

Sampler bias in the quantitative study of deep-sea meiobenthos*

B. J. Bett¹, A. Vanreusel², M. Vincx², T. Soltwedel³, O. Pfannkuche³,
P. J. D. Lamshead⁴, A. J. Gooday¹, T. Ferrero⁴, A. Dinet⁵

¹Institute of Oceanographic Sciences Deacon Laboratory, Brook Road, Wormley, Godalming, Surrey GU8 5UB, United Kingdom

²University of Gent, Zoology Institute, Marine Biology Section, K. L. Ledeganckstraat 35, B-9000 Gent, Belgium

³Institut für Hydrobiologie und Fischereiwissenschaft, Universität Hamburg, Zeiseweg 9, D-22765 Hamburg, Germany

⁴Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom

⁵Observatoire Oceanologique de Banyuls, CNRS URA 117, F-66650 Banyuls-sur-Mer, France

ABSTRACT: The influence of sampler type on quantitative estimates of deep-sea meiobenthos is examined by an indirect statistical comparison of box corer and multiple corer samples collected throughout the northeast Atlantic, and by a direct comparison of contemporaneously collected multiple corer and box corer samples from a single abyssal location. The data strongly support the suggestion that the greater down-wash/bow wave associated with box corers results in displacement of surface sediments and any superficial detritus layer together with their associated fauna. Total metazoan meiobenthos density estimates from box corer samples are about half those from corresponding multiple corer samples. Sampler type may also influence the faunal composition of both the metazoan and protozoan components of the meiobenthos.

KEY WORDS: Meiobenthos · Deep sea · Sampling · Box corer · Multiple corer · Northeast Atlantic

INTRODUCTION

In preparing a review of the meiobenthos of the northeast Atlantic (Vincx et al. in press) we compiled quantitative data from both published and unpublished sources. A concern in attempting to analyse such data is the comparability of results obtained by different workers employing different sampling methods. Initial results suggested that the type of sampler used to collect the material is potentially a major source of bias.

Methods for the quantitative sampling of the meiobenthos have been reviewed by Fleeger et al. (1988). They report that 'many workers have severe reservations' about the quality of samples recovered from various grab samplers, concluding that this type of equipment should be avoided if possible. Deep-sea studies have generally avoided the use of grab

samplers and have instead relied upon box corers and, more recently, multiple corers. There is, however, reason to suspect that these 2 types of sampler do not recover samples of the same quality. Multiple corers (Barnett et al. 1984) are designed specifically to collect undisturbed sediment cores. Box corers (Hessler & Jumars 1974) may disturb the surface of the sediment, to a greater or lesser degree, as a result of their more rapid sediment penetration and associated down-wash/bow wave.

Thistle (1983) and Thistle & Sherman (1985) found no evidence of a significant bow wave effect on the densities of meiobenthos from sub-divisions of individual 'vegetatic' box corer samples, although Jumars (1975) had previously detected a significant effect on the densities of macrobenthos. Thiel et al. (1988/1989) reported on the relative recovery of phytodetritus in multiple corer and box corer samples taken from the same abyssal location in the northeast Atlantic: 'The smaller amounts of detritus material in box cores compared to multiple corer samples demonstrates that the

* IOSDL DEEPSEAS programme contribution number 9, BIOTRANS contribution number 32

bow wave of a box corer, despite an optimized flow of water before and during sediment penetration, still washes away loose, light material'. It is therefore reasonable to suspect that even perfect box corer samples (with clear overlying water, etc.) may recover less of the superficial layer of sediment and its associated fauna. This is consistent with the conclusion of Blomqvist (1991) that the multiple corer is the 'best device available for general sampling of open-sea, soft-bottom sediments at present'.

Here, we test whether box corers are as effective as multiple corers in the quantitative sampling of meiobenthos, using data from a range of locations in the northeast Atlantic.

