ON THE UTILITY OF METAZOAN MEIOFAUNA FOR STUDYING THE SOFT-BOTTOM DEEP SEA

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BIOGEOGRAPHY
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ABSTRACT. – The deep sea, an environment of great ecological interest, is difficult to study because of the thick layer of water that overlies it. As a consequence, choosing a target taxon well suited for the question to be addressed is particularly advantageous. I suggest that metazoan meiofauna have attributes that make them the best choice for some deep-sea questions. To illustrate their properties, I discuss their suitability for use with a potentially powerful technique for the study of deep-sea communities and for the testing of a major theory of deep-sea diversity. I also argue that meiofauna can provide a more complete understanding of deep-sea biogeography.

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RÉSUMÉ. – L'étude des grands fonds marins, un environnement de haut intérêt écologique, est difficile en raison de l'importante hauteur d'eau qui la surmonte. En conséquence, le choix d'un taxon cible bien adapté aux questions posées est particulièrement important. Je propose que les métazoaires de la méiofaune possèdent les caractères qui en font le meilleur choix pour traiter certaines questions. Pour illustrer leurs propriétés, l'intérêt de leur utilisation à l'aide d'une technique potentiellement performante pour l'étude des communautés profondes et pour tester une théorie majeure de la diversité en mer profonde est discuté. Je suggère aussi que la méiofaune peut permettre une meilleure compréhension de la biogéographie dans les grands fonds.

INTRODUCTION

The deep sea is a vast habitat, occupying 49% of the Earth's surface (Hessler 1974). In most of this area, the seabed consists of sediment, making the soft-bottom deep sea (hereafter the deep sea) arguably the largest biome on the planet. The deep sea is interesting for many reasons. For example, conditions there are at the extreme of the range for several gradients of ecological stress (*e.g.*, pressure, food supply), and the deep sea has unexpectedly high species richness (Hessler & Sanders 1967). The deep sea is a difficult environment to study. Its large size and considerable heterogeneity (Gage & Tyler 1991) prevent drawing universal conclusions from the investigation of a small number of sites. At least 200 m of water overlies it (Murray 1895), so the environment is remote and cannot be studied with the techniques used in shallower habitats. The tools needed for its study (*e.g.*, large ships) are expensive, limiting the number of investigations. Quantitative sampling (Gage 1975, Fleeger *et al.* 1988, Bett *et al.* 1994) and experimentation are more difficult in the deep sea than in shallow water (Thistle 2003). As a consequence, selecting organisms for study that are well suited to the question at hand is particularly important.

In most deep-sea studies, megafauna (*e.g.*, sea urchins, sea stars) or macrofauna (*e.g.*, polychaete worms, bivalve mollusks) (Table I) have been the focus. I will argue that metazoan meiofauna (hereafter meiofauna; *e.g.*, nematode worms, harpacticoid copepods) have attributes that make them better choices in some circumstances. To illustrate these features, I will discuss the suitability of meiofauna as target organisms for use with a potentially powerful technique for the study of deep-sea communities and for testing a major theory of deep-sea diversity. I will also argue that the study of meiofauna can provide a more complete understanding of deep-sea biogeography.

The utility of meiofauna for use with a technique: caging experiments

In shallow water, caging experiments have been used with great success to dissect community organization (Connell 1961, Virnstein 1977). In these experiments, mesh-covered frames designed to exclude larger animals are placed on the seabed, and

Table I. – The size categories of benthic organisms.

Category	Lower size limit	Representative taxa
Megafauna	centimeters	fishes, sea urchins
Macrofauna	250–500 μm	polychaetes, bivalves
Meiofauna	32–62 μm	nematodes
Microbiota	microns	protists

after a suitable period, the infauna inside is compared to that of controls.

The deep sea contains animals of the same sort (*e.g.*, sea stars, fishes, crabs) that have been found to be important in shallow-water soft bottoms. Caging experiments would allow the roles that such organisms play in deep-sea communities to be investigated, but one concern is that individuals of the target taxa might move in or out of the cage during the experiment. Because the amount of distance moved per unit time increases with body size to a first approximation (Peters 1983), meiofaunal individuals are likely to move less than larger individuals. Meiofaunal species also lack the planktonic larval stages common in larger animals (Por 1965, Warwick 1984) and therefore are less likely to have moved into or out of a cage during the experiment.

