Metazoan meiobenthos along continental margins: a review

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Abstract

The sediment-inhabiting meiofauna is a major component of benthic ecosystems, particularly in the deep sea. Knowledge on the deep-sea meiobenthos has increased considerably during recent decades, and attempts have been made to relate standing stocks with various environmental factors. The flux of organic matter from surface productivity to the seafloor has been proven to exert considerable control on benthic standing stocks. The energy content of sedimentating organic matter generally decreases with water depth because of degradation processes within the water column. Consequently, benthic standing stocks decrease with increasing water depth. Generally enhanced densities of benthic animals are to be expected in areas of increased surface production and subsequently enhanced flux of organic matter to the seafloor. Thus, meiobenthic densities and biomasses should show perceptible differences not only with water depth, but also between areas with different primary productivity in surface layers. The objective of this paper is to condense current information focusing on the abundance of metazoan meiofauna along continental margins, and to compare meiofauna stocks from various climatic regions of the world, representing areas of diverse productivity in the water column. Results clearly demonstrate regional differences on global scale: richer communities were generally found in areas with increased productivity and enhanced input of organic matter to the seafloor. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Review; Meiobenthos; Metazoa; Abundances; Biomasses; Continental margins; Global distribution patterns

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Contents

1. History of meiofauna research

The term meiofauna was introduced and defined by Mare (1942). It derived from the Greek word 'meio' meaning 'the smaller'. Quantitative studies on sediment-inhabiting organisms have been restricted to those faunal components that are retained on sieves used to wash off the finer sediment particles. Although Mare (1942) suggested 2 mm for the topmost size limit for meiofauna organisms, today 1 mm is commonly accepted as the upper size limit for meiobenthic investigations.

The lower size limit for the meiobenthos differs widely between researchers. Wigley and McIntyre (1964), who carried out the first quantitative sampling of meio-benthic organisms below the shelf break, used a 74 μm sieve. Thiel (1966) reduced the lower size limit to 65 μm, whereas in the 1970s Dinet (1973) and Thiel (1971) set the lower limit to 50 and 42 μm, respectively, in order to include smaller abundant specimens. Today a lower size limit of 32 μm, separating meiofauna from the so-called nanofauna (mainly consisting of flagellates, ciliates and yeasts), seems to be commonly accepted (SCOR Working Group 76, 1994).

Before 1970, quantitative information on deep-sea meiofauna from below the shelf break was available only from the upper continental slope off the eastern coast of Northern America (Wigley & McIntyre, 1964) and from bathyal and abyssal depths

off Eastern Africa (Thiel, 1966). Since then, data on the deep-sea meiobenthos have been gathered from all oceans and from all ocean depths, allowing attempts to be made to relate the large-scale geographical patterns observed to various environmental patterns. Thiel (1983) summarised the quantitative information available for the meiofauna up to 1980, and a decade later Tietjen (1992) presented further data concentrating mainly on information collected during the 1980s. The objective of this paper is to condense current information focusing on the abundance of metazoan meiofauna along continental margins, from the shelf down to abyssal depths. Half of the papers summarised in this review (i.e. 19 documents) have been written during the last decade.

2. Comparability of meiofauna data from the literature

There has been a lack in standardisation of sampling, sorting and biomass determination techniques, so comparisons of meiobenthic stocks on a world-wide basis is fraught with problems. The use of different sampling devices, subsampling strategies and extraction methods (especially the use of different lower size limits of sieve meshes) makes a comparison of meiofauna data from the literature a challenge.

2.1. Different sampling devices and strategies

Sediment samples for meiofauna investigations have been obtained using a variety of sampling devices with assumed differing sampling efficiencies (Table 1). Spade corers (Reineck box corer and, in more recent studies, an USNEL-type box corer) were used for sampling in almost one third of the studies considered in this review. Various grabs (e.g. Van Veen grab, Smith McIntyre grab, Okean grab) were used for about 20% of the investigations. However bow wave effects in front of spade corers and especially grabs introduce a strong bias, because the pressure wave tends to blow away light surficial materials from the sediment surface, which include many attached meiofaunal individuals (Bett et al., 1994). Most recently meiobenthos investigations have been using multiple corers based on the design described by Barnett, Watson and Conelly (1984), which collect sediment samples with an almost undisturbed sediment–water interface. For a description of the various sampling devices see Fleeger, Thistle and Thiel (1988).

Bearing in mind the well-known fine-scale variability in meiofauna abundances (which probably result from the complex microhabitat structure of the sediment surface), the quality of data is seriously biased by the small numbers of replicate samples collected per station, and by the subsample volume, as defined by the subsampled area and the overall sediment depth investigated. The number of samples per station is often dependent on logistical prerequisites and also the 'environmental' conditions during sampling (e.g. ship time, weather conditions, sea states, ice-conditions for investigations in polar regions). Hence, the data compiled in this review have resulted from 1 to 10 replicate samples per station (Table 1), although more than 50% of the data were based on 3 or more replicates per station and are presumed

Table 1
Summary of information on standing stocks of metazoan meiobenthos along continental margins off various climatic regions of the world[a]

Area	Sampling Date	Depth Range (m)	Corer Type	Number Of Stations	Number Of Replicates Per Station	Number Of Subsamples Per Gear	Subsample Area (cm²)	Sampling Depth (cm)	Size Limits (µm)	Total Abundances (ind./10 cm²)	Total Biomass (mg/10 cm²)	References
POLAR REGIONS												
NORTHERN POLAR REGIONS												
SE-Svalbard, Nansen Basin, 79–82°N	July '80	226–3920	BC	9	1	up to 9	4	9	42–1000	233–4339	0.35–2.38	Pfannkuche and Thiel, 1987
W-Novosibirskye Island, Nansen Basin, 77–79°N	September '93	65–3237	MC	5	1	4	1.5	10	40–1000	700–2683	—	Vanaverbeke et al., 1997a
Eastern Greenland, Greenland Abyssal Plain, 75°N	October/November '65	250–2250	RC	4	1	1–2	10	4	40–1000	550–1470	—	Thiel, 1975
Northern Norway, Norwegian Basin, 69°N	October/November '65	750–3250	RC	4	1	1	10	4	40–1000	450–1920	—	Thiel, 1975
NORTHERN SUBPOLAR REGIONS												
Norway, Norwegian Basin, 64–65°N	August '74	440–2000	RC	3	1–2	1	?	5	40–2000	92–932	—	Dinet, 1974
SOUTHERN POLAR REGIONS												
Antarctica, Lazarev Sea, 66–71°S	January '82	227–3580	PG	6	3	1	15.9	10	44–500?	111–2977	0.02–0.54	Parulekar et al., 1983
Antarctica, Kapp Norvegia, 71–72°S	January–March 89	211–2080	MC/MBC	6	1	2–4	10	5	38–?	850–5120	0.11–0.69	Vanhove et al., 1995
Antarctica, Ross Sea, 72–74°S	November–January '94	432–587	BC	2	6	3	10.7	15	32–1000?	192–1191	0.009–0.05	Fabiano and Danovaro, 1999
Antarctica, Weddel Sea, 74–75°S	January–March '89	339–1958	MC	10	1	4	10	15	38–1000	792–3119	—	Herman and Dahms, 1992
TEMPERATE REGIONS												
WESTERN ATLANTIC												
NE-America, Scotian Basin, 40–41°N	June '62	40–567	SMG	10	1	1	9.5	4	74–1000	113–974	0.10–0.77	Wigley and McIntyre, 1964
NE-America, Hatteras Abyssal Plain, 34°N	?	50–2500	GC	21	1	1	?	10	44–500	41–1174	—	Tietjen, 1971
NE-America, Hatteras Abyssal Plain, 34°N	May '74	400–4000	RC	3	2–4	3–6	10	6	42–?	26–597	—	Coull et al., 1977
EASTERN ATLANTIC												
SW-Ireland, Porcupine Seabight, 52°N	May '91	600–1500	MC	4	1	2	25.5	10	32–?	1283–1523	—	Vanreusel et al., 1995

(continued on next page)

Table 1 (*continued*)