METHODS

We adopted 2 approaches. The first was an indirect statistical comparison of box corer and multiple corer samples collected throughout the northeast Atlantic. The second was a direct statistical comparison of box corer and multiple corer samples collected contemporaneously at a single abyssal location. To maintain the independence of the 2 approaches, the data used in the direct comparison were not used in the indirect analyses.

Indirect comparison. Data on the abundance of meiobenthos were compiled from a number of published and unpublished sources. This data-set was then reduced to single records for what will be referred to as individual 'stations'. An individual station is defined as an intended nominal location sampled by one investigator on (typically) one occasion, irrespective of the total number of samples collected. Where replicate data were available, meiofaunal densities were summarised as geometric mean values. At all stations, only data on the density of meiobenthos in the top 5 cm layer of sediment were used. Fig. 1 and Table 1 show the locations of the 49 sampling stations, their depths and the sources of the data. Note that complete data on meiobenthic taxon composition and density are available for 35 of the stations, that total metazoan density is available for a further 13 stations, and that nematode density alone is available for one other station.

The various statistical methods employed in the analyses are detailed in Sokal & Rohlf (1969) and Steel & Torrie (1981) and, in the main, were implemented using the 'Minitab' (Minitab Inc., USA) statistics software package.

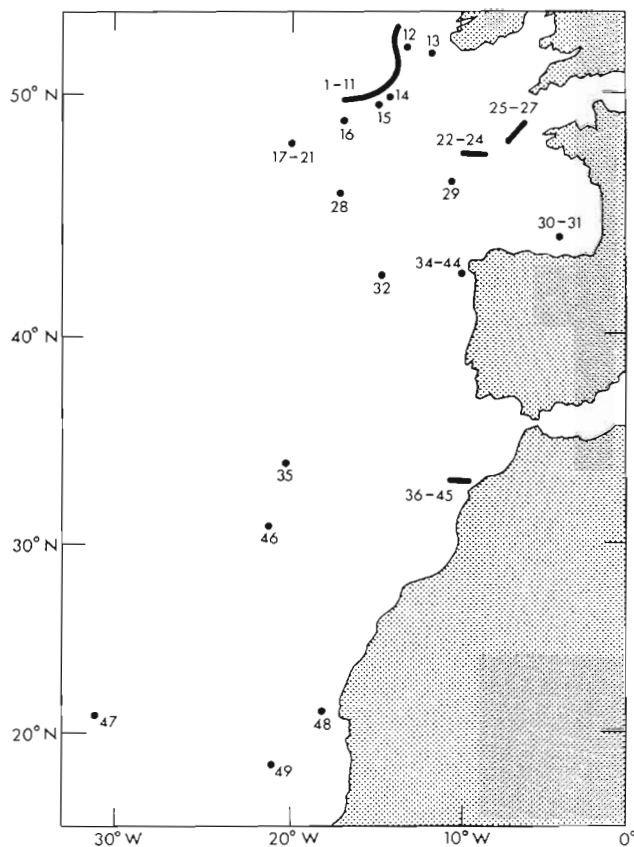


Fig. 1 The northeast Atlantic, showing the positions of the sampling stations from which data were drawn for the study of sampler bias (see also Table 1)

Table 1. List of stations used in the analysis of sampler bias. Station numbers correspond to those shown in Fig. 1. MC: multiple corer samples; BC: box corer samples. Data for each station are coded: C, complete data on meiobenthic taxon composition and density; T, total metazoan density only; N, nematode density only

