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Temporal variabilities in benthic activity and biomass on the western European continental margin

Temporal variability
Benthic activity
Benthic biomass
Biogenic sediment compounds
Continental margin

Variabilité temporaire
Activité benthique
Biomasse benthique
Composants biogéniques du sédiment
Marge continentale

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ABSTRACT

Temporal variations in activity and biomass of the smaller benthic biota (size range: bacteria up to small meiofaunal organisms) were investigated on the Goban Spur continental margin (NE Atlantic) within the framework of the multidisciplinary research programme OMEX ("Ocean Margin EXchange") sponsored by the European Union. Activities and biomasses were estimated analysing a series of biogenic sediment compounds (enzymes, adenylates, DNA, phospho-lipids, particulate proteins). In contrast to the very time-consuming sorting, enumeration and weighing of organisms, the determination of biochemical sediment parameters represents a useful method to obtain rapid information on ecological dynamics within benthic systems.

Measurements of activity and biomass parameters on the Goban Spur continental margin showed a strong seasonal cycle with two peaks in spring (May) and autumn (September/October), and a rapid response within days and/or a few weeks of the most reactive part of the benthic community, *i.e.* bacteria and protozoans (flagellata, ciliata, amoeba, foraminifera), following episodic inputs of organic matter via phytodetritus sedimentation.

In general, benthic activities and biomasses decrease with increasing water depth and distance from the shelf, and the seasonal signal fades with increasing depth. However, still high and sometimes even increasing values were found on a terrace in about 3600 m water depth (Pendragon Escarpment) and also on the continental rise, indicating the presence of deposition centres for a down-slope transport of organic material.

RÉSUMÉ

Variabilité temporelle de l'activité benthique et de la biomasse sur la marge continentale d'Europe occidentale.

La variabilité temporelle de l'activité biologique et de la biomasse de la faune benthique (de tailles allant des bactéries aux petits organismes de la méiofaune) a été étudiée sur l'éperon « Goban Spur » de la marge continentale du nord-est de l'Atlantique, dans le cadre du programme pluridisciplinaire Ocean Margin Exchange (OMEX) parrainé par l'Union Européenne. L'activité biologique et la biomasse ont été déterminées par l'analyse biochimique d'une série de composants biogéniques du sédiment (enzymes, adénylates, DNA, phospholipides, protéines particulaires). Par comparaison aux méthodes traditionnelles (tri, comptage, estimation du poids) qui exigent beaucoup de temps, l'analyse biochimique du sédiment a l'avantage de fournir rapidement des informations sur la dynamique écologique d'un système benthique.

Sur la marge continentale de l'éperon « Goban Spur », les paramètres biochimiques révèlent un cycle saisonnier prononcé avec deux maxima, au printemps (mai) et en automne (septembre-octobre), et un temps de réaction très court (quelques jours à quelques semaines) pour la partie la plus active de la communauté benthique, bactéries et protozoaires, lors des apports épisodiques de matière organique par la sédimentation de détritus végétaux.

En général, l'activité et la biomasse benthiques diminuent en profondeur et loin du plateau continental. Le cycle saisonnier s'estompe également lorsque la profondeur augmente. Cependant, un accroissement marqué des paramètres précédents a été observé sur une terrasse (Pendragon Escarpment) vers 3600 m de profondeur, indiquant la présence de zones d'accumulation dans le transport de marériel organique le long de la pente continentale.

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INTRODUCTION

The aim of the European multidisciplinary project "Ocean Margin EXchange" (OMEX) is to obtain a better understanding of the physical, chemical and biological processes occurring in the outer shelf – upper slope region, which are responsible for the exchange of matter and energy between the neritic zone and the open ocean. Thus, OMEX serves as a link between large international programmes devoted to similar objectives in oceanic regions ("Joint Global Ocean Flux Study", JGOFS) and in the coastal zone ("Land-Ocean Interactions in the Coastal Zone", LOICZ).