Area	Sampling Date	Depth Range (m)	Corer Type	Number Of Stations	Number Of Replicates Per Station	Number Of Subsamples Per Gear	Subsample Area (cm²)	Sampling Depth (cm)	Size Limits (µm)	Total Abundances (ind./10 cm²)	Total Biomass (mg/10 cm²)	References
SW-Ireland, Porcupine Seabight, 49–52°N	May '81/April '82	500–4850	MC	11	1	4	3.4	5	42–1000	315–2604	0,35–1,16	Pfannkuche, 1985
SW-Ireland, Porcupine Abyssal-Plain, 49–50°N	October '93	206–2760	BC	7	2	1	10	5	32–1000	178–970	—	Vanaverbeke et al., 1997b
WESTERN PACIFIC												
NE-Japan, NW Pacific Basin, 39°N	July '87–May '87	120–7460	BC/OG	13	1	2	8	3	63–?	191–2060	—	Shirayama and Kojima, 1994
SUBTROPICAL REGIONS												
ATLANTIC OFF IBERIAN PENINSULA												
Iberian Peninsula, Biscay Abyssal Plain, 44–45°N	October '73–October '74	1913–4460	RC	9	1–2	2–5	10	5	50–?	7–808	—	Dinet and Vivier, 1977
Iberian Peninsula, Biscay Abyssal Plain, 43–44°N	September '89	190–325	BC	2	1	2	10	10	?	864–915	—	Vanreusel et al., 1992
Iberian Peninsula, Tagus Abyssal Plain, 38°N	Jan./Feb. '67/ March '70	250–5250	RC/VVG	6	1–3	1–4	10	4	40–1000	123–1387	—	Thiel, 1975
Iberian Peninsula, Tagus Abyssal Plain, 38°N	March '70– May/June '71	1469–5112	RC/VVG	10	1–2	1	10	2–7	50–?	18–294	0,02–0,26	Rachor, 1975
ATLANTIC OFF NORTHERN AFRICA												
NW-Africa, Seine Abyssal Plain, 35°N	March '80	131–3088	BC	10	1	?	3.8	5	42–1000	550–2656	0,52–1,40	Pfannkuche et al., 1983
NW-Africa, Seine Abyssal Plain, 33°N	January '67	250–4750	RC/VVG	5	1	2	10	4	40–1000	130–629	—	Thiel, 1975
MEDITERRANEAN SEA												
Alborian Sea, 36–37°N	October '70	750–2750	RC	4	1	2–10	10	4	40–1000	370–1414	—	Thiel, 1975
Gulf of Lions, Northwestern Mediterranean, 43°N	March '72– June '73	168–810	RC	20	1	2	10	7	40–?	16–801	—	Vivier, 1978
Gulf of Lions, Northwestern Mediterranean, 42–43°N	August–November '86	672–2334	BC	9	1–7	2–4	?	10	40–?	78–592	—	DeBovée et al., 1990
Gulf of Lions, Northwestern Mediterranean, 42–43°N	November–December '91	70–2725	RC	5	1	5	1.8	10	50–?	70–1105	—	Tahey et al., 1994
Ligurian Sea, Northern Mediterranean, 43°N	September '85/June '86	160–1220	RC	6	1–2	1	10	5	38–500?	369–724	—	Soetaert et al., 1991
Northern Aegean Sea, 39–40°N	March–May '72	130–1137	RC	3	1–3	1	10	4	50–?	124–427	—	Dinet, 1976
Southern Aegean Sea, 36°N	September '89	533–1840	BC	10	1	2	4.9	6	45–500?	4–107	0,003–0,16	Danovaro et al., 1995
Ionian Sea, 36°N	September '89	550–2401	BC	4	1	2	4.9	6	45–500?	66–290	0,03–0,75	Danovaro et al., 1995

Table 1 (*continued*)

Area	Sampling Date	Depth Range (m)	Corer Type	Number Of Stations	Number Of Replicates Per Station	Number Of Subsamples Per Gear	Subsample Area (cm²)	Sampling Depth (cm)	Size Limits (μm)	Total Abundances (ind./10 cm²)	Total Biomass (mg/10 cm²)	References
GULF OF MEXICO												
Central America, Gulf of Mexico, 22–24°N	April/May '93	196–540	BC	16	1	3	12.6	5	54–175	0–382	—	Escobar et al., 1997
Central America, Gulf of Mexico, 26–29°N	Spring '84	355–2602	BC	15	1	6	9.6	?	63–300	115–700	0,08–0,48	Pequegnat et al., 1990
TROPICAL REGIONS												
EASTERN ATLANTIC												
W-Africa, Sierra Leone Basin, 4–10°N	January '88	37–4327	BC	16	1	3	3.5	5	42–1000	159–638	0,06–0,72	Soltwedel, 1997
W-Africa, Guinea Basin, 3–6°N	January/February '88	39–4449	BC	18	1	3	3.5	5	42–1000	221–2201	0,12–1,64	Soltwedel, 1997
W-Africa, Golf of Guinea, 0–6°N	February '88	27–2860	BC	11	1	3	3.5	5	42–1000	253–1556	0,06–0,63	Soltwedel, 1997
INDIAN OCEAN												
W-India, Arabian Sea, 15°N	?	20–840	VVG	7	3	1	4.5	10	44–500?	222–957	—	Ansari et al., 1980
SOUTHWESTERN PACIFIC												
SE-New Guinea, Coral Sea Basin, 12–15°S	July–September '88	695–4350	SMG	4	2	3	6.6	10	45–500?	99–1570	—	Alongi, 1992
NE-Australia, Coral Sea Basin, 17–18°S	May '86	298–1096	SMG	12	1–2	3–5	6.6	10	45–500?	23–168	—	Alongi and Pichon, 1988
ARID REGIONS												
ATLANTIC OFF NORTHWESTERN AFRICA												
NW-Africa, Canary Basin, 24–25°N	March '72	125–3000	RC	8	1	2	10	4	42–1000	290–2200	—	Thiel, 1982
NW-Africa, Cape Verde Abyssal Plain, 21°N	..., '85	110–1116	OG	4	1	?	10	4	?	1940–3100	—	Kamenskaya and Galtsova, 1996
NW-Africa, Cape Verde Abyssal Plain, 20–21°N	February '72	30–3050	RC	9	1	2	10	4	42–1000	410–2700	—	Thiel, 1982
NW-Africa, Cape Verde Abyssal Plain, 20°N	January/February '91	1650–4550	BC	3	7–11	2–3	5.3	5	40–?	128–1039	0,01–0,12	Relexans et al., 1996
ATLANTIC OFF SOUTHWESTERN AFRICA												
SW-Africa, Angola Basin, 6–17°S	February '88	30–4601	BC	15	1	3	3.5	5	42–1000	358–2876	0,05–0,89	Soltwedel, 1997

Table 1 (continued)

Area	Sampling Date	Depth Range (m)	Corer Type	Number Of Stations	Number Of Replicates Per Station	Number Of Subsamples Per Gear	Subsample Area (cm²)	Sampling Depth (cm)	Size Limits (µm)	Total Abundances (ind./10 cm²)	Total Biomass (mg/10 cm²)	References
NORTHWESTERN INDIAN OCEAN												
NE-Africa, Arabian Basin, 23°N	November '78	800–2900	RC	2	1	1	6.6	4	40–?	229–712	0,02–0,06	Romano and Dinet, 1981
NE-Africa, Arabian Basin, 16–18°N	November '78	200–4010	RC	4	1	1	6.6	4	40–?	11–698	0,002–0,06	Romano and Dinet, 1981
NE-Africa, Somalia Basin, 5–8°N	December '64/ January '65	1050–5030	VVG	7	1	1–4	25	4	65–?	18–168	—	Thiel, 1966
NE-Africa, off Kenya, 2–5°S	June/July '92	50–2000	BC	12	1	2	3.33	5	32–1000	131–1189	—	Duineveld et al., 1997
RED SEA												
NE-Africa, Central Red Sea, 21°N	October '77	507–1977	BC	5	1	5	3.8	4	40–1000	39–407	—	Thiel, 1979
48 sampling sites	1962–1994	20–7460		389 stations	1–11	1–10	1,5–25,5	2–15	32–2000	0–5120	0,002–2,38	38 references

[a] Different corer types: BC=box corer (USNEL), GC=gravity corer, MC=multiple corer, MBC=multi box corer, OG=Okean grab, PG=Petersen grab, RC=Reineck corer, SMG=Smith McIntyre grab, VVG=Van Veen grab, ?=no information, —=no data available.

to be characteristic of the individual locations. The area subsampled per replicate has varied between 1.5 and 25.5 cm^2 ($>$10 cm^2 in about 50% of the cited papers); sampling depths have ranged between 2 and 15 cm (down to max. 5 cm sediment depth in about two third of the cited papers), so quite a variety of sediment volumes have actually been investigated (Table 1). However, in most cases, variations in the depth of sediment investigated has been of little consequence, because the majority of the deep-sea meiobenthos generally inhabits the uppermost 5 cm of the sediment (cf. Thiel (1983)). To make the sorting process easier, and also to investigate gradients in distribution, sediment cores have usually been sliced into 1-cm-layers, which have been sorted individually.