Station	Sampler	Depth (m)	Data	Source
1-11	MC	500-4850	C	Pfannkuche (1985)
12-15	MC	398-4495	C	Gooday (unpubl.)
16	MC	4850	N	Ferrero (unpubl.)
17	MC	4560	C	Soltwedel (unpubl.)
18	MC	4560	C	Gooday (unpubl.)
19-21	MC	3900-4550	T	Pfannkuche et al. (1990)
22-24	BC	2127-4178	C	Dinet & Vivier (1977)
25-27	BC	70-170	C	Vanreusel & Vincx (unpubl.)
28	BC	4466	C	Rutgers van der Loeff & Lavaleye (1986)
29	BC	4641	C	Dinet & Vivier (1977)
30-31	BC	2016-4397	C	Dinet & Vivier (1977)
32	BC	5314	C	Thiel (1972)
33-34	BC	123-300	C	Vanreusel & Vincx (unpubl.)
35	MC	5120	C	Soltwedel (unpubl.)
36-45	BC	132-3046	T	Pfannkuche et al. (1983)
46	MC	4950	C	Gooday (unpubl.)
47	BC	4594	C	Dinet (unpubl.)
48	BC	1789	C	Dinet (unpubl.)
49	BC	3124	C	Dinet (unpubl.)

Direct comparison. Four box corer (modified USNEL type; Hessler & Jumars 1974) and 4 multiple corer (Barnett et al. 1984) samples were collected from the Porcupine Abyssal Plain (4850 m water depth; 48° 50' N, 16° 30' W, Location 16 on Fig. 1) during RRS 'Challenger' Cruise 79 in May 1991. The box corer samples used had clear overlying water and apparently undisturbed sediment surfaces marked by animal tracks and other biogenic structures. These box corer samples were subsampled with a 'randomly' located standard multiple corer core tube (internal diameter 57 mm). Both the multiple corer samples and the box corer subsamples were sectioned into 1 cm horizons down to 5 cm depth in the sediment. On return to the laboratory, the preserved (formalin) samples were sieved on a 32 μm mesh. Meiobenthos were extracted from the sieve residues using a Ludox centrifugation technique, as detailed in Heip et al. (1985). The extracted material was then sorted, and all specimens identified to major taxa and counted. To ensure consistency, these data (Vanreusel unpubl.) were all produced by a single laboratory.

RESULTS

Indirect comparison

The most obvious source of variation in the data-set is attributable to factors related to water depth. Spearman's rank correlations of total metazoan, nematode, and harpacticoid densities with depth, treating box corer and multiple corer samples separately, give highly significant values ($p < 0.002$), with the exception of nematode densities from box corer samples where the value is nevertheless significant ($p < 0.05$).

The relationships between meiofaunal densities and water depth were examined further by regression of log-transformed densities on depth (see Fig. 2). The F -values for all the regressions are highly significant ($p < 0.001$), or significant ($p < 0.02$) in the case of nematodes from box corer samples. In the 3 cases examined, total metazoans, nematodes, and harpacticoids, a comparison of the regressions of data from box corer and multiple corer samples indicates that, for a given depth, estimates of density based on box corer samples are lower than those from multiple corer samples.

Differences between the pairs (box and multiple corer) of regressions were tested by analysis of covariance. The use of this technique requires a number of assumptions to be made about the data. These assumptions, and their validity in the present case, are as follows. (1) The values of the independent variable, water depth, should be fixed, measured without error, and independent of sampler type; this assumption is