It is well known that coastal and marginal seas account for a significant portion of the primary productivity in the oceans. Furthermore, these regions could also act as sources or sinks for several biogenic elements relative to the open ocean. Much of the terrestrial material transported into the oceans by rivers settles on the continental shelves. In this connection, temporal (seasonal and inter-annual) and spatial variability in primary productivity, the balance between the production and consumption of organic matter and temporal and spatial variations in the burial of biologically relevant elements are of great importance.

The largest proportion of particulate organic matter (POM) reaching the sea bed is degraded by bacteria and protozoans (Pfannkuche, 1993), which stresses the importance of the small size classes of the benthic community in carbon degradation. In off shore regions, bacteria and protozoans seem to be the main generators of observed increases in the sediment community oxygen consumption (Pfannkuche, 1992; 1993) and other parameters of metabolic activity, e.g. enzymatic activity (Boetius and Lochte, 1994), after POM pulses. Thus, measurements of biochemical sediment parameters for activities and biomasses of the smaller benthic biota permit the identification of zones of relatively high carbon remineralization. In contrast to very time-consuming traditional sorting, counting and weighing methods, the determination of activities and biomasses *via* measurements of biogenic sediment compounds is a useful tool to obtain rapid information on the impact of episodic POM pulses on the most reactive part of the benthic community, *i.e.* bacteria and protozoans (e.g. Altenbach, 1985; Gooday and Lambshead, 1989; Lochte, 1992; Meyer-Reil, 1983).

To survey the reaction of the benthic community to temporally varying organic matter input, sediment samples were analysed from a total of five cruises during spring 1988 (not within the OMEX project) and between summer 1993 and fall 1994 (OMEX cruises) to the western European continental margin.

Study area

Sampling on each cruise was conducted along a single transect across the Goban Spur continental margin, between 48° 30′ N/16° 30′ W and 49° 30′ N/11° 10′ W (Fig. 1). This margin embodies the transitional zone between the Celtic shelf and the Porcupine Abyssal Plain (PAP) bordered to the north-west by the Porcupine Seabight (PSB) and to the south-east by the King Arthur Canyon, separating the Goban Spur region from the entire Celtic continental margin.

Below the shelf edge, the Goban Spur displays a smoothly falling slope (on average < 1° angle of inclination) over about 90 nautical miles (Fig. 2). In 1300 m water depth the slope becomes abruptly steeper (on average ~ 2.5°).

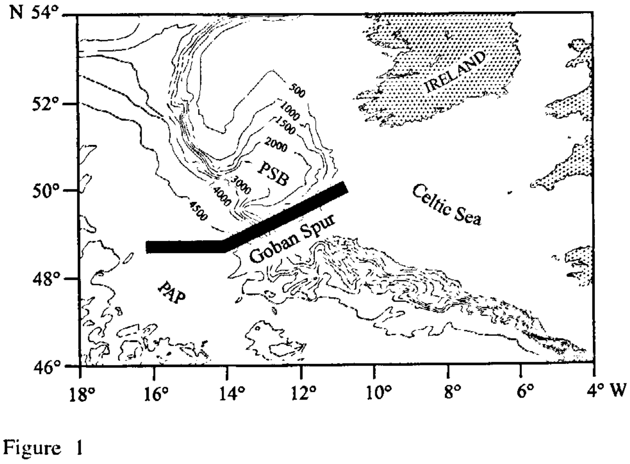

Figure 1

Transect of 35 stations from a total of five cruises across Goban Spur continental margin (PAP: Porcupine Abyssal Plain; PSB: Porcupine Seabight).

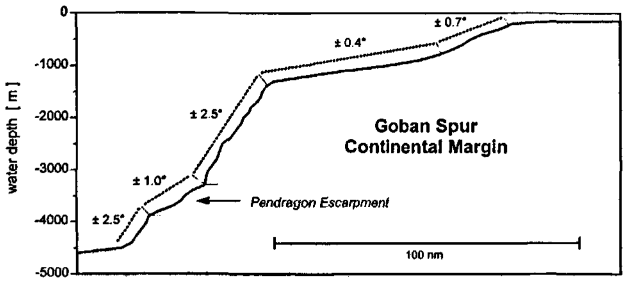

Figure 2

Morphology and average angles of inclination of the Goban Spur continental margin.