Cages impose boundaries that can affect the enclosed animals, *e.g.*, by interfering with their normal movement. Experimenters strive to maximize the surface area enclosed by their cages to reduce the probability that an individual of a target species will encounter a boundary. Because of the limitations of the vehicles used to emplace cages in the deep sea, cages tend to be ≤ 1 m^2 (see, *e.g.*, Eckman *et al.* 2001). A way to decrease the effects of boundaries on motile target organisms is to study those that, however fast they move in terms of body lengths per unit time, do not move far in terms of distance per unit time, those of meiofaunal size.

Over time, cages foul and are overgrown, increasing the potential for experimental artifacts. Selecting the metrics that have the shortest response times can minimize this problem. Because meiofauna have higher metabolic rates than larger organisms (Mahaut *et al.* 1995), changes in their condition (*e.g.*, amount of energy reserves) should occur more quickly than for larger organisms. Because meiofauna have shorter generation times

than larger organisms (Warwick 1984), their reproductive responses should be more rapid. The low movement rates, lack of pelagic larvae, high metabolic rates, and rapid reproduction of meiofauna make them particularly suitable for use in caging and perhaps other types of deep-sea experiments.

The utility of meiofauna for testing a theory

The question of why the species richness of many taxa increases with depth (Hessler & Sanders 1967, Sanders 1968), at least into the bathyal zone (Rex 1973, 1976, Boucher & Lambshead 1995, Paterson & Lambshead 1995), has been central to deep-sea ecology since its discovery in the late 1960's. Among theories proposed to explain the pattern (Gage & Tyler 1991, Gage 1996), the grain-matching hypothesis (Jumars 1975a, 1976, Thistle 1979, Jumars & Gallagher 1982) is prominent. The theory weaves together several threads. First, the intensity of the motion of the near-bottom water declines as depth increases, decreasing the frequency of hydrodynamic sediment disruption. Second, the amount of food that reaches the seabed declines as depth increases (Rowe 1971). The decrease in food causes a decrease in the standing stock of animals (Murray 1895) and their activity, so bioturbation rates should also decline with depth (see DeMaster *et al.* 1994). The combination of reduced hydrodynamic disruption and reduced bioturbation create a gradient of increasing sediment stability with increasing depth. Third, most sediment-dwelling animals modify their local environment. For example, some build structures in which to live, some alter the local microbial community by feeding, and some produce piles of fecal pellets. In shallow water, the rate of sediment disruption is so great that these modifications of the habitat are quickly obliterated, but as depth increases and the physical environment becomes more stable, more and more of these modifications
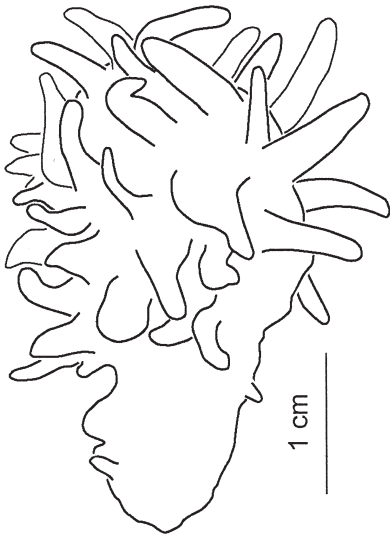
Fig. 1. – The test constructed by the polychaete *Tharyx luticastellus* as an example of a biologically produced structure in the deep sea. The lower third of the test would be below the sediment surface in nature. Modified from Jumars (1975b).

persist long enough for other animals to perceive them as habitat heterogeneity. That is, as depth increases, animals themselves produce increasing amounts of ecologically important "grain" in the habitat. The increase in grain should allow increasing numbers of species to coexist, for example, by providing more opportunities for habitat partitioning, more refuges from predation, or a more complex template for contemporaneous disequilibrium. The grain-matching hypothesis brings the threads together to suggest that the increase in diversity with increasing depth arises because more and more animal-created habitat heterogeneity is present as depth increases.

The best target species for investigating this hypothesis are those whose space and time scales best match the space and time scales of the effects of the animal-created grain. Many structures created by deep-sea organisms are millimeters to a few centimeters in largest dimension (Thistle 1979, Levin *et al.* 1986), *e.g.*, the test built by the deep-sea polychaete *Tharyx luticastellus* (Jumars 1975b) (Fig. 1). Target species with ambits (*sensu* Lloyd 1967) on this scale and with generation times less than the persistence times of the structures should be able to pass their entire lives in the heterogeneity the structures create. As ambit sizes and generation times increase, individuals of potential target species will fit the effects of the structures less well. For example, a 3-cm-diameter test cannot be used as a place to live by a 10-cm-long polychaete as well as it can by a 0.05-cm-long nematode. Therefore, the suitability of target species should decrease with increasing size and generation time. Meiofauna are the smallest metazoans and have the shortest generation times (Warwick 1984). They should therefore be particularly suitable for testing the grain-matching hypothesis.