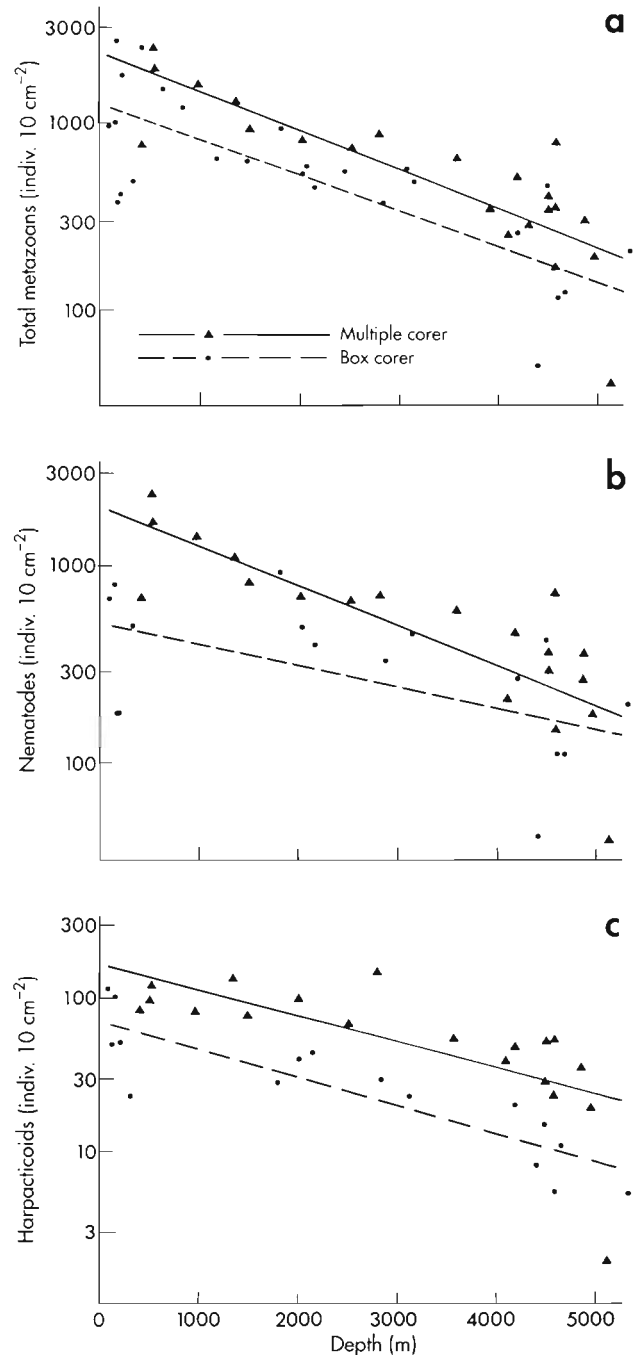


Fig. 2. Plots of the density of meiobenthos (log scale) against depth for (a) total metazoans, (b) nematodes, and (c) harpacticoids. The data, and corresponding regressions, for box corer and multiple corer samples are keyed separately

clearly met in the present case. (2) After removal of the effect of gear type, the regression of meiobenthos densities on water depth should be linear and independent of gear type. This assumption was tested (t -test) by comparing the slopes of the regressions based on box corer and multiple corer data separately. No significant

difference ($p > 0.05$) in slope was detected in any case (total metazoans, nematodes, and harpacticoids). (3) The residuals (the differences between observed values and those predicted by the regressions) should be normally distributed and have a common variance. The residuals from each separate regression were plotted against their corresponding ranked normal deviates (rankits); in all cases, the relationships were approximately linear. These observations were confirmed by calculation of product-moment correlations between the residuals and the rankits, all the values being highly significant ($p < 0.002$). Homogeneity of variance about each pair (box corer and multiple corer) of regressions was assessed using an *F*-test; in all 3 cases, total metazoans, nematodes, and harpacticoids, no significant difference ($p > 0.05$) in variance was detected.

There being no apparent violation of any of the major assumptions of analysis of covariance, this technique was applied to the present data. The effect of sampler type on meiofaunal density was tested using depth as a standardizing covariate. The effect of sampler type on meiofaunal density was highly significant in all 3 cases: total metazoans ($p < 0.005$), nematodes ($p < 0.005$), and harpacticoids ($p < 0.001$). The adequacy of the covariance model in removing the influence of water depth was assessed by calculating rank correlation coefficients between the model residuals and depth; in all cases, the values were not significant ($p > 0.05$). As a further test, 2 other variables potentially related to meiofaunal density were examined, the latitude and distance from continental shoreline of each sampling station. Neither of these variables exhibited a significant rank correlation with the covariance model residuals. Given this reasonable confidence in the covariance model, it was further employed to produce adjusted mean values of meiofaunal densities for each of the 2 sampler types. These mean values enable the magnitude of the sampler effect to be quantified. Box corer density estimates derived by this method, expressed as a percentage of corresponding multiple corer estimates, are: total metazoans 59.4%, nematodes 46.4%, and harpacticoids 37.1%.