2.2. Differences in sample processing

The majority of sediment samples for meiofaunal investigations have been fixed and preserved using a 4% solution of formaldehyde, buffered with borax to inhibit dissolution of carbonate structures. Several extraction methods (i.e. decantation, elutriation, separation in a density gradient using e.g. Ludox™) have been described for the quantitative isolation of meiofauna organisms from sediments (Pfannkuche & Thiel, 1988). However, no single extraction technique will remove all the specimens of all taxa from a given sample. Therefore, sieving and subsequent hand sorting under a low power microscope is most frequently used to extract the bulk of meiofauna from the fixed samples.

To evaluate meiofauna size spectra (and also to make the sorting process easier), sediments are usually passed through a series of sieves with progressively decreasing mesh sizes. The smallest mesh size used has varied between 32 and 74 μm. Meiobenthologists contributing data to this review have, in most cases, used a lower size limit of 40–45 μm for their studies (over 55% of the cited papers). In about 25% of the papers, larger mesh sizes (50–74 μm) have been used (Table 1). In the most recent contributions minimum sieve size has generally been reduced to 32–38 μm. 1 mm as the upper limit for meiofauna is commonly accepted. Probably for that reason, almost two thirds of the meiofauna papers used in this review give no clear information about the sieve used to separate macrofauna from meiofauna (Table 1). Dinet (1974) extended the upper size limit to 2000 μm, whereas Pequegnat, Gallaway and Pequegnat (1990) and Escobar, López, Soto and Signoret (1997) reduced the upper limit to 300 and 175 μm, respectively, probably preventing a direct comparison of results with the majority of meiofauna investigations presented here (see below).

Selective staining improves sorting efficiency by identifying the organisms better. Residues retained on the sieves are commonly stained with Rose Bengal, with added phenol. Good colouring of most organisms normally takes only a few minutes. Although the protoplasm of foraminiferans generally stains as well as any other organism, in many cases it is difficult to decide whether or not the specimen was alive at the time of collection. This is because Rose Bengal can stain the stable inner organic lining of the foraminiferans tests, giving a false impression of a 'living' specimen (Douglas, 1979). These uncertainties may be contributing to why, in most meiofauna investigations, foraminiferans are not taken into account despite their

numerical (and ecological) importance. In addition, many meiofaunal studies have ignored the foraminiferans because they cannot be accurately quantified using techniques such as elutriation or Ludox™ extraction. The lack of foraminiferal data from continental margins has also been the reason why, in this review, the focus has been purely on the metazoan meiofauna.

2.3. Biomass determination techniques

The determination of biomasses for meiofauna organisms is an extremely laborious task, and plagued with methodological problems. Thus, it is rarely done in deep-sea studies. Moreover, meiofauna biomasses in the literature are presented in a wide variety of units (wet, dry, or ash free dry weight) or have been derived from body measurements, using various formulas and conversion factors. In this review, an attempt was made to convert these divers meiofauna biomass data available in the literature into a standardised coherent compilation to allow a comparison of biomass values on a global scale.

Most of the biomass data are given as AFDW or 'ash free dry weight' (>50% of the data), all the other available biomass values (i.e. wet weights, dry weights, carbon weights derived from volumetric measurements) have been transformed into AFDW, using a variety of conversion factors. According to Wieser (1960) and Ankar and Elmgren (1976), 100% wet weight corresponds to ~20% dry weight and 100% dry weight corresponds to ~85% ash free dry weight (Widbom, 1984). Jensen (1984) provided a conversion factor for wet weight to carbon equivalents (100% wet weight corresponding to 12.4% carbon weight). Results given below show clear trends in the compiled biomass data, and demonstrate that the conversion factors have proved sufficiently precise for our purpose.

2.4. Temporal variabilities in the meiofauna data

Seasonal and interannual fluctuations in primary and export production are expected to generate temporal variations in food supply to the benthos in different oceanic regions. These may result in temporal variability in benthic standing stocks, so complicating direct comparisons of deep-sea meiobenthic data from the literature.

Gooday (1988) and Pfannkuche (1993) described a pronounced response of deep-sea foraminiferans to the pulsed input of phytodetrital matter in some areas of the North-eastern Atlantic. DeBovée, Guidi and Soyer (1990) detected changes in the taxonomic composition of the metazoan meiofauna at deep stations (>2000 m) in the North-western Mediterranean Sea between summer and autumn, and Soltwedel, Pfannkuche and Thiel (1996) found some indications of deep-sea nematode assemblages showing growth responses to an episodic food supply. However, a measurable response in metazoan abundances to a seasonal input of particulate organic matter has yet to be observed in oceanic regions (Pfannkuche, 1993; Gooday, Pfannkuche & Lambshead, 1996).

The absence of any overall increase in metazoan abundance (and biomass) following phytodetrital sedimentation events probably reflects slower rates of somatic

growth in the metazoans and their energy requirements of egg production. Consequently, responses of higher trophic levels in deep-sea communities even to temporal fluctuations in food supply generally appear to be damped, so that comparisons of metazoan meiofauna data also from a variety of sampling programmes conducted in different times of the year may be possible.

3. Standing stocks of metazoan meiobenthos along continental margins

This review compiles abundance and biomass data from a total of 38 papers, describing metazoan meiofauna assemblages along the continental margins from various climatic regions around the world (Table 1). Only those investigations covering two or more stations at depths deeper than the shelf break have been taken into consideration. When available, data from shelf stations have been included to complete the information for specific transects. Thus, water depths of stations for which data are used range between 20 and 7460 m (Table 1). Presumably for logistic reasons, the overall number of stations sampled decreases with increasing water depth on a logarithmic scale. Compared to 205 observations made to a maximum depth of 1000 m, only 21 stations have been sampled at the continental rise between 4000 and 5000 m water depth.

All in all, 48 sampling areas have been visited (Table 1): 9 in polar and subpolar regions, 7 off temperate regions, 16 off subtropical regions (including 8 sites in the Mediterranean Sea and 2 in the Gulf of Mexico), 6 off tropical and 10 off arid regions (Fig. 1). About one third of the sampling areas were situated in the Eastern Atlantic.

As explained above, the evaluation of the meiofauna data from the literature depends on the comparability of the available data. Despite the lack in standardisation in the methodologies used, meiofauna abundances and biomasses as given in each paper (converted to standard units, i.e. individuals/10 cm^2 and mg AFDW/10 cm^2) have been taken to be characteristic, and all differences between sampling and/or sample processing methods have been neglected.

Values for meiobenthic biomass were reported in only about one third of the papers used in this review. Thus, the comparisons of data on a global scale focuses mainly on meiofaunal densities.

3.1. Overall trends and regional characteristics

One of the major environmental gradients is that created by the slope of the ocean floor. Faunal abundances generally show a trend for numbers to decrease as water depths increase, which can be related to the amount and nature of organic matter reaching the seafloor (see below). However, these general patterns are locally influenced by a number of abiotic factors, such as the hydrographic regime and varying sediment types.