A terrace at about 3600 m water depth (Pendragon Escarpment) constitutes another prominent feature of the Goban Spur continental margin. A relatively steep slope (on average ~2.5°) below this terrace leads to the adjacent PAP.

The Goban Spur region exhibits a very complex hydrography with wind-induced currents, internal waves and strong tidal influences in shallow water depths, and also changes in the along-slope current direction in different seasons. For a detailed hydrographic description of the area of investigations see Pingree and Le Cann (1989).

Recent results from the nearby PSB and PAP demonstrated a strong seasonality in phytoplankton production and subsequently a pulsed supply of organic matter (phytodetritus) to the benthic community (Billett *et al.*, 1983; Lampitt, 1985; Rice *et al.*, 1986; 1994). Thus, benthic activity and biomass should be subject to spatial, but also to seasonal variations in response to the sedimentation of particulate organic matter.

MATERIALS AND METHODS

Data from four German, English and Dutch OMEX cruises in 1993 and 1994, together with results from an earlier RV *METEOR* cruise in 1988 (not within the OMEX project) are the basis for these investigations. Sediment sampling was carried out with a multiple corer (Barnett *et al.*, 1984) and a modified version of the USNEL spade box corer (Fleeger *et al.*, 1988). A total of 35 stations was sampled (four to eight stations per cruise) ranging between 135 m on the shelf (Great Sole Bank) and 4808 m on the PAP. For logistic reasons (e.g. weather conditions, ship time and wire length), it was not always possible to sample exactly the same stations along this transect during the various cruises (Table 1). However, a comparison of results from stations on fairly similar depth levels allows temporal changes to be identified.

Subsampling for biochemical analyses was performed with small piston-style corers (5 ml and 20 ml disposable syringes) down to 10 cm sediment depth. To evaluate small-scale variations, five replicates from each multiple corer or box corer were analysed for the various biochemical parameters. To investigate gradients within the sediment column, subsamples were sectioned horizontally in 1-cm-layers and analysed separately.

Table 1

Station water depths occupied and sampling devices (BC = box corer; MC = multiple corer) deployed during five cruises between April 1988 and September 1994.

cruise *date*	**METEOR 6/7** 5.4.-6.4.1988	**VALDIVIA 137** 29.6.-5.7.1993	**PELAGIA** 18.10.-25.10.1993	**DARWIN** 23.5.-1.6.1994	**METEOR 30/1** 12.9.-17.9.1994
number of stations:	8	4	7	8	8
corer type:	BC	MC	MC	BC	MC
water depth:					
< 1000 m	182	135	206	218	224
	410	571/580	670	666	674
1000-2000 m	1013	1216/1252	1034	1016	1148
		1630/1680	1425	1146	1535
			1961	1423	
2000-3000 m	2084		2182	2266	2269
			2760		
3000-4000 m	3552			3663	3629/3666
	3889				
4000-5000 m	4470			4500	4471
	4772				4804/4808

The input of 'fresh' phytodetritus to the benthos was assessed by measurements of sediment-bound chlorophyll *a* concentrations. Chloroplastic pigments were extracted in 90% acetone and measured with a TURNER fluorometer according to Yentsch and Menzel (1963) and Holm-Hansen *et al.* (1965).

Differences in activities and biomasses within the sediment samples were determined by a series of biochemical assays commonly used in ecological investigations of the deep sea (see Greiser and Faubel, 1988): esterase turnover rates with fluorescein-di-acetate (FDA) for bacterial enzymatic activity, and total adenylates (ATP+ADP+AMP), DNA, phospho-lipids and particulate proteins for biomass of the smaller benthic fauna.

Fluorescein-di-acetate measurements, estimating the activity of extracellular and intracellular microbial ester-cleaving enzymes, were made according to Köster *et al.* (1991). Total adenylates and particulate proteins, operationally defined as ATP and γ-globulin equivalents respectively, were measured following instructions given by Greiser and Faubel (1988). Phospho-lipids from cell walls were determined with a modification of the method of Findlay *et al.* (1989), whereas for DNA measurements the method of Kapuscinski and Skoczylast (1977) was applied.

