Advances in MARINE BIOLOGY

VOLUME 30

Edited by

J H S Blaxter and A J Southward

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FRONTISPIECE

Examples of invertebrate aggregations. (A) School of spawning squid, *Loligo opalescens*. (B) Swarm of mysids in shallow coastal water, south east Tasmania, Australia. (C) School of mysids, *Paramesopodopsis rufa*. (A, courtesy of Planet Earth Pictures, photograph by Norbert Wu; B and C, courtesy of Jon Bryan.)

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Meiobenthos of the Deep Northeast Atlantic

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1. INTRODUCTION

Although the first ecological investigations on the meiobenthic communities of the deep northeast Atlantic were carried out 20 years ago (Thiel, 1972b), it is only recently (1990) that co-operative research has been initiated by the European Community under the EC MAST I (Marine Science and Technology I 1990–1992) programme: "Natural variability and the prediction of change in marine benthic ecosystems". The general objectives of this EC programme, which continues in a MAST II project (1993–1996), are (i) to describe the natural structure and variability of offshore benthic populations in the northeast Atlantic, (ii) to relate the structure and variability to processes in the physical, chemical and biological environment, (iii) to describe the trophic network in the benthic boundary layer and to estimate the organic carbon flux through the deep-sea benthic ecosystem, and (iv) to attempt to predict the changes that are likely to be associated with natural and anthropogenic disturbance. An important component of benthic ecosystems, particularly in the deep sea (Thiel, 1975, 1983), is the meiobenthos, generally considered to include organisms in the size range 31–500 μm. The combined efforts of five laboratories in four of the countries participating in the MAST project have highlighted the gaps that exist in our knowledge of the meiobenthos of the northeast Atlantic and have prompted this review. Our main purpose is to summarize literature data and new results from an area lying between 15°N and 53°N and extending from the continental margin of western Europe and northwest Africa to the Mid-Atlantic Ridge (Figure 1).

Since the first quantitative investigation by Wigley and McIntyre (1964), data on deep-sea meiobenthos have been gathered from all oceans and attempts made to relate the broad geographical patterns observed to various environmental factors. On a planetary scale, one of the major environmental gradients is created by the slope of the ocean floor, a gradient which has important effects on benthic communities. As in the case of macrobenthos (Lampitt *et al.*, 1986), the data available on meiobenthic densities in deep-sea environments also show trends which can be related to the amount and nature of organic matter reaching the seafloor (Thiel, 1983; Shirayama, 1983; Pfannkuche, 1985; Pfannkuche and Thiel, 1987). The distribution patterns of deep-sea organisms are