The 389 data points of meiofauna densities from continental margins compiled in this review confirm this overall trend of decreasing abundances with increasing water depth (Fig. 2). Mean values for 1000 m depth horizons, although subjected to very
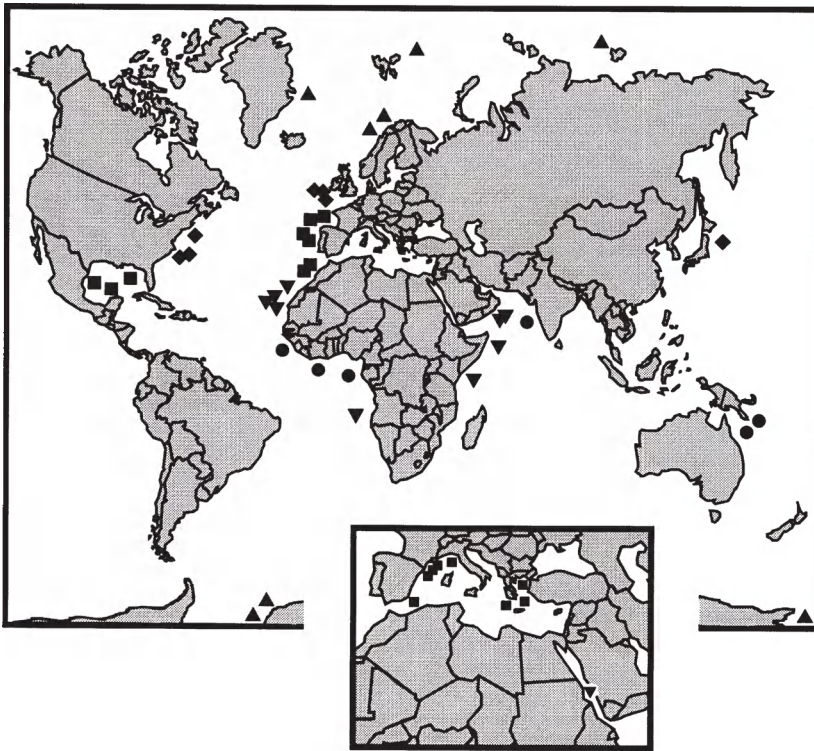
Fig. 1.   Sampling sites off various climatic regions of the world (▲: polar, ◆: temperate, ■: subtropical, ●: tropical, and ▼: arid regions) at which meiofauna investigations have been conducted along continental margins.

large variations, show a highly significant inverse logarithmic relationship (p <0.001) between meiofauna densities and water depth; the same holds for maximum values per depth horizon (Fig. 3).

Total meiofaunal biomass data (153 data points) show a similar decline with water depth (Fig. 2), as shown by the abundance data. Given the fact that meiobenthic communities are dominated by two taxa (i.e. nematodes and harpacticoid copepods), such a relationship might be expected. However, differences in the taxonomic composition and the considerable depth-related variations in individual body sizes of meiofauna organisms may be severely effecting this relationship. Deviations from the overall trend of decreasing meiofauna biomass with increasing water depth may also result from combining biomass data (although standardised) assessed by a variety of methods.

3.1.1. Polar regions

Nine transects (5 in the Northern, 4 in the Southern Hemisphere) with 49 stations have been sampled crossing continental margins in polar and subpolar regions (Dinet,

Fig. 2.   Bathymetric distribution of metazoan meiofauna standing stocks (abundances and biomasses) along continental margins.
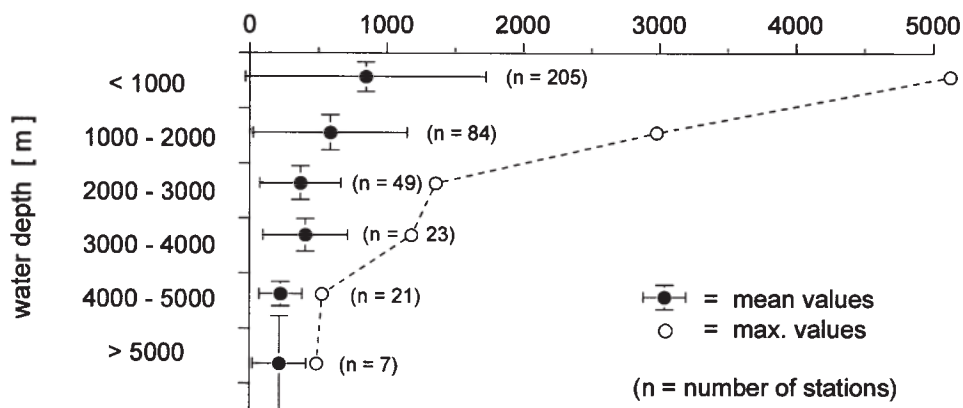

Fig. 3.   Mean and standard deviations of meiofauna densities together with maximum values for 1000 m depth horizons from shallow to hadal depths.

1974; Thiel, 1975; Parulekar, Ansari & Harkantra, 1983; Pfannkuche & Thiel, 1987; Hermann & Dahms, 1992; Vanhove et al., 1995). Meiofaunal abundances have ranged from 111 to 5120 ind./10 cm^2 and total biomass (ash free dry weight) from 0.009 to 2.38 mg/10 cm^2 (Table 1). Meiofaunal abundances show a highly significant correlation ($p<0.001$) with water depth, and biomasses followed the same general trend, although with greater variability (Fig. 4). Biomasses in northern polar regions appear to be on a (non-significantly) higher level than those in southern polar regions.

Fig. 4.   Comparison of bathymetric distributions of meiofauna standing stocks along continental margins in northern and southern polar oceans.

However, it is uncertain whether these relatively small differences truly reflected fundamental ecological differences or are the result of the different biomass determination techniques used.

3.1.2. Temperate regions

There were highly significant correlations between meiofauna abundances and water depth for continental margins off temperate regions (Fig. 5). However, densities off the north-eastern American coast (Wigley & McIntyre, 1964; Tietjen, 1971; Coull et al., 1977) were significantly lower ($p<0.05$) than those found on the European continental margin (Pfannkuche, 1985; Vanreusel, Vincx, Schram & Van Gansbeke, 1995; Vanaverbeke, Soetaert, Heip & Venreusel, 1997b) and off Japan, in the North-western Pacific (Shirayama & Kojima, 1994). The data suggest that the rate of decline in metazoan meiofauna abundances with increasing water depth is greater in the Eastern than in the Western Atlantic.

Differences between sampling and sample processing methods may partly explain the comparably lower values along the Western Atlantic depth transects. Sediment sampling off the north-eastern American coast was conducted using grabs and (Reineck) box corers, whereas along Eastern Atlantic depth transects most sampling was done using multiple corers. In addition, the use of sieves with smaller minimum mesh sizes (32–42 μm) in Eastern Atlantic investigations may also explain the higher meiofaunal densities found along the European continental margin. However, there are overall differences in primary production between the two sides of the North Atlantic, as demonstrated in satellite-derived figures on pigment concentrations in the upper water masses (Yoder, Lewis & Blanchard, 1989). These differences are
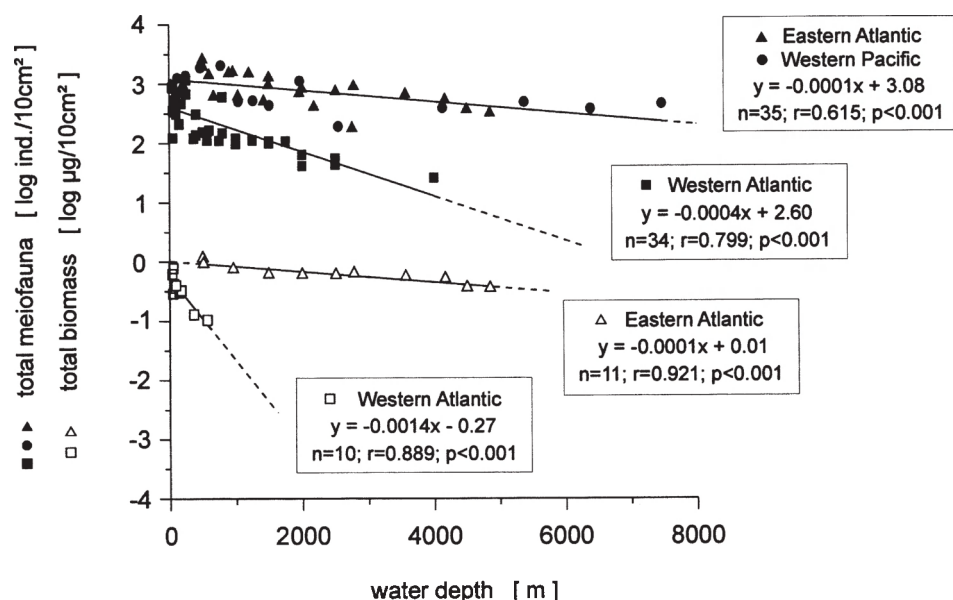
Fig. 5.   Meiofauna standing stocks along continental margins off temperate regions.

most likely to lead to differences in standing stocks between off North-eastern America (26–1174 ind./10 cm²) and along the European continental margin (178–2604 ind./10 cm²).