Table 2 explains which biochemical analyses were performed on the sediment samples from the various cruises and stations between spring 1988 and fall 1994.

RESULTS

Biochemical analyses were carried out on samples to a maximum sediment depth of 10 cm. However, the following detailed description and interpretation of temporal variations within the data is mainly restricted to values from the uppermost centimetre of the sediment column. Although gradients within the sediment column (*see below*), especially at shallow stations, often showed strong heterogeneity, presumably due to bioturbation effects and hydrodynamic sediment reworking, cumulative values over several centimetres and values of the uppermost centimetre in general exhibited rather similar trends.

Although pieced together from observations collected in different months over a period of several years, and probably influenced by interannual variations, the results show a pronounced seasonal pattern in food availability and biomass of the smallest benthic organism size groups, with two major peaks in May and September/October.

Temporal and spatial variations in organic matter input

Chlorophyll *a* concentrations, indicating phytodetritus sedimentation, varied considerably between April and October. Lowest values were measured in early April (1988) and at the beginning of July (1993); maximum values occurred at the end of May (1994). Increased chlorophyll *a* concentrations were also found during September (1994) and October (1993). These results indicate a two-peak input of primary organic matter to the benthos over the year (Fig. 3). Enhanced variations (high standard deviations) between replicates at certain stations and at different times of the year reveal periods of increased patchiness of phytodetritus on the sea floor. However, the pronounced seasonality in phytodetritus sedimentation could be observed in various water depths on the Goban Spur transect, at least down to ~2200 m. Below this depth horizon there is insufficient pigment data for a direct temporal comparison. A compilation and processing (inverse distance interpolation) of all chlorophyll *a* data available from the various cruises (35 stations; 135-4808 m water depth) suggests that seasonality in organic matter

Table 2

Biochemical analyses performed (•) to assess benthic activity and biomass as well as organic matter input to the benthos during five cruises between April 1988 and September 1994.

cruise *date*	**METEOR 6/7** 5.4.-6.4.1988	**VALDIVIA 137** 29.6.-5.7.1993	**PELAGIA** 18.10.-25.10.1993	**DARWIN** 23.5.-1.6.1994	**METEOR 30/1** 12.9.-17.9.1994
number of stations:	8	4	7	8	8
corer type:	BC	MC	MC	BC	MC
activity:					
FDA			•		•
biomass:					
DNA		•	•	•	•
ADENYLATES	•		•		•
LIPIDS		•	•	•	•
PROTEINS		•	•	•	•
primary organic matter:	•	•	•	•	•
PIGMENTS					