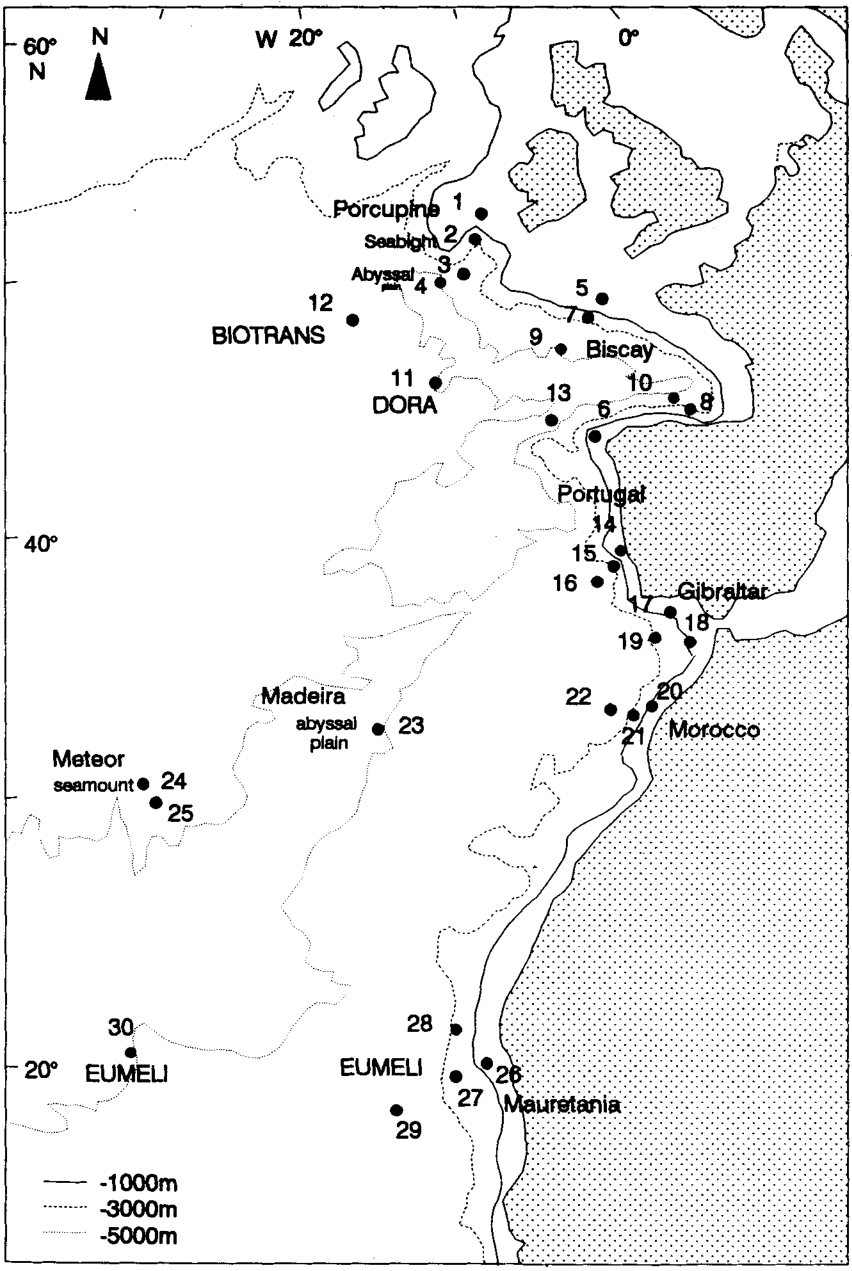

Figure 1 The northeast Atlantic showing the positions of the 30 sampling *areas*.

influenced by other variables such as sediment type, bottom currents and bottom water masses. Local topographic and hydrodynamic features, such as canyons, seamounts and deep boundary currents, are also important. In addition, the ever-improving resolution of the physical structure of the deep sea, and technical advances in sampling gear and surface navigation, have permitted biologists to address small-scale variability, on scales ranging from centimetres to kilometres.

In this review we consider first the nature and scope of meiofaunal research in the northeast Atlantic and then discuss the environmental parameters which are believed to influence meiofaunal organisms. Next, we discuss the various types and scales of pattern observed among meiofaunal populations within our study area, progressing from the large-scale bathymetric and latitudinal trends and then to small-scale horizontal patterns within particular areas. Faunal densities and faunal composition are considered separately and compared with data from other regions. Finally, we discuss the distribution of meiofauna within sediment profiles and the temporal variability of populations. Our approach differs, therefore, from that adopted in Tietjen's (1992) recent review of deep-sea meiofauna which focused mainly on abundance and biomass data from different oceans and on the relationship between the biomass of the meiofauna and that of other faunal components.

2. MEIOBENTHOS IN THE NORTHEAST ATLANTIC

2.1. Physiographic Setting

The area under investigation consists of a series of deep basins separated by ridges. Basin depth tends to increase from north to south, with depths in excess of 5000 m occurring in basins to the west and northwest of the Cape Verde Islands.

A number of physiographic zones can be recognized within this region: continental shelf, continental slope, continental rise, abyssal apron and abyssal plain (Emery and Uchupi, 1984; see also Rona, 1980; Udintsev *et al.*, 1989–1990). Secondary features include the zone of abyssal hills which separates the continental rise from the Mid-Atlantic Ridge and a number of major seamounts and volcanic islands. Notable aspects include the abyssal aprons (sediment masses deposited by geostrophic bottom currents) of the northwest African margin and around and to the west of the Rockall Trough (Hill, 1987) and the series of abyssal plains (from north to south the Porcupine, Biscay, Iberian, Tagus, Horseshoe, Seine, Madeira, Cape Verde, Gambia) which lie seaward of the continental rise.

The area consists of different biogeochemical provinces of plankton productivity, such as upwelling (NW-Africa), trade wind regime, subtropical gyre, etc., which are of great consequence to the supply of food to the seabed and ultimately for the sediment type where pelagic sedimentation prevails.