Meiofaunal biomasses generally paralleled abundance values. Thus, biomasses in the Eastern Atlantic (0.35–1.16 mg/10 cm²) exceeded those in the Western Atlantic (0.10–0.77 mg/10 cm²). Although the biomass data from a transect off North-eastern America only covers water depths of between 40 m and 567 m, the rate of decline in metazoan meiofauna biomass with increasing water depth seems to be greater in the Eastern than in the Western Atlantic. However, the biomass data available for the Western Atlantic is probably too sparse to allow any significant conclusion to be drawn.

3.1.3. Subtropical regions

Data from transects off subtropical regions originate from three different areas: the North-eastern Atlantic (Rachor, 1975; Thiel, 1975; Dinet & Vivier, 1977; Pfannkuche, Theeg & Thiel, 1983; Vanreusel et al., 1995), the Mediterranean Sea (Thiel, 1975; Dinet, 1976; Vivier, 1978; DeBovée et al., 1990; Soetaert, Heip & Vincx, 1991) and the Gulf of Mexico (Pequegnat et al., 1990; Escobar et al., 1997).

Highest values (up to 2656 ind./10 cm²) and a highly significant ($p<0.001$) decrease with increasing water depth were found along the transects off the Iberian peninsula and Northern Africa (Fig. 6). Lower meiofauna densities were reported for the Mediterranean Sea, but there were also pronounced regional differences: (nonsignificantly) higher values (16–1414 ind./10 cm²) were registered for the western

$$y = -0.0003x + 3.13$$
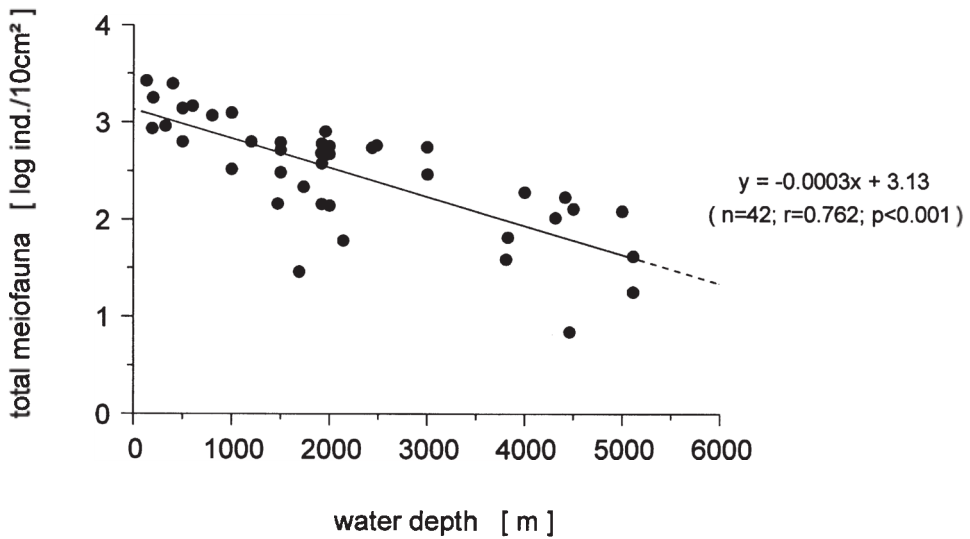$$(n=42; r=0.762; p<0.001)$$

Fig. 6. Meiofauna abundances along continental margins off subtropical regions: the North-eastern Atlantic.

and northern areas (Alborian Sea, Gulf of Lions, Ligurian Sea), than for the central and eastern parts (Ionian Sea, Aegean Sea), where not only meiofauna densities were lower (4–724 ind./10 cm^2) but also decreased more rapidly with increasing water depth (Fig. 7). These regional differences may be explained by the variations in
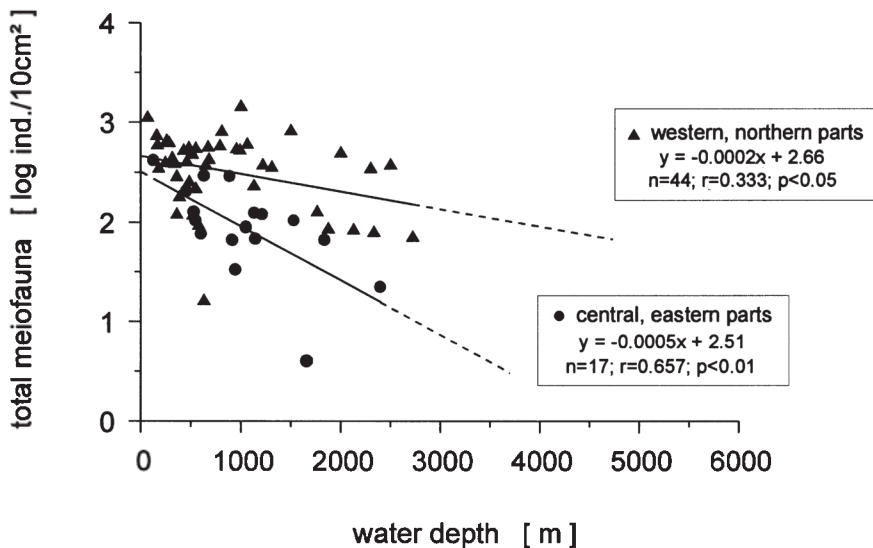

▲ western, northern parts
$$y = -0.0002x + 2.66$$
$$n=44; r=0.333; p<0.05$$

● central, eastern parts
$$y = -0.0005x + 2.51$$
$$n=17; r=0.657; p<0.01$$

Fig. 7. Meiofauna abundances along continental margins off subtropical regions: the Mediterranean Sea.

primary production rates (and a subsequently varying input of organic matter to the seafloor) between the north-western and eastern parts of the Mediterranean Sea; as confirmed in satellite-derived figures on pigment concentrations in the upper water masses (Crispi, Crise & Solidoro, 1998). According to Crispi et al. (1998) chlorophyll *a* concentrations in Aegean Sea and Ionian Sea waters ranges from 0.05 to 0.3 mg Chl./m^3, whereas in north-western parts of the Mediterranean Sea chlorophyll *a* concentrations are generally higher (up to 2.5 mg Chl./m^3).

A very few data are available from the Gulf of Mexico, mainly from depths down to 500 m water depth. The densities reported from shallow stations (<500 m) are slightly (non-significantly) lower than in the Mediterranean Sea. However, the use of different size limits (54–175 µm and 63–300 µm, respectively) in meiofauna investigations from the Gulf of Mexico (Escobar et al., 1997; Pequegnat et al., 1990) prevents any confidence in the conclusions drawn. Within the data for the Gulf of Mexico, there is a vague trend for meiofaunal densities to decrease from northern to western and southern slopes (Fig. 8).