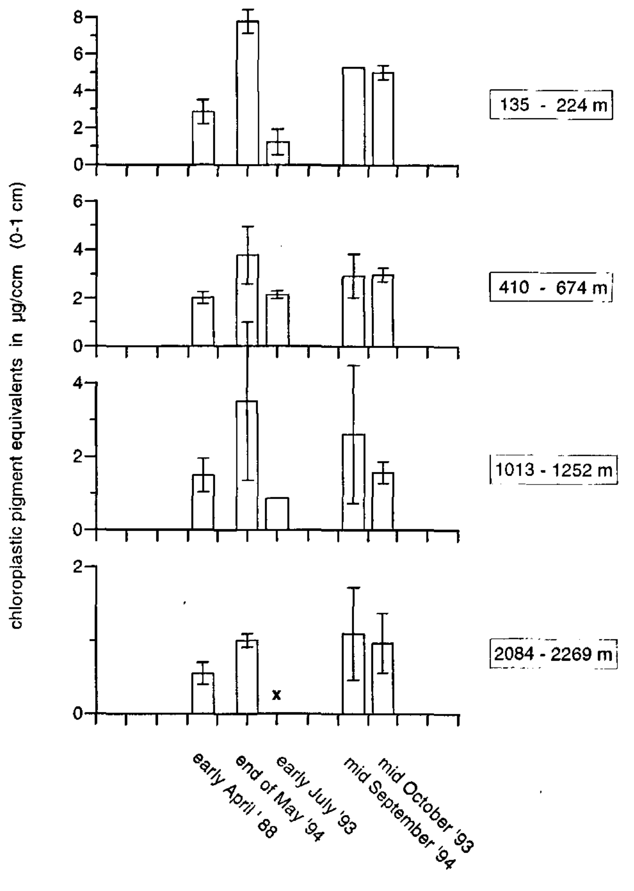

Figure 3

Chlorophyll a *concentrations and standard deviations (five replicates) in the top 1-cm-layer of the sediments at different water depth horizons between April and October (x = missing value).*

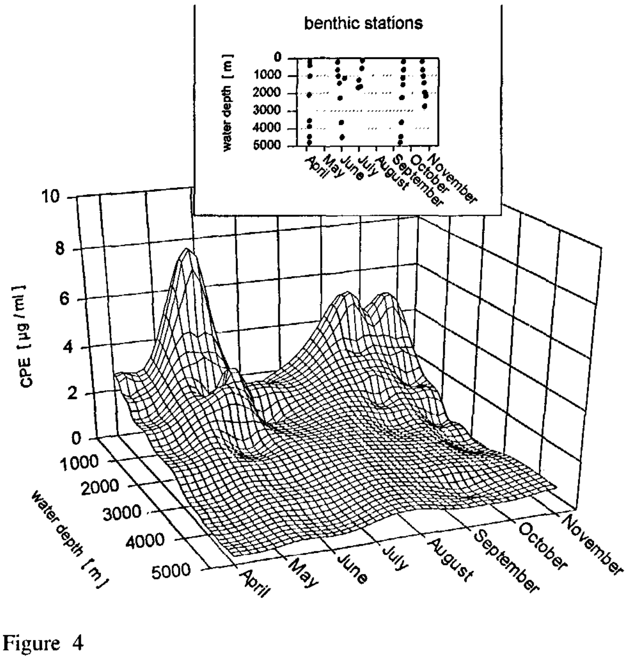

Figure 4

Temporal development of food availability from phytodetritus input, indicated by sediment-bound chlorophyll a *concentrations on the Goban Spur transect between April (1988) and October (1993).*

input may be detectable throughout the transect and not only in its upper part (Fig. 4).

Temporal and spatial variations in benthic activities and biomasses

Concentrations of particulate proteins in the sediments, indicating 'living' and 'dead biomass' (micro-organisms and detritial organic matter, respectively), generally followed sediment-bound pigment concentrations over the year (for shelf stations *see* Fig. 5). This suggests that a significant proportion of particulate proteins represents primary organic matter and/or organisms closely associated with the phytodetritus and its degradation.

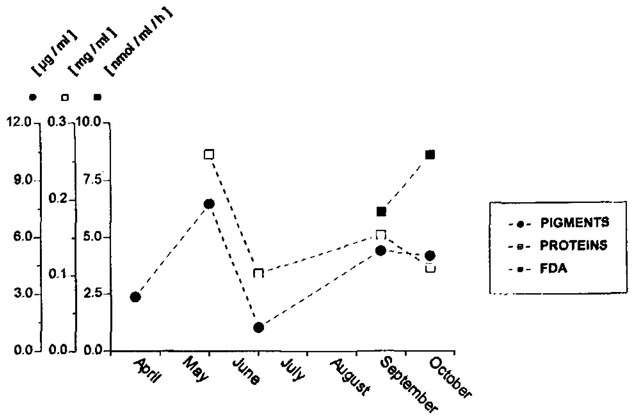

Figure 5

Sediment-bound chloroplastic pigments as well as activity and biomass parameters in 200 m water depth (uppermost centimetre) on the Goban Spur transect between April and October.

