REPLY COMMENT

Macroecology and meiobenthos: Reply to Warwick (2014)

Brian J. Bett*

National Oceanography Centre, Empress Dock, Southampton SO14 3ZH, UK

ABSTRACT: Warwick (2014; Mar Ecol Prog Ser 505:295–298) suggests that my claim that the biology of marine metazoan benthos may scale continuously with body mass (Bett 2013; Mar Ecol Prog Ser 487:1–6) is an overstatement. His alternative hypothesis is that there is a 'step-change' in allometric relationships between the meio- and macrobenthos. I continue to propose that simple null hypotheses for standing stock size spectra and species size spectra of the metazoan benthos, consistent with metabolic theory and macroecology, offer parsimonious solutions. For standing stock and species size spectra I present field data that conform to these null hypotheses. Data from other studies, such as those suggested by Warwick (2014), may be difficult to place in the macroecological context, as those studies are constructed or presented in a different manner (e.g. they lack data on the number of individuals identified). I suggest that it may be useful to consider 'evolutionary species size spectra' separately from 'macroecological species size spectra'. Both are valid testable hypotheses, and are not necessarily contradictory.

KEY WORDS: Meiobenthos · Macrobenthos · Metabolic theory · Macroecology · Metazoan evolution · Body size spectra

Introduction

My original contribution (Bett 2013) was based on simple numerical simulations of standard benthic sampling practices. This approach seems reasonable in the case of standing stock (abundance and biomass) assessments, but is certainly more questionable in relation to species richness studies. The outcomes of my simulations provide null hypotheses that can readily be rejected with appropriate data. The following questions could be asked of such data: (1) Are particular taxa restricted in their body mass ranges to the groups referred to as meio- and macrobenthos? (2) Do standing stocks exhibit distinct boundaries (troughs) between these groups? (3) Does species richness exhibit distinct boundaries between these groups? To frame these questions, some working definition of the meiobenthos is needed.

Molly Mare's meiobenthos

Molly Mare defined meiobenthos as

> fauna of intermediate size, such as small Crustacea (copepods, cumaceans, etc.) small polychaetes and lamellibranchs, nematodes and foraminifera
> (Mare 1942, p. 519)

In defining her scheme for the benthos, Mare noted that, in addition to differences in body size,

> generation time … varies enormously between the groups and is important in considering the role of the various organisms in the community
> (p. 518)

This link between body mass and biological rate processes is fundamental to early allometric research (Peters 1983) and the more recent metabolic theory of ecology (Brown et al. 2004). Mare's objective was an 'understanding of that part of the marine food cycle

which takes place on the sea bottom', a quantitative investigation of benthic biogeochemistry (Mare 1942, p. 517). How do Mare's data fare against metabolic theory? I have regressed Mare's (1942) data for standing stock biomass and abundance on corresponding values for geometric mean body mass (Fig. 1), yielding close approximations to Brown et al.'s (2004) predictions from metabolic theory, biomass having a mass exponent of +0.25 (theory +0.25), and abundance an exponent of −0.81 (theory −0.75).

Modern meiobenthos

Higgins & Thiel (1988) noted that definition of the meiobenthos remained controversial, and argued for a strict size category, considering it essential when conducting quantitative investigations. However, variant definitions of meiobenthos have continued to proliferate, as illustrated by the use of the qualifiers sensu lato and sensu stricto. The former represents a size-based category (e.g. Mare 1942, Higgins & Thiel 1988), the latter a taxonomically restricted unit that excludes taxa based on a preconceived notion of which ecological trait (size) group they belong to.

Higgins & Thiel (1988) found that size categories have a weak relationship with higher taxonomic classifications. Some taxa (Tardigrada, Gastrotricha, Gnathostomulida) may be exclusively meiobenthic. The Loricifera and Kinorhyncha were included with the latter taxa but have since been placed in the Cephalorhyncha (Schmidt-Rhaesa 2013), a phylum that spans the meio-, macro- and megabenthos.
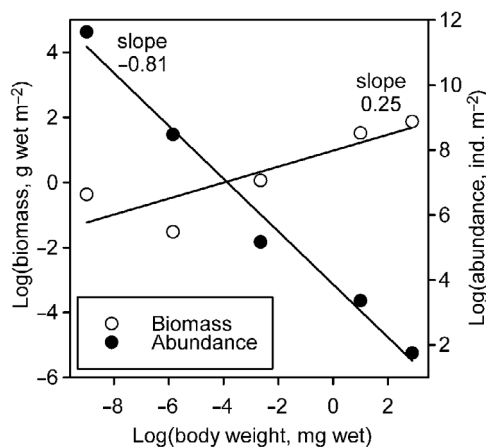