Biomass data for transects off subtropical regions are restricted to a total of 44 stations off the Iberian peninsula (Tagus Abyssal Plain), off North-western Africa, in the northern Gulf of Mexico and in the central Mediterranean Sea (Ionian and Aegean Sea). Biomass values decline significantly ($p<0.001$) with increasing water depth (Fig. 9). Off North-western Africa, meiofaunal biomasses (0.52–1.40 mg/10 cm^2) are significantly higher ($p<0.05$) than those reported from off the Iberian peninsula (0.02–0.26 mg/10 cm^2) and in the northern Gulf of Mexico (0.08–0.48 mg/10 cm^2). Biomasses in the Mediterranean Sea (0.003–0.75 mg/10 cm^2) showed the steepest decrease with increasing water depth.
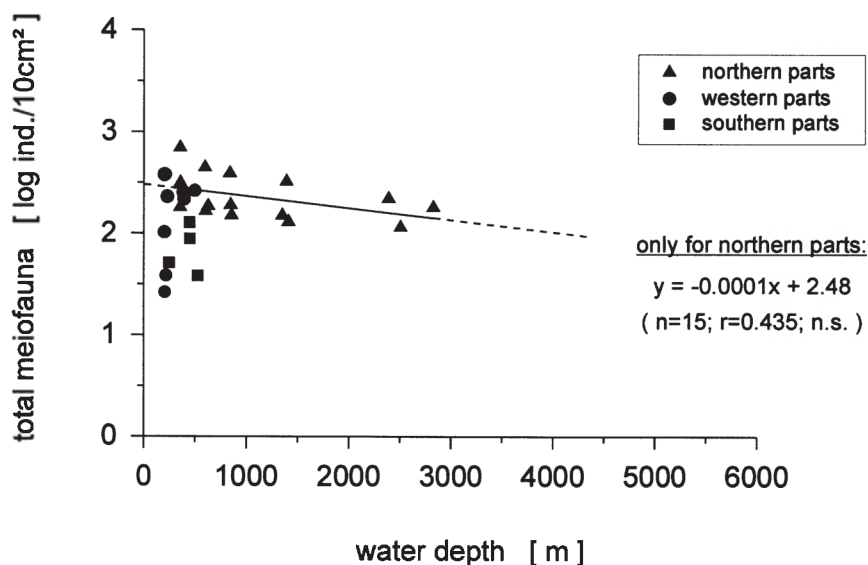

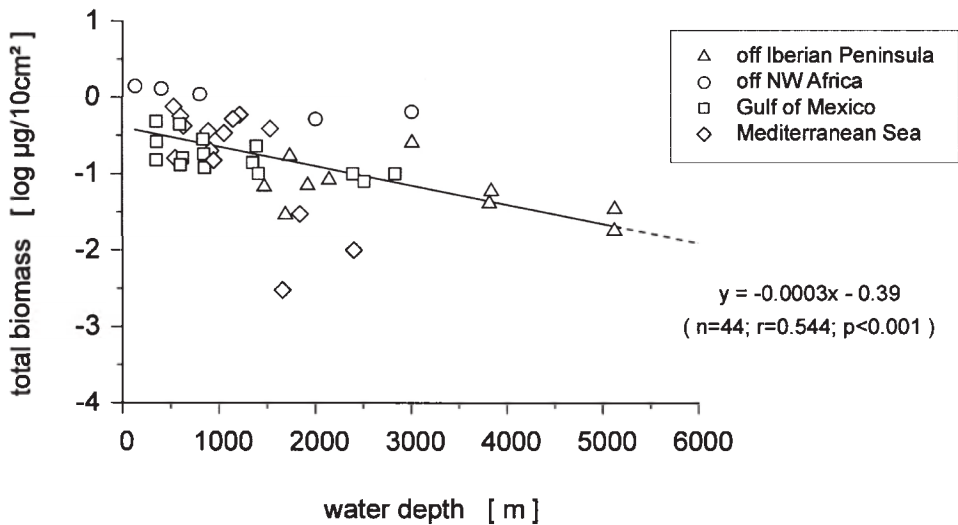Fig. 8.   Meiofauna abundances along continental margins off subtropical regions: the Gulf of Mexico.

Fig. 9.   Meiofauna biomasses along continental margins off subtropical regions.

3.1.4. Tropical regions

Meiobenthic densities off tropical regions have been registered for transects off Western Africa (Soltwedel, 1997), off Western India (Ansari, Parulekar & Jagtap, 1980), off South-eastern New Guinea (Alongi, 1992) and off North-eastern Australia (Alongi & Pichon, 1988). Except for the latter investigation, meiofauna abundances are within the same range of 99–2201 ind./10 cm^2, and show a highly significant ($p<0.001$), but rather slow decline with increasing water depth (Fig. 10). A similar smooth gradient was found along transects across the European continental margin and off the Eastern Japanese coast (see Fig. 5). Meiofauna densities along a transect off North-eastern Australia (23–168 ind./10 cm^2) were significantly lower ($p<0.05$), and also decreased much faster with increasing water depth.

All biomass data available from transects off tropical regions derive from stations in the eastern equatorial Atlantic (Soltwedel, 1997). Biomass values (0.06–1.64 mg/10 cm^2) generally followed meiofauna abundances and exhibiting a highly significant correlation ($p<0.001$) with water depth (Fig. 10).

3.1.5. Arid regions

Meiofauna densities along transects off arid regions showed a rather smooth gradient with water depth (Fig. 11). Abundances off North-western and South-western Africa (128–3100 ind./10 cm^2) (Thiel, 1982; Kamenskaya & Galtsova, 1996; Relexans, Deming, Dinet, Gaillard & Sibuet, 1996) were on a slightly higher level than those reported for transects off most tropical regions (see above). Meiofauna densities along depth transects in the Western and North-western Indian Ocean (11–1189 ind./10 cm^2) (Thiel, 1966, 1975; Romano & Dinet, 1981; Duineveld, De Wilde, Berghuis, Kok, Tahey & Kromkamp, 1997) were significantly lower ($p<0.05$), but
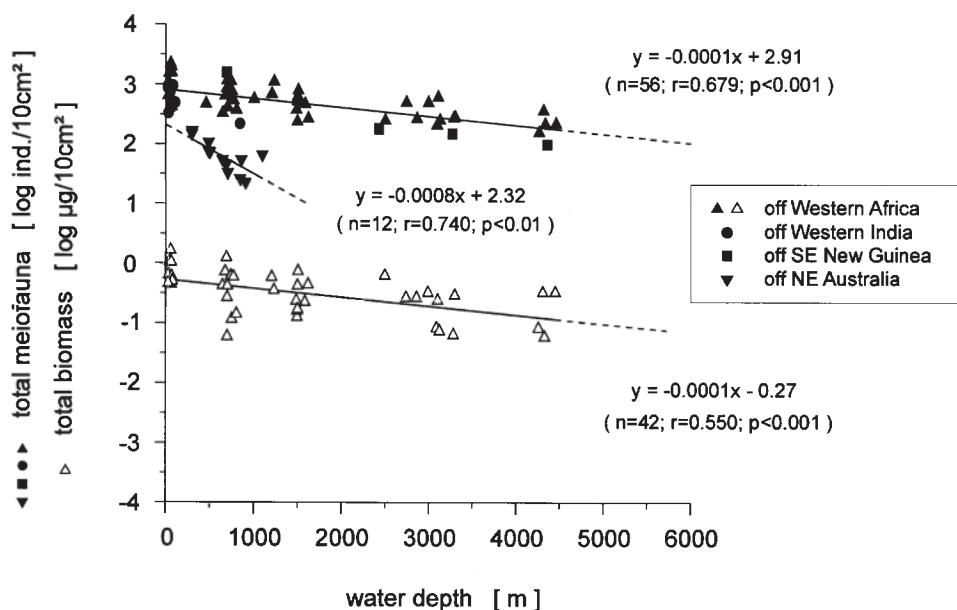
Fig. 10.   Metazoan meiofauna standing stocks along continental margins off tropical regions.
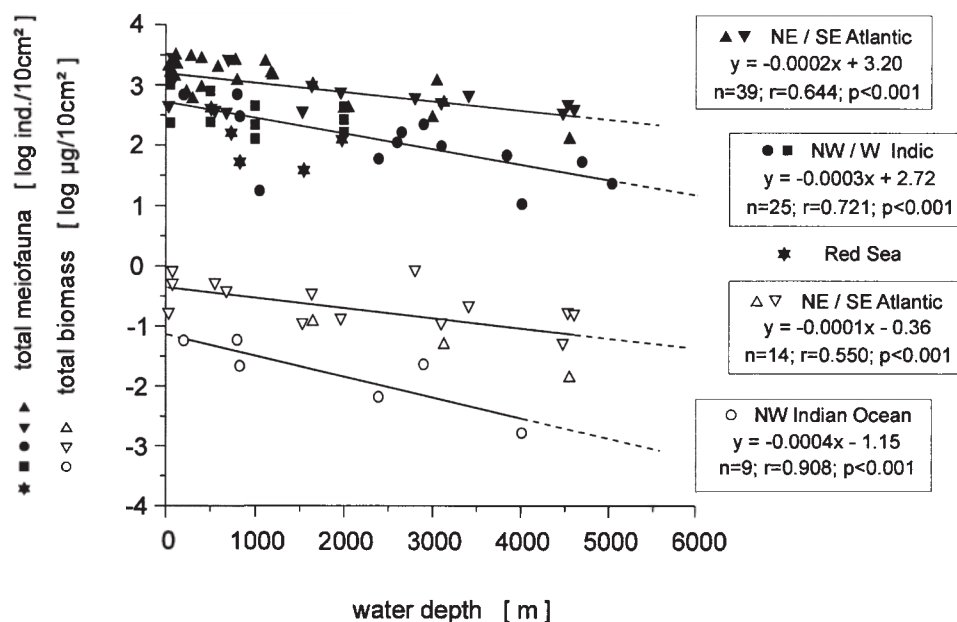

Fig. 11.   Metazoan meiofauna standing stocks along continental margins off arid regions.

also with a smooth gradient (Fig. 11). Lowest reported abundances for transects off arid regions (39–407 ind./10 cm^2) were from the central Red Sea (Thiel, 1979).