However, in September/October, during or shortly after organic matter input from a phytoplankton bloom, a strong increase of 'living biomass' and bacterial enzymatic activity (FDA turnover) in the sediments was detectable at some stations, while pigment and protein concentrations decreased slightly (Fig. 5). The fast benthic response, manifested by an increase of organism biomass within a few days or weeks, was indicated by a considerable increase in total adenylates, DNA and phospho-lipids within the sediments during this period (for shelf stations *see* Fig. 6).

These indications of increase in activity and biomass were observed throughout the Goban Spur transect, with high, and in some cases increased, values on and below the Pendragon Escarpment. This terrace and the foot of the continental margin may be deposition centres for a downslope transport of organic matter. Figure 7 illustrates depth variations in enzymatic activity and biomass on the Goban Spur transect (uppermost centimetre) in April (1988), September (1994) and October (1993), with low values in spring and increased values from September to October.

Activities and biomasses within the sediment column

Changes in heterotrophic activities and biomasses were also observed within the sediment columns, *i.e.* the upper ten

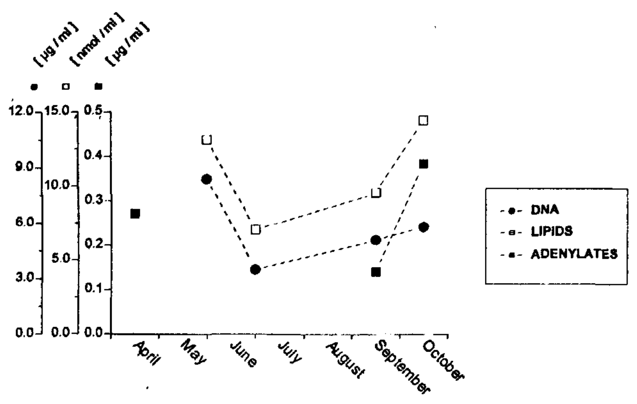

Figure 6

Benthic biomass parameters in 200 m water depth (uppermost centimetre) on the Goban Spur transect between April and October.

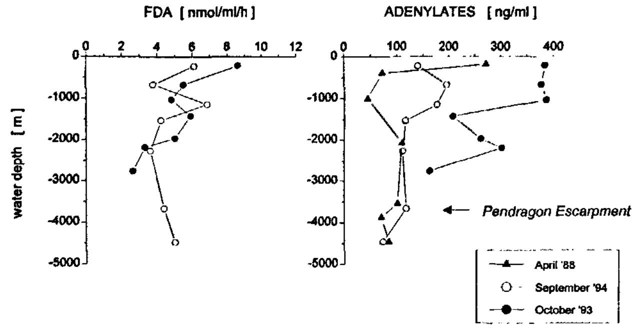

Figure 7

FDA turnover (bacterial enzymatic activity) and total adenylate concentrations ('living biomass') in the sediments on the Goban Spur transect (uppermost centimetre) in various months.

centimetres of the sediments. For instance, October (1993) values in bacterial enzymatic activity (FDA) and DNA concentrations at the shallower stations (~200, ~650 m) were about twice as high as September (1994) values (Fig. 8), also indicating a rapid transfer of detritus to deeper sediment layers *via* bioturbation by macro- and megafaunal organisms. This was especially obvious at the shelf and upper slope stations, but a rapid response of the benthic infauna to an enhanced organic matter input was indicated by most biochemical parameters at almost all station depths.

DISCUSSION

The top several centimetres of the sediment and the overlying water represent the most active zone of the benthal. This zone receives material from the water column, transforms it in a variety of chemical and biological reactions, and exchanges material both with the underlying sediment and with the overlying water column. Sedimentation fluxes occur vertically to the sea floor, but also laterally along it. In contrast to fluxes measured by sediment traps, benthic investigations of activity and biomass integrate both vertical and lateral