Fig. 1. Benthic body size spectra from Mare (1942), showing large macrobenthos, small macrobenthos, meiobenthos, protozoan microbenthos and bacterial microbenthos (body weights are geometric means of reported ranges)

Warwick (2014) noted that the dominant metazoan groups of the meiobenthos, nematodes and harpacticoids, have macrobenthic-sized representatives, citing the oncholaimids (Bett & Moore 1988) and the genera *Tisbe* and *Bulbamphiascus* (Moore & Bett 1989). Polychaetes, the dominant macrobenthos group, span 3 categories: meiobenthic (*Parapodrilus psammophilus*, Struck 2006; 0.003 mg) to megabenthic (*Eunice aphroditois*, Campoy 1982; 2 000 000 mg). The foraminifera (part of Mare's meiobenthos) span the nano- (Gooday et al. 1995), meio-, macro-, and megabenthos (Tendal & Gooday 1981), at least in terms of the physical dimensions of their tests.

Real size spectra

My own investigations (Kelly-Gerreyn et al. 2014) suggest that I should not reject my null hypothesis (Bett 2013) in the case of standing stocks (Fig. 2). Across 3 highly contrasting sites, I see no evidence of a trough in these abundance size spectra. Nematode
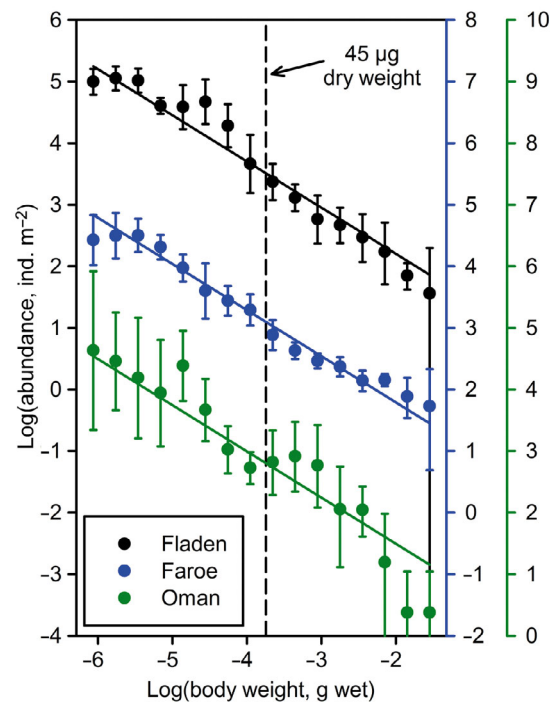

Fig. 2. Geometric mean (with 95% CI) benthic abundance in X2 geometric size classes from contrasting sites: Fladen Ground (temperate sublittoral, 150 m depth); Faroe-Shetland Channel (Arctic deep sea, 1600 m depth); and Oman Margin (tropical, hypoxic, deep sea, 500 m depth) (see Kelly-Gerreyn et al. 2014). Fitted lines are predictions from metabolic theory. Dashed line indicates proposed meio- to macrobenthos trait transition at 45 µg dry weight (Warwick 2014). Note: *y*-axes are offset to avoid overlap of data points
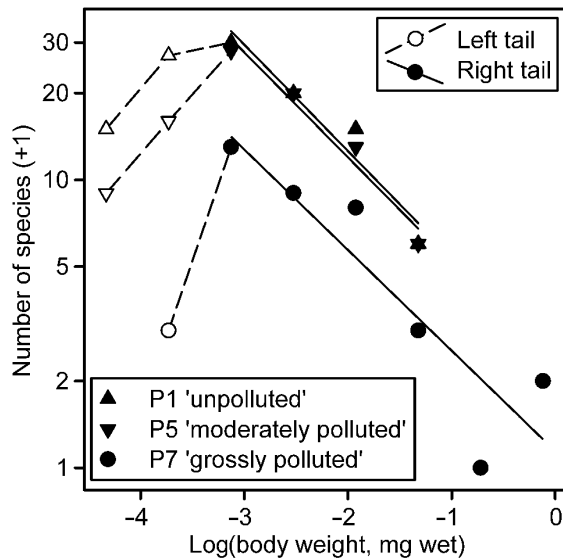
Fig. 3. Nematode species size spectra from 3 sites in the vicinity of the Garroch Head sewage sludge dump ground in the Firth of Clyde (UK) based on data from Bett (1991). Species abundance is plotted against typical adult body mass in X4 geometric size classes. Data represent 2629 to 2693 meiobenthic (> 45 μm, <1000 μm) nematodes identified at each site, and an additional 1137 macrobenthic (>1000 μm) nematodes identified at P7. Linear regression of the right tail data gives slope and r^2 adjusted values as follows — P1: −0.37, 90%; P5: −0.36, 94%; P7: −0.35, 78%. Note: *y*-axis values are plotted as (*y* + 1) to accommodate a zero value. (✶) confluent P1 and P5 data points