Biomass data along transects off arid regions are from the continental margins off North-western and South-western Africa, and off the Arabian peninsula (Romano & Dinet, 1981; Relexans et al., 1996; Soltwedel, 1997). Values from the North-eastern and South-eastern Atlantic were in a similar range (0.01–0.89 mg/10 cm^2), whereas those from the North-western Indian Ocean were an order of magnitude lower (0.002–0.06 mg/10 cm^2).

High levels of meiofauna densities and biomasses along depth transects crossing the continental margins off arid regions exhibiting smooth depth-related gradients may be explained by primary production rates being high in the particular areas studied (see below). Off both North-western and South-western Africa as well as off the Arabian peninsula and North-eastern Africa, there is coastal upwelling of nutrient-rich deep water masses which enhances primary production and conse-quently increases fluxes of particulate organic matter to the deep-sea floor. The high faunal abundances and biomasses reflect the increased food/energy availability in benthic environments. The Indian Ocean coastal waters off Kenya, Somalia and Oman are influenced by the monsoon winds, which also create upwelling conditions. However the upwelling occurs for less than half the year, since seasonally the mon-soonal winds reverse direction stopping the upwelling and diminishing the productivity (as well as sedimentation of phytodetritus). Under these monsoon con-ditions standing stocks are lower than off North-western and South-western Africa, where along parts of the coast the winds can blow offshore at any season so upwelling persists throughout most of the year (Thiel, 1978).

3.2. Relationship between meiobenthic abundances and biomasses

A comparison of abundances with biomasses at each station may indicate whether there are regions where mean sizes of meiobenthic organisms are larger or smaller. The data set compiled in this review exhibits a highly significant ($p < 0.001$) corre-lation between meiofauna densities and weights (Fig. 12). The rather large variability within the data could partially be explained by variations in the taxonomic compo-sition of the meiobenthic community. For example, enhanced relative proportions of copepods in specific samples could substantially influence the total meiofauna biomass, because of their comparably high average individual body weight. In addition, the body sizes of individual meiofauna organisms can vary considerably (Shirayama, 1984; Jensen, 1988; Tietjen, 1989), so biomass estimates based on aver-age weights of specimens may be misleading. Another source of variation may come from the variety of methods of determining biomasses used in the compiled data set.

Within this data set the biomass values given by Vanhove et al. (1995) for the Kapp Norvegia region, Antarctica (Fig. 13), appear to be relatively small for the abundances of meiobenthic organisms. The possible explanation lies in the extremely high relative proportions (~ 90%) of nematodes (with comparably low individual body weights) in these samples.
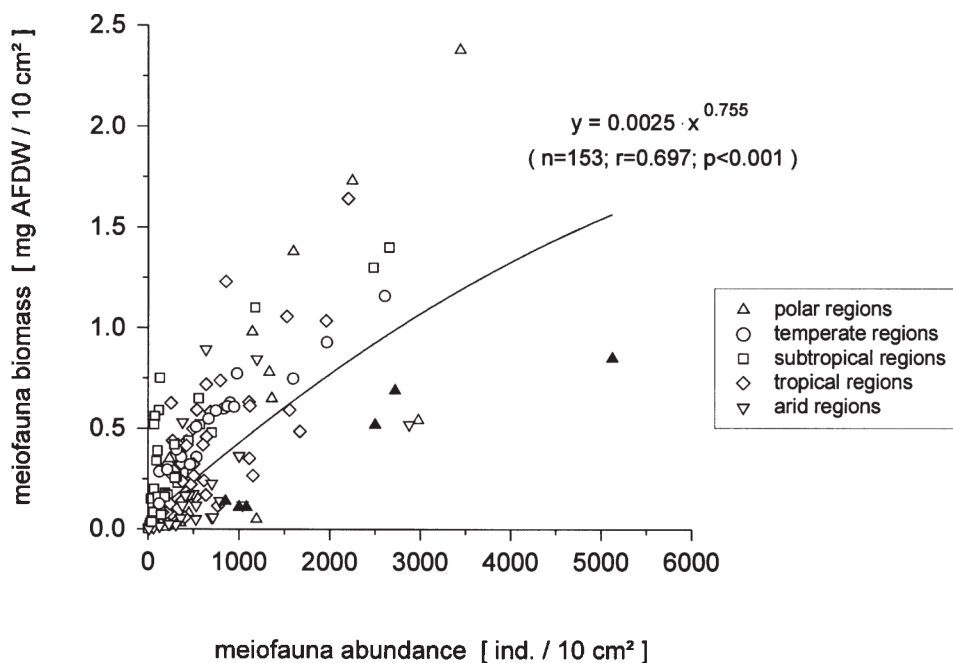
$$y = 0.0025 \cdot x^{0.755}$$
$$(n=153; \; r=0.697; \; p<0.001)$$

Fig. 12.   Relationship between meiofauna abundances and biomasses (▲: abundance and biomass data given by Vanhove et al. (1995)
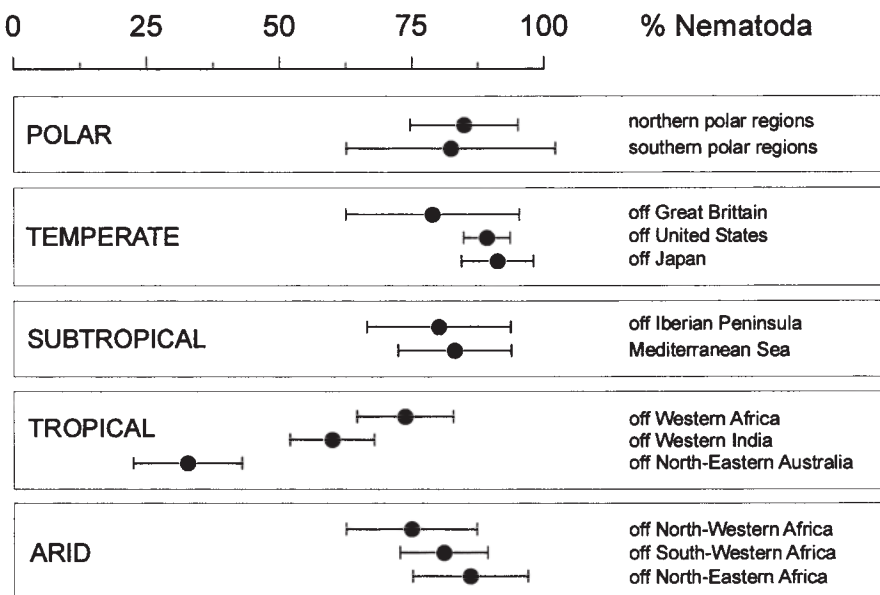

Fig. 13.   Relative proportions of nematodes in various climatic regions.

3.3. Faunal composition of meiobenthic communities

Nematodes dominate the metazoan meiobenthic community, and in the data set compiled for this review on average almost 80% of the metazoans are nematodes. Harpacticoid copepods (including nauplii) are second in the abundance ranking, contributing about 12% of individuals. Polychaetes and other taxa (e.g. ostracods, kinorhynchs, turbellarians, gastropods and bivalves) occur in small numbers at most water depths, but are most abundant in shallower water.

In contrast to meiofauna densities and biomasses along depth transects, changes in meiofauna composition with increasing water depth are less apparent. Nevertheless, Vincx et al., 1994 and Soltwedel (1997) have demonstrated some bathymetric trends in the taxonomical composition of meiofauna from the North-eastern Atlantic and the tropical Eastern Atlantic, respectively. The relative abundance of nematodes generally increases with water depth, while the percentage of all other taxa decreases.