Direct comparison

The data from the 4 multiple corer samples and the 4 box corer subsamples do not meet the assumptions of parametric statistical analyses; comparisons between samplers were, therefore, restricted to a simple non-parametric method (Mann-Whitney *U*-test). (Note that, in the following, 'other taxa' refers to all metazoans other than nematodes and harpacticoids.) Table 2

Table 2. Mean densities (ind. 10 cm^{-2}) of selected meiobenthic taxa ('other taxa', all metazoans excluding nematodes and harpacticoids) in the top 5 cm sediment layer, based on multiple corer samples and box corer subsamples from the Porcupine Abyssal Plain. (* $p < 0.05$, Mann-Whitney *U*-test)

Taxon	Multiple corer	Box corer
Nematodes	685.3	269.6*
Harpacticoids	25.7	33.1
'Other taxa'	12.2	1.7*
Total metazoans	723.2	304.4*

details the mean densities of meiobenthic taxa in the top 5 cm sediment layer, as estimated from the 2 sampler types. In those taxa, where a significant ($p < 0.05$) difference between samplers was detected, box corer estimates expressed as a percentage of corresponding multiple corer estimates are as follows: nematodes 39.3%, 'other taxa' 13.6%, and total metazoans 42.1%. No significant difference ($p > 0.05$) in harpacticoid densities was detected.

Between-sampler variations were also examined in the individual 1 cm sediment horizons (see Fig. 3). For nematodes, 'other taxa', and total metazoans, multiple corer density estimates exceed those from the box corer in all 5 sediment layers (0–1 to 4–5 cm). These differences are only significant ($p < 0.05$) in the top 2 layers (0–1 and 1–2 cm) for 'other taxa', and in the top 3 layers (0–1 to 2–3 cm) for nematodes and total metazoans.

In the case of harpacticoids, in the surface layer (0–1 cm) there is a significant ($p < 0.05$) difference between samplers, with the multiple corer estimate exceeding that from the box corer. However, in all subsurface layers (1–2 to 4–5 cm) box corer estimates are greater than those from the multiple corer, significantly ($p < 0.05$) so in the 1–2 and 4–5 cm layers. Overall, there is a marked difference in the apparent distribution of harpacticoids with depth between the 2 samplers. The multiple corer data indicate a rapid decline in harpacticoid numbers with depth in the sediment, whereas little or no change with depth is apparent in the box corer data.

DISCUSSION

Overall, the analyses strongly support the intuitive notion that, because of their greater down-wash, box corers are less efficient collectors of meiobenthos than multiple corers. In detail, the results differ from these expectations in 2 respects.

Firstly, in the case of the harpacticoids in the direct comparison analysis, no significant difference in densities was detected between samplers over the full