species size spectra constructed from my own data (Bett 1991; present Fig. 3) suggest a close match to simple macroecology predictions, e.g. if abundance (A) in geometric size classes is related to body mass (m) with −3/4 power (A ≈ $m^{-0.75}$; Brown et al. 2004), and species richness (S) in geometric size classes is related to abundance with 1/2 power (S ≈ $A^{0.5}$; Siemann et al. 1999), then species richness in geometric size classes should be related to body mass with −0.38 power [S ≈ $(m^{-0.75})^{0.5}$, S ≈ $m^{-0.375}$]. The right tails of my nematode species size spectra (Fig. 3) have slopes of −0.35 to −0.37. The 3 sites studied span an extreme range of organic matter supply and a corresponding dramatic reduction in total species richness (107 to 32 species), but have very similar slopes that are a close approximation of the macroecology prediction.

The original species size spectra study of Warwick (1984) proposed an attractive and appealing case for the meio- and macrobenthos being distinct entities. His work further provided plausible evolutionary drivers for the distinctiveness that are revisited in Warwick (2014). Although he made a very thorough census of the species pool, Warwick (1984) did not control sampling and identification effort across the

size spectra. Consequently, it is almost impossible to place Warwick's species size spectra in the same context as the species size spectra from macroecological studies (e.g. McClain 2004; present Fig. 3). For example, it is difficult to assess the significance of the relative species richness of the meio- and macrobenthos modes without knowledge of the number of specimens identified in the corresponding body size classes. It becomes impossible to judge whether a bimodal distribution is a better summary than a unimodal distribution, as would be suggested from macroecology (Siemann et al. 1999) or my simple simulations (Bett 2013).

Warwick (2014) indicated that the work of Warwick et al. (2006) provided additional evidence for the distinctiveness of meio- and macrobenthos. The latter authors demonstrated a very convincing dichotomy in the diversity and species composition of samples collected on smaller (63, 125, 250 μm) and larger (500, 1000 μm) sieves. However, that study is difficult to interpret for 2 reasons: (1) Only a single sieve mesh size was used in the processing of any sample, and (2) the number of specimens recovered and identified in any sample was not reported. Consequently, the degree of body size range overlap between samples from different sieve meshes is unknown and uncontrolled. I would suggest that without that control or knowledge, it is not possible to interpret whether those data provide support for the suggestion that the meio- and macrobenthos are discrete ecological entities.

Beyond meio- and macrobenthos

In attempting an 'understanding of that part of the marine food cycle which takes place on the sea bottom' (Mare 1942), it is necessary to consider those organisms that are both smaller (nano- and microbenthos) and larger (megabenthos) than the meio- and macrobenthos. Some size spectra have been produced for the megabenthos (Thurston et al. 1994), but they were derived from trawl samples and therefore suffer from a lack of truly quantitative data—a problem that today might be solved by photographic survey methods (Jones et al. 2005). The Archaea, Bacteria, and nanobenthos remain difficult subjects for quantitative study (see e.g. Epstein 1995, Amalfitano & Fazi 2008). The foraminifera, however, are a practical taxon for further study at the lower end of the benthic body size range. Gerlach et al. (1985) provided benthic biomass spectra for foraminifera, in addition to the metazoan meio- and macrobenthos, which appeared to show some differentiation of the

protozoan and metazoan response in the meiobenthic size range. Further development of macroecology and the metabolic theory of ecology (as applied to the marine benthos) would benefit from work beyond the metazoan meio- and macrobenthos.

Conclusions

I continue to propose that simple null hypotheses for metazoan benthos size spectra, consistent with metabolic theory and macroecology, offer parsimony. Such hypotheses can readily be rejected with appropriate data. The characteristic biomass spectra of Schwinghamer (1981) may well be simple sampling artefacts and should not constrain macroecological study of the marine benthos. Macroecological species size spectra (e.g. McClain 2004; present Fig. 3) appear to be a valuable tool, and are not necessarily contrary to the evolutionary species size spectra of Warwick (1984). The bimodal form and proposed drivers of Warwick's characteristic species size spectra remain valuable hypotheses in the evolution of the metazoan marine benthos that warrant further study. Following Mare's (1942) lead, it is useful to provide both an upper and lower limit (e.g. sieve mesh size) for all groups of the benthos reported in quantitative studies. Indeed we would do well to acquiesce to Higgins & Thiel's (1988) plea for a common set of sieve mesh sizes for benthic studies. This area of research would particularly benefit from additional data on the size spectra of groups beyond the metazoan meio- and macrobenthos (e.g. foraminifera and megabenthos).

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