Regional differences in the composition of the metazoan meiofauna along continental margins are hard to detect, because of the pronounced local variations. Only two sampling sites off tropical regions exhibited significantly different faunal compositions with the overall data set. Off Western India (Ansari et al., 1980) and especially off North-eastern Australia (Alongi & Pichon, 1988; Alongi, 1992), the relative abundance of nematodes was unusually low averaging 60% and 33%, respectively (Fig. 13). The highest proportions of nematodes (~90%) were in data sets from the Western Pacific (off Japan) and the North-western Atlantic (off the United States).

Differences in food availability both quantitative and qualitative, may be the most important factors controlling total abundances and the faunal composition of the metazoan meiobenthos at the taxonomic level; richer communities are tending to develop in shallower areas where there is a higher overall input of organic matter (cf. Vincx et al., 1994; Soltwedel, 1997).

4. Meiofauna in relation to food availability

All transects exhibit a general trend for faunal abundances and biomass to decrease with increasing water depth, probably reflecting an overall decrease in food availability for the benthos. Exceptions along individual transects (e.g. off North-western africa; Thiel, 1982) may fully, or partially, be explained by subsurface currents hindering the sedimentation of the rather light particulate organic matter. If these currents are strong enough, they may erode these materials and transport them in suspension in nepheloid layers to sometimes far distant, but calmer habitats. When combining meiofauna data from various transects in specific climatic regions, those exceptions often vanish from the general trend.

Intercomparisons of meiofauna data from depth transects off different climatic regions imply that deviations in trends in distributions of standing stocks can be explained by variations in local productivity. Fig. 14a,b compare levels and slopes in meiofauna densities for the various regions. The global comparison shows that the highest abundance levels occurred in upwelling regions off the North-western
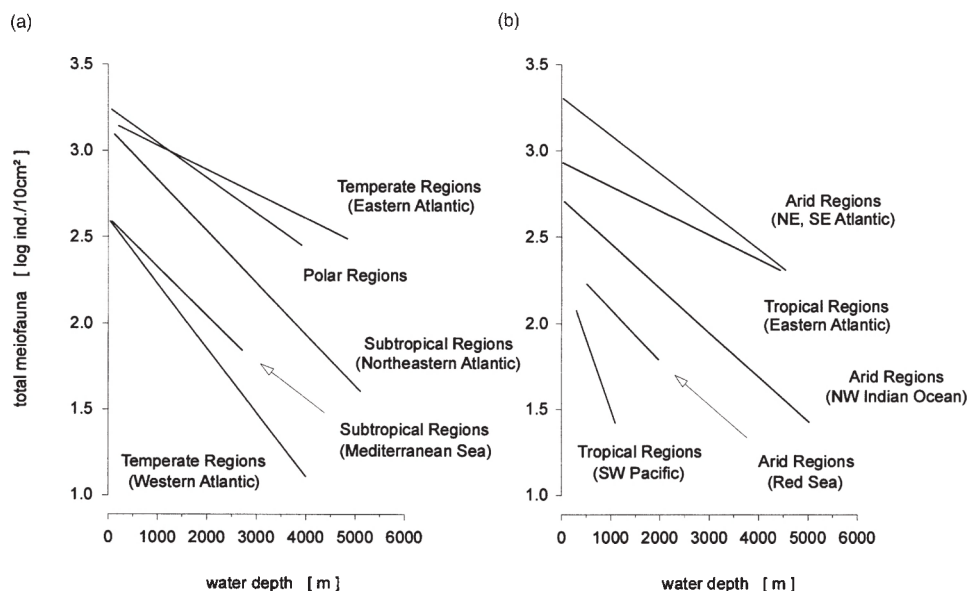
(a)   (b)

Fig. 14.   (a, b) Gradients in meiofauna abundances in various climatic regions.

and South-western African coast. High abundance levels were also found in polar regions, in the temperate North-eastern Atlantic and in the tropical Eastern Atlantic. In subtropical regions of the North-eastern Atlantic (off the Iberian peninsula and North-eastern Africa, north of 30°N) there were rather high abundances in shallower water, which declined more rapidly with increasing water depth (relative to those in the regions mentioned above). Similar steep declines were found along depth transects in the North-western Indian Ocean, and in the Mediterranean Sea and the Red Sea. However, the declines in the latter two seas were significantly lower level ($p<0.05$). The steepest gradients in the decline of meiofauna abundances were along transects off the North-eastern American coast and especially off North-eastern Australia, where the transects exhibited some of the lowest meiofaunal densities reported from continental margins.

Several indices have been used to estimate flux rates of sedimenting organic matter to the seafloor. Thiel (1978) introduced analysis of sediment-bound pigments as an indicator of the input of phytodetrital organic matter, in which fluorometric measurement of chloroplastic pigment equivalents (CPE), which comprises the bulk of intact chlorophyll a and its derivatives, was carried out according to the methodology of Shuman and Lorenzen (1975). Faunal data together with CPE concentrations have been given in a number of papers dealing with meiofauna standing stocks along continental margins, from all climatic regions of the world (Pfannkuche et al., 1983; Pfannkuche, 1985; Pfannkuche & Thiel, 1987; Soetaert et al., 1991; Vanhove et al., 1995; Soltwedel, 1997). Fig. 15 summarises these data, and illustrates the significant logarithmic relationship between meiofauna abundances and CPE values, indicative of close pelago-benthic coupling. Although there is a significant statistical relation-
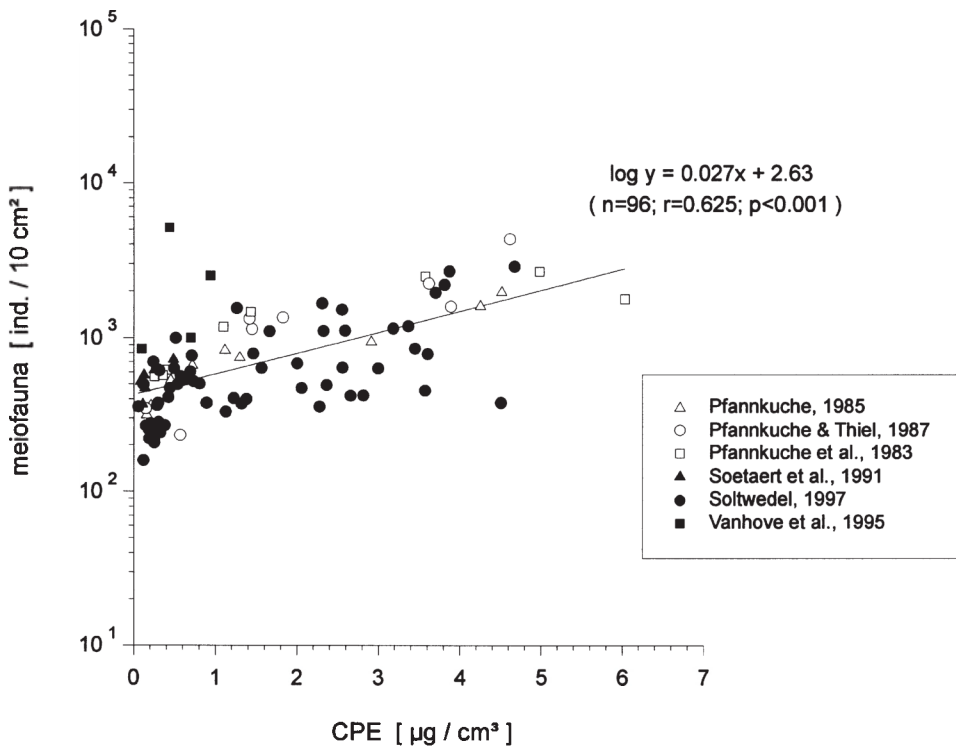
Fig. 15. Correlation between sediment-bound chloroplastic pigment equivalents (CPE) and meiofauna densities.

ship between primary production and meiobenthic standing stocks, there is large variation in the data, indicating that their relationship is complex, as a result of the influence of abiotic factors (pressure, water temperature, oxygen concentrations, sediment granulometry), biological processes in the water column (degradation of organic matter in the pelagic food web) and interactions with other faunal groups (competition, predation).

Acknowledgements

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