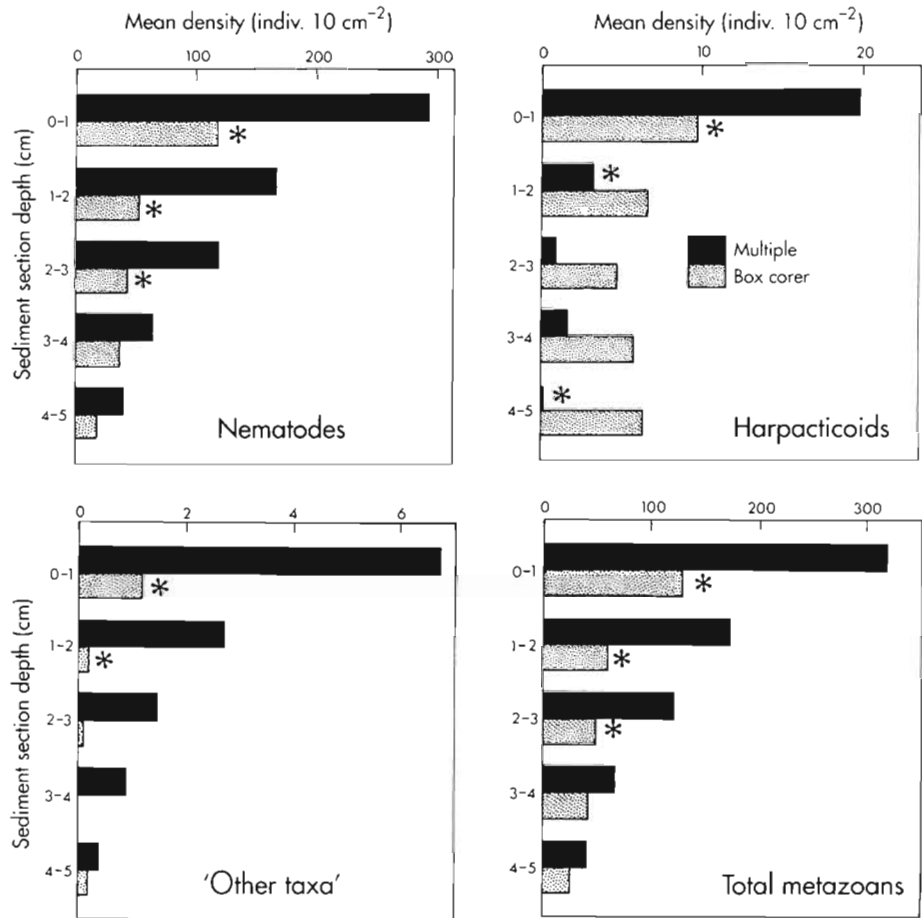


Fig. 3. Mean sediment depth distributions of selected meiobenthic taxa ('other taxa', all metazoans excluding nematodes and harpacticoids) in multiple corer samples and box corer subsamples from the Porcupine Abyssal Plain. (* $p < 0.05$, Mann-Whitney U -test)

0–5 cm layer, although the multiple corer did recover significantly higher numbers of harpacticoids in the 0–1 cm horizon than the box corer. At present, we can offer no explanation for this result, nor for the unusually even vertical distribution of harpacticoids in the box corer subsamples, and we omit these observations from the general considerations below.

Secondly, we had expected the effect of any down-wash to be detectable in the surface sediment layers. However, the observation that multiple corer density estimates always exceeded those of the box corer in all sediment layers down to 5 cm suggests something more than simply a down-wash effect, possibly a difference in the degree of core compaction produced by the 2 samplers.

Assuming that the difference between box corer and multiple corer meiobenthos density estimates results primarily from the greater down-wash of box corers, then the effect is likely to be greatest on the surface sediment layer. If this is the case then the apparent magnitude of the effect, when considered over the upper 5 cm of sediment, may vary depending on the within-sediment vertical distribution of the fauna. It is possible that the difference in the magnitude of the

effect recorded for nematodes (or perhaps more reliably, total metazoans) and harpacticoids, in the indirect comparison analysis, could have resulted from this. Harpacticoids are generally more concentrated in the surface sediment layers than nematodes (Hicks & Coull 1983), as is evident in a comparison of nematode and harpacticoid vertical distributions from multiple corer samples collected on the Porcupine Abyssal Plain (see Fig. 3). Similarly, the marked difference in the magnitude of sampler bias recorded for nematodes (39.3%) and 'other taxa' (13.7%) in the direct comparison analysis could be attributed to the same effect. In consequence, both the apparent vertical distribution of the fauna and its composition summed over, for example, 0–5 cm may vary depending on sampler type.