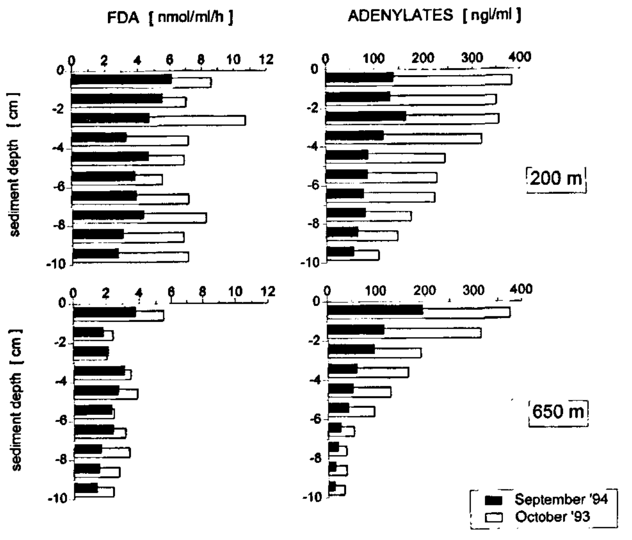

Figure 8

FDA turnover (bacterial enzymatic activity) and total adenylate concentrations ('living biomass') in the upper 10 cm of the sediments on shelf and upper slope stations in September (1994) and October (1993).

fluxes. Therefore, to evaluate the quantity and quality of POM finally reaching the sediments in space and time, and to understand the timing and extent of the benthic response, extensive investigations of benthic activities and biomasses seem to be essential.

Biogenic sediment compounds as indicators of benthic life

The determination of biogenic compounds constitutes a practical method of estimating activities and biomasses in sediment samples. In contrast to the very time-consuming sorting, enumeration and weighing of organisms (especially for the smaller size classes), these biochemical techniques rapidly lead to reliable information on ecological dynamics within the benthic system (e.g. Graf *et al.*, 1983; Pfannkuche *et al.*, 1983; Soltwedel and Thiel, 1995). The comparatively rapid biochemical assays also allow the processing of a larger number of samples. This fact led to an extensive spatial and especially temporal coverage with activity values (15 stations) and biomass data (27 stations) for the smallest sediment-inhabiting biota along the Goban Spur continental margin. Organic matter input from phytoplankton production (indicated by sediment-bound pigment concentrations) could be assessed for every station of the various cruises (35 stations).

Analyses of biogenic compounds from relatively small sediment samples, of course, register mainly the smallest size classes of the benthic community, *i.e.* bacteria, protozoans and small meiofaunal organisms; larger meiofaunal and small macrofaunal organisms may contribute to variabilities in the biochemical data. However, bacteria and protozoans account for more than 90% of the deep-sea benthic biomass (Pfannkuche, 1993; Rowe *et al.*, 1991; Tietjen, 1992). Moreover, these organisms represent the most reactive part of the benthic community (*see* *below*), thus playing an important role in remineralization processes in the benthal and the biogeochemical ocean carbon cycle as a whole.

Despite their ecological importance, benthic bacteria and protozoans have not been the subject of specific investigations within the OMEX project. Analyses of biogenic sediment compounds, however, allow rough estimations of population densities and activity patterns for this prominent group.

Effect of sampler bias on activity and biomass data

Sediment sampling during the various cruises was done either with box corers or multiple corers. The influence of the sampler type on quantitative estimates has been demonstrated e.g. for deep-sea meiobenthos by Bett *et al.* (1994). A direct comparison of results from box and multiple corer samples from the same spot supported the notion that box corers, because of their greater bow wave effect, are less efficient collectors than multiple corers, especially in the presence of a fluffy layer of phytodetritus on the sediment surface (Bett *et al.*, 1994).

In general, similar effects on sampling efficiency are to be expected for estimates of activity and biomass *via* analyses of biogenic sediment compounds, since the highly active micro-organisms may be blown away before box penetration. However, a comparison of results from the Goban Spur continental margin from different cruises, e.g. the consistent decrease in biomass values between the end of May (1994; box corer samples) and the beginning of July (1993; multiple corer samples) suggests that the identified tendencies are 'real', although the data may be biased to some extent by the differing sampling efficiency of gears.

