence of a dense population of a species at that site.

This emphasis on locally abundant species may have serious consequences for the outcome of the relationships studied by Compton et al. (2008). Low- and high-density (<10 vs. >100 ind. m^{-2}) bivalve populations showed differential distribution patterns over the Balgzand tidal flats (Fig. 1b). At sites with fine-grained sediments, the 2 types of populations were encountered at an almost equal frequency: sampling of ~1 m^2 yielded on average about 1 high- and 1 low-density bivalve population. As sites were characterized by increasingly coarse sediments, the incidence of high-density populations declined significantly, whereas that of low-density populations increased significantly (Fig. 1b). At all sites, low-density populations contribute little (<20%) to species counts in samples of 0.02 m^2. On the other hand, dense populations, where they were frequent, contributed substantially to species numbers in 0.02 m^2 samples, i.e. particularly at sites with fine sediments. As a consequence, species numbers in small samples were low at coarse-sediment sites (as none of the density groups contributed substantially), whereas relatively high species numbers were found at fine-sediment sites, due to the relatively high contribution of dense populations. More than half of the dense populations belonged to only 2 species (*Macoma balthica* and *Abra tenuis*). On Balgzand, for the 11 years around 2003 (i.e. the year of observation by Compton et al. 2008), dense populations of these 2 species were either restricted (*A. tenuis*) or nearly restricted (*M. balthica*) to sites with fine sediments.

Our counts of species numbers revealed that the contribution of low-density species was much greater in large samples (1 m^2 or more) than in small samples, whereas those of high-density species were hardly higher. This is so, because for a record of the mere presence of a species it does not matter how many individuals (after the first one) were found within the sample (and usually at least 1 specimen of a dense population will be found in even a small sample). The increase in species numbers with sampled area does not follow an identical course at the various sediment types, as low-density species are more numerous in coarse than in fine sediments (Fig. 1b). As a consequence, the maximal species number per sample is no longer found in the finest sediments — as reported by Compton et al. (2008) for small samples — but shifts to coarser sediments when larger samples are used. In Fig. 1a, the solid points and curvilinear fit represent an aggregated sample area of no less than ~40 m^2 and show maximal species richness values at median grain sizes of 140 to 180 µm (as compared to <140 µm when small samples of 0.02 or 0.1 m^2 are used). The species numbers observed in large samples better represent the species richness of a site, because at increasing sample areas, the accumulation curve asymptotically approaches the true species richness. The maximal species richness of bivalves at intermediate sediment coarseness agrees with observations of maximal diversity in tidal flat macrozoobenthos at environmental conditions that are intermediate with regard to sediment coarseness, intertidal height, and exposure to wave action or tidal currents (Beukema 1976, 1988, Dankers & Beukema 1983: their Figs. 11 & 12, Armonies & Hellwig-Armonies 1987).

CONCLUSION

Maximal species numbers in the finest sediments, as observed by Compton et al. (2008), are an artifact originating from the use of small sample areas. Their other conclusion (regarding the relationship between species richness and sediment heterogeneity) might also change if they had increased sample areas by aggregation of samples. Thus, their study of relationships between sediment characteristics and species richness might have been more conclusive if they had used some measure of γ- rather than α-diversity, i.e. they should have aggregated samples from neighbouring sites and/or sites having similar sediment composition.

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