The problem of sampler bias is not limited to the metazoan meiobenthos. The relative and absolute abundance of foraminifera, a taxon not included in our analyses, may also be influenced substantially by the type and quality of corer samples (Douglas 1979). In some samples, approximately 10% of live specimens reside in phytodetritus, a flocculent sediment-surface layer that is only reliably recovered in multiple corer samples (Goody 1988, Goody & Lamshead 1989,

Lambshhead & Gooday 1990). Some species of foraminifera with calcareous or proteinaceous tests are concentrated in phytodetritus, and so the loss of this material undoubtedly will bias the taxonomic composition of the live assemblages in favour of agglutinated taxa. The inability of box corers to reliably sample sediment surface accumulations of phytodetritus is a particularly serious problem. Although significant phytodetritus deposition may occur only in certain regions (Billett et al. 1983, Lampitt 1985, Rice et al. 1986, Thiel et al. 1988/1989, Hecker 1990), in areas where it does occur, this superficial layer plays a very important role in total benthic processes (Gooday & Turley 1990, Pfannkuche 1992, 1993).

Our results indicate that the apparent density of metazoan meiobenthos can differ by around 50% depending on sampler type. However, it is possible that the magnitude of sampler bias may vary between taxa (see above), between times and places dependent on the presence or absence of phytodetritus, or between muddy and sandy sediments, such that no simple 'correction' can be applied when comparing data from different samplers.

Acknowledgements. We thank all those colleagues who assisted in the collection and processing of material and who commented on the manuscript. This collaborative effort was made possible through funding by the CEC MAST programme [contracts: MAST I, 0037-C(EDB); MAST II, MAS2-CT92-0033].

LITERATURE CITED

- Barnett, P. R. O., Watson, J., Connelly, D. (1984). A multiple corer for taking virtually undisturbed samples from shelf, bathyal and abyssal sediments. *Oceanol. Acta* 7: 399–408
- Billett, D. S. M., Lampitt, R. S., Rice, A. L., Mantoura, R. F. C. (1983). Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature* 302: 520–522
- Blomqvist, S. (1991). Quantitative sampling of soft-bottom sediments: problems and solutions. *Mar. Ecol. Prog. Ser.* 72: 295–304
- Dinet, A., Vivier, M.-H. (1977). Le meiobenthos abyssal du Golfe de Gascogne. I. Considerations sur les donnees quantitatives. *Cah. Biol. mar.* 18: 85–97
- Douglas, R. G. (1979). Benthic foraminiferal ecology and paleoecology: a review of concepts and methods. In: Lipps, L. H., Berger, W. H., Buzas, M. A., Douglas, R. G., Ross, C. A. (eds.) *Foraminiferal ecology and paleoecology*. Society of Economic Paleontologists and Mineralogists, Short Course notes Vol. 6, Houston, p. 21–53
- Fleeger, J. W., Thistle, D., Thiel, H. (1988). Sampling equipment. In: Higgins, R. P., Thiel, H. (eds.) *Introduction to the study of meiofauna*. Smithsonian Institution Press, Washington, D.C., p. 115–125
- Gooday, A. J. (1988). A response by benthic foraminiferans to the deposition of phytodetritus in the deep sea. *Nature* 332: 70–73
- Gooday, A. J., Lambshhead, P. J. D. (1989). Influence of seasonally deposited phytodetritus on benthic foraminiferal populations in the bathyal northeast Atlantic: the species response. *Mar. Ecol. Prog. Ser.* 58: 53–67
- Gooday, A. J., Turley, C. M. (1990). Response by benthic organisms to input of organic material to the ocean floor. *Phil. Trans. R. Soc. Lond.* 331A: 119–138
- Hecker, B. (1990). Photographic evidence for the rapid flux of particles to the sea floor and their transport down the continental slope. *Deep Sea Res.* 37: 1773–1782
- Heip, C., Vincx, M., Vranken, G. (1985). The ecology of marine nematodes. *Oceanogr. mar. Biol. A. Rev.* 23: 399–489
- Hessler, R. R., Jumars, P. A. (1974). Abyssal community analysis from replicate box cores in the central North Pacific. *Deep Sea Res.* 21: 185–209
- Hicks, G. R. F., Coull, B. C. (1983). The ecology of marine meiobenthic copepods. *Oceanogr. mar. Biol. A. Rev.* 21: 67–175
- Jumars, P. A. (1975). Environmental grain and polychaete species' diversity in a bathyal community. *Mar. Biol.* 30: 253–266
- Lambshhead, P. J. D., Gooday, A. J. (1990). The impact of seasonally deposited phytodetritus on epifaunal and shallow infaunal benthic foraminiferal populations in the bathyal northeast Atlantic: the assemblage response. *Deep Sea Res.* 37: 1263–1283
- Lampitt, R. S. (1985). Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep Sea Res.* 32: 885–897
- Pfannkuche, O. (1985). The deep-sea meiofauna of the Porcupine Seabight and abyssal plain (NE Atlantic): population structure, distribution, standing stock. *Oceanol. Acta* 8: 343–353
- Pfannkuche, O. (1992). Organic carbon flux through the benthic community in the temperate abyssal northeast Atlantic. In: Rowe, G. T., Pariente, V. (eds.) *Deep-sea food chains and the global carbon cycle*. Kluwer Academic, Dordrecht, p. 183–198
- Pfannkuche, O. (1993). Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station, 47° N, 20° W. *Deep Sea Res.* 40: 135–149
- Pfannkuche, O., Theeg, R., Thiel, H. (1983). Benthos activity, abundance and biomass under an area of low upwelling off Morocco, Northwest Africa. *'Meteor' Forsch.-Ergebn.* 36: 85–96
- Pfannkuche, O., Beckmann, W., Christiansen, B., Lochte, K., Rheinheimer, G., Thiel, H., Weikert, H. (1990). BIOTRANS, Biologischer Vertikaltransport und Energiehaushalt in der bodennahen Wasserschicht der Tiefsee. *Berichte aus dem Zentrum für Meeres- und Klimaforschung der Universität Hamburg*, Nr. 10, 159 pp.
- Rice, A. L., Billett, D. S. M., Fry, J., John, A. W. G., Lampitt, R. S., Mantoura, R. C. F., Morris, R. J. (1986). Seasonal deposition of phytodetritus to the deep-sea floor. *Proc. R. Soc. Edinb.* 88B: 265–279
- Rutgers van der Loeff, M. M., Lavaleye, M. S. S. (1986). Sediments, fauna and the dispersal of radionuclides at the N.E. Atlantic Dumpsite for low-level radioactive waste. Report of the Dutch DORA Program. Netherlands Institute for Sea Research, Texel
- Sokal, R. R., Rohlf, F. J. (1969). *Biometry. The principles and practice of statistics in biological research*. W. H. Freeman & Co., San Francisco
- Steel, R. G. D., Torrie, J. H. (1981). *Principles and procedures of statistics a biometrical approach*. McGraw-Hill International Book Co., London