2.2. Historical Background

The study of some meiobenthic taxa, particularly foraminifera, living in this region has a long history (e.g. Parker & Jones, 1856; Brady, 1884). However, sampling for meiobenthos was incidental until the 1960s and 1970s when the first quantitative meiobenthic samples were collected from the German research vessel *Meteor*; numerical abundance data from these samples were published by Thiel (1972a, b, 1975, 1978, 1983) and Rachor (1975). Another quantitative investigation which included the meiobenthos was the BIOGAS programme, carried out during the 1970s in the Bay of Biscay (Dinet and Vivier, 1977; see also Dinet *et al.*, 1985). More recent papers devoted partly or exclusively to the meiobenthos are those of Pfannkuche *et al.* (1990), Pfannkuche (1992, 1993b) in the BIOTRANS area and Rutgers van der Loeff and Lavaleye (1986) at the DORA site.

Other studies have focused on particular aspects of the meiobenthos. Some authors have considered just the nematodes (Riemann, 1974; Dinet and Vivier, 1979, 1981). Desbruyères *et al.* (1985) evaluated meiobenthic taxa as part of a recolonization experiment in the Bay of Biscay. Another approach has been to look for correlations between meiobenthic densities and environmental parameters such as bathymetric depth and the amount of organic matter in the sediment (Thiel, 1979b, 1983; Dinet and Khripounoff, 1980; Sibuet *et al.*, 1989; Vanreusel *et al.*, 1992). Although taxonomic studies of deep-sea meiobenthos are fairly rare in our area, some new taxa have been described among the harpacticoids (Bodin, 1968; Dinet 1977), nematodes (Decraemer, 1983), ostracods (Kornicker, 1989, van Harten, 1990) and tardigrades (Renaud-Mornant, 1989). Some of these investigations have dealt exclusively with the metazoans while others have included foraminifera within the scope of the meiobenthos. Several papers by Gooday (1986a, b, 1988), Gooday and Lambshead (1989), Lambshead and Gooday (1990) have described the foraminiferal meiobenthos in the northeast Atlantic. Gooday and Turley (1990) presented some additional data and Gooday (1990) established a new, ecologically important allogromiid species. The numerous geologically orientated studies of modern deep-sea foraminifera in the northwest Atlantic (Murray, 1991) deal only with the hard-shelled taxa and are not considered further.

2.3. Sampling Areas

Nine of the papers cited above provide data on the density and composition of metazoan and foraminiferal meiobenthos in the area under consideration and are further treated in a general data analysis (Thiel, 1972a, 1975; Dinet and Vivier, 1977; Pfannkuche *et al.*, 1983, 1990; Pfannkuche, 1985, 1992; Rutgers van der Loeff and Lavaleye, 1986; Vanreusel *et al.*, 1992). Information on foraminifera published by Gooday (1986a, b, 1988) and Gooday and Lambshead (1989) is not considered in the general approach because no total meiobenthic data are given in these articles. However, this information is discussed in the sections on foraminifera. For reasons explained below, we exclude the data of Rachor (1975) from this survey. Additional unpublished results are available from the Porcupine Seabight (Gooday, IOSDL benthic biology programme), Porcupine and Madeira Abyssal Plains (Gooday and Ferrero, IOSDL DEEPSEAS and EC MAST Programmes), Bay of Biscay (Vincx and Vanreusel, EC MAST programme), BIOTRANS site (Soltwedel and Gooday, BIOTRANS Programme) and from off northwest Africa (Dinet, EUMELI and EC MAST programmes).

In order to recognize general trends among the meiobenthos, we have grouped all the stations sampled during these published and unpublished studies into 30 *areas* (identified by number in Table 1) on the basis of geographical and bathymetric proximity. In what follows, density data and other relevant abiotic information on *areas* will always be an average value of the sampling stations situated within one of the 30 *areas* as defined in Table 1. References to *area* numbers in the following text refer always to one of the *area* numbers shown in Figure 1. Bathymetric proximity is arbitrarily defined with limits of following depth zones: < 1000 m, 1000–3000 m, 3000–4500 m and > 4500 m. Inevitably, most of these *areas* are broader in their areal and bathymetric extent than the stations described in the original publications. *Area* locations and numbers are summarized in Figure 1. The original data from all sampling stations are summarized in Table 2.

2.4. Collection and Processing

Methods for the collection and processing of meiobenthic samples are discussed by Thiel (1983), Fleeger *et al.* (1988) and Pfannkuche and Thiel (1988). The data reviewed in the present chapter were obtained from samples collected with various kinds of coring devices (Table 1). A Reineck box corer was used in some of the early studies (Thiel, 1972b, 1975; Dinet and Vivier, 1977) but most investigators have used either an