Temporal variations in benthic and biomasses

A comparison of benthic biotic parameters (*i.e.* food availability, activity and biomass) obtained in different years is affected by interannual variability, because timing, amount and composition of the annual sedimentation of phytodetritus as the major food resource for benthic organisms and the related response of the benthos can vary considerably. Therefore, the presentation of data from different months within a six-year period as an annual cycle may have inherent uncertainties. However, the fact that rises in sediment-bound chlorophyll *a* concentrations were measured in autumn of different years (September 1994 and October 1993) provides evidence that these increases are not peculiar to one particular year, but are part of a regular seasonal cycle, as confirmed also by multi-year Continuous Plankton Recorder (CPR) data for this region (Colebrook, 1979). Together with significantly high chlorophyll *a* values at the end of May (1994) and low values in early April (1988) and at the beginning of July (1993), the data presented in this paper reveal a two-peak seasonal input of phytodetritus to the benthos in spring and autumn. Unfortunately, there are no winter data available to cover a complete composite annual cycle.

Gradients of benthic activity and biomass along the Goben Spur transect

According to a suggested decrease in sedimentated organic matter quantity and quality, activities and biomasses of the smallest benthic biota along the Goban Spur continental margin generally decline with increasing water depth and distance from the continental shelf (Fig. 7). Variations within these gradients are probably due to sediment reworking by meso-scale hydrodynamics (e.g. tides, internal waves, small scale eddies) causing resuspension and resettling of organic material, and/or bioturbation activities of larger sediment-inhabiting organisms, especially at the shallower stations.

Moreover, there are indications from light attenuation profiles of a distinct near-bottom, down-slope transport of material to greater depths (OMEX subproject "Recent sediments, boundary layer dynamics and sediment accumulation at the Goban Spur margin"; van Weering, pers. comm.), which may also determine the dispersion of organic matter on the sea floor and subsequently the dispersion pattern of benthic organisms feeding on it. Confirmation of lateral transport of organic matter to upper and mid-slope depths in the Porcupine Seabight region has also come from measurements of sediment community oxygen consumption in relation to measured vertical fluxes (Lampitt *et al.*, 1995).

Evidence for deposition centres of organic material along the Goban Spur transect, as indicated by relatively high and sometimes even slightly increased activities and biomasses of the benthic micro-biota compared to shallower stations, was found on the Pendragon Escarpment and on the continental rise. However, organic matter in these greater depths is probably mainly refractory and available only to metabolically-specialized bacteria (Boetius and Lochte, 1994).

The benthic response

The biochemical data suggest a reaction of the benthic infauna to the episodic input of phytodetritial matter within days, confirming a very close pelago-benthic coupling. Although probably complicated by interannual variations, results show strongly increasing values in bacterial enzymatic activity (FDA turnover) and organism biomass (total adenylates, DNA, phospho-lipids) in October during or shortly after phytodetritus sedimentation. As stated above, these shifts in benthic activity and biomass probably can be attributed mainly to bacteria and protozoans (Gooday, 1988; Gooday and Lambshead, 1989; Lochte, 1992; Pfannkuche, 1993; Pfannkuche and Thiel, 1987), because these organisms are obviously able to respond quickly to a sedimentation event due to their short generation times and potentially by activation of resting stages and dormant cells.

A measurable response of metazoan size groups (meio-, macro- or megabenthos) to a seasonal input of particulate organic matter has never been observed in oceanic regions

(Gooday *et al.*, 1996; Pfannkuche, 1993). Meio- and macrobenthos density and biomass data from the Goban Spur continental margin produced by partners within the OMEX project (OMEX subproject "Benthic community and species diversity gradients") showed differences between early summer values (end of May 1994) and fall values (August 1995 and October 1993), with significantly increased values only on the upper part of the slope (< 1500 m water depth) in early summer suggesting seasonal variations (Flach and Heip, 1996). However, meio- and macrobenthos data from these two time periods are so far the only faunal data from the Goban Spur continental margin evaluated within the OMEX project, and allow no clear statement concerning temporal variabilities over the year. In contrast, as demonstrated within this paper, the analysis of biogenic sediment compounds definitely confirms, at least for the smallest benthic organism size classes, pronounced temporal variabilities in benthic activity and biomass values within the area of investigations.

Acknowledgements

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