- Thiel, H. (1972). Meiofauna und Struktur der benthischen Lebensgemeinschaft des Iberischen Tiefseebeckens. 'Meteor' Forsch.-Ergebn. 12: 36–51
- Thiel, H., Pfannkuche, O., Schriever, G., Lochte, K., Gooday, A. J., Hemleben, CH., Mantoura, R. F. G., Turley, C. M., Patching, J. W., Riemann, F. (1988/1989). Phytodetritus on the deep-sea floor in a central oceanic region of the north-east Atlantic. Biol. Oceanogr. 6: 203–239
- Thistle, D. (1983). The role of biologically produced habitat heterogeneity in deep-sea diversity maintenance. Deep Sea Res. 30: 1234–1245
- Thistle, D., Sherman, K. M. (1985). The nematode fauna of a deep-sea site exposed to strong near-bottom currents. Deep Sea Res. 32: 1077–1088
- Vincx, M., Bett, B. J., Dinert, A., Ferrero, T., Gooday, A. J., Lamshead, P. J. D., Pfannkuche, O., Soltwedel, T., Vanreusel, A. (in press). Meiobenthos of the deep northeast Atlantic: a review. Adv. mar. Biol. 30

This article was submitted to the editor

Manuscript first received: July 20, 1993

Revised version accepted: November 3, 1993