Meiofauna and deep-sea biogeography

Biogeographic patterns provide foci for the investigation of forces that have molded faunas on regional scales, so the discovery of these patterns and their study are of interest (MacArthur 1972). Investigation of such patterns in the deep sea is in its infancy because of the mismatch between the large size of the environment and the small amount of sampling that has been done.

Biogeographic investigations become more difficult as the samples on which they are based become increasingly biased. At present, most of the information about the biogeography of macrofauna comes from samples collected by box corer (see for example, Hessler & Jumars 1974, Grassle & Maciolek 1992). This device undercollects animals living on or near the surface of the sediment (Jumars 1975a, Bett *et al.* 1994). In contrast, unbiased samplers for meiofauna have been used since the 1980's (*e.g.*, the SMBA multiple corer, Barnett *et al.* 1984, and its descendents). Although most of our knowledge of deep-sea biogeography is based on larger organisms (see, *e.g.*, Grassle & Maciolek 1992, Allen & Sanders 1996, Glover *et al.* 2001), studies of meiofauna should provide a clearer view of biogeographic patterns until data accumulate from unbiased macrofaunal sampling.

Biogeographic patterns of meiofauna might not be the same as those of the larger organisms or arise for the same reasons. For example, isopods (Sanders *et al.* 1965) and harpacticoid copepods (Vincx *et al.* 1994) are major crustacean components respectively of the macrofauna and the meiofauna of the deep sea. Most deep-sea isopod species belong to families that evolved in the deep sea (Hessler & Thistle 1975). In contrast, most deep-sea harpacticoid species belong to shallow-water genera and families (Por 1965, personal observation), suggesting a very different evolutionary history of the two taxa in the deep sea.

Ecological time-scale processes also affect biogeographic patterns, and meiofauna and larger organisms might not respond in the same way. For example, deep-sea polychaetes are the major vermiform component of the deep-sea macrofauna (Sanders *et al.* 1965), and nematodes are the major vermiform component of the deep-sea meiofauna (Vincx *et al.* 1994). Because the mouths of nematodes are much smaller than those of polychaetes, nematodes can make selections at a much smaller scale as to which particles to ingest, scrape, or bite, so their choices of food could differ from those of polychaetes. The nematodes should also be able to

use more of the biologically produced environmental heterogeneity than polychaetes.

Such contrasts suggest that ecological forces could affect nematodes and polychaetes differently. Investigation of macrofaunal patterns will therefore not suffice for a complete understanding of deep-sea biogeography. For example, Rex *et al.* (1993) studied the diversity of the macrofaunal taxa Bivalvia, Gastropoda, and Isopoda in the deep North Atlantic and showed that diversity decreased significantly along a gradient of increasing productivity. In contrast, Lambshead *et al.* (2002) found an increase in nematode diversity along a gradient of increasing productivity in the equatorial Pacific. Although the two studies are not exactly comparable, the opposite directions of the trends of diversity with productivity raise the possibility that meiofauna and macrofauna respond differently to ecological forces and will therefore have different biogeographic patterns.

Challenges of using meiofauna

The study of meiofauna has its challenges. Meiofauna are less well known taxonomically than larger organisms. That is, deep-sea meiofaunal species are probably more numerous than larger species (Lambshead 1993), but deep-sea taxonomic work has been concentrated on the latter (see for example the reports of the *Challenger* and *Galathea* expeditions). For some questions, this shortcoming is critical (*e.g.*, species-level biogeography), but for others, it is unimportant because meiofaunal individuals from a sample can be readily separated into working species. Another concern is that the number of meiofaunal individuals in a sample can be overwhelming, but methods for truly random subsampling have been developed (Sherman *et al.* 1984). Despite these potential problems, meiofauna have properties (Table II) that make them good choices for some investigations in deep-sea biology.

Table II. – Traits that make meiofauna particularly useful for the study of some deep-sea questions.

Meiofaunal traits compared to those of larger organisms
Shorter generation time
Higher metabolic rate
Slower movement
Nonplanktonic larvae
Smaller body size
More nearly quantitative sampling

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