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# Annual Course of Sediment Parameters and Meiofauna on a Sandy Tidal Flat in the Wadden Sea after the Severe Winter of 1995/96

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## Summary

Local abiotic and biotic data are presented from the Gröninger Plate (a sandy tidal flat south of Spiekeroog Island) covering a period of one year (February 1996 – February 1997), which includes the coldest part of the ice winter of 1995/96 as well as the winter of 1996/97. The thickness of the visible oxidized layer revealed a clear seasonality. Regarding sandy sediments, values were generally low and ranged between 2.9 cm in winter and 0.9 cm in summer. Biotic and abiotic data are restricted to composition and abundance of meiofauna taxa, total organic carbon, Chl *a* and phaeopigments as well as temperature and salinity. A significant reduction of meiofaunal abundance, particularly of nematodes, in the top 2 cm was recorded in samples taken in sediments covered by ice, as compared to sediments without an ice cover. However, vertical distribution of meiofauna under ice cover showed that nematodes had migrated to deeper sediment layers. The meiofauna appeared to have overcome the stress of low temperatures and ice formation better than the macrofauna.

## Jährlicher Verlauf von Sedimentparametern und Meiofauna auf sandigen Wattflächen des Wattenmeeres nach dem extremen Winter 1995/96 (Zusammenfassung)

Örtliche abiotische und biotische Daten von der Gröninger Plate, einer sandigen Wattfläche südlich von Spiekeroog werden über einen Zeitraum von einem Jahr (Februar 1996 – Februar 1997) dargestellt. Dieser Zeitraum schließt die kälteste Phase des Eiswinters 1995/1996 ein sowie den moderaten Winter 1996/1997. Die Dicke der sichtbaren oxidierten Schicht zeigt eine klare saisonale Schwankung. Angesichts des sandigen Sediments sind die Werte allgemein niedrig und schwankten zwischen 2,9 cm im Winter und 0,9 cm im Sommer. Die biotischen und abiotischen Daten sind beschränkt auf die Zusammensetzung und Abundanz von Meiofauna-Taxa, den gesamten organischen Kohlenstoff, Chl *a*- und Phaeopigment sowie Temperatur und Salinität. Eine eindeutige Reduktion der Meiofauna-Abundanz, speziell von Nematoden, wurde in Proben aus den oberen 2 cm sowohl des eisbedeckten wie des eisfreien Sediments registriert. Allerdings zeigte die vertikale Verteilung der Meiofauna unter der Eisdecke, daß die Nematoden in die unteren Sedimentschichten gewandert waren. Die Meiofauna schien den Streß der niedrigen Temperaturen und der Eisbildung besser überstanden zu haben als die Makrofauna.

## Introduction

Several species inhabiting the tidal flats of the Wadden Sea have been found sensitive to low temperatures, showing high rates of mortality or even local extinction during extremely cold winters (CRISP [1964]; BEUKEMA [1979, 1985]; REICHERT AND DÖRJES [1980]). The build-up of an ice cover means mechanical destruction of habitat, increase of surface and pore water salinity, and sometimes oxygen depletion and sulfide formation. The immediate and direct effect of a cold winter is a strong reduction in the abundance of the numerous cold-sensitive benthic species (BEUKEMA [1990]). Since in the intertidal zone temperature variations are more extreme in the upper sediment than in the overlying water (DE WILDE AND BERGHUIS [1979]), the negative effects are more noticeable in benthic fauna inhabiting the upper tidal flats than in that living in lower situated ones (BEUKEMA [1985]).

In most of the investigations carried out on effects of severe winters, primarily the macrofauna has been considered (ZIEGELMEIER [1964]; BEUKEMA [1979, 1985, 1990]; BUHR [1981]). In contrast, there is only scarce information about possible effects of severe winters on meiobenthic organisms (JANSSON [1968], LORENZEN [1968]). Although the importance of temperature in determining distribution patterns of marine interstitial organisms is well known (MCINTYRE [1969], KRAUS AND FOUND [1975], VERNBERG AND COULL [1975]), WESTHEIDE AND VON BASSE [1978] reported that no noticeable meiobenthic population changes occurred in a year following a cold period. Laboratory experiments using meiobenthic organisms revealed different capabilities between species to tolerate freezing and supercooling (PURSCHKE [1981], FARKE ET AL. [1985]).

The unusually cold winter of 1995/96 ("Ice Winter") was characterized by air temperatures below 0 °C for several weeks in succession causing the build-up of a relatively long-lasting ice cover in the German Wadden Sea (STRÜBING [1996]). Against this more general background we present local abiotic and biotic data from the Gröninger Plate (south of the East Frisian Spiekeroog Island) covering a period of one year (February 1996 – February 1997), which includes the coldest part of the ice winter as well as the „normal" winter of 1996/97, as temperatures were close to the long-term average (MURSYS [1996]). Biotic and abiotic data are restricted to meiofauna taxa composition and abundance, total organic carbon, Chl *a* and phaeopigment as well as temperature and salinity.

## Site and Methods

The study area was the Gröninger Plate, a sandy tidal flat situated between the island of Spiekeroog and the East-Frisian mainland coast (Station 63 located at 53° 43' 00" N and 07° 45' 54" E). It is far away from tidal channels and emerges for four hours during low tide. The sediment of the area consists mainly of well sorted fine sand ranging from 125 µm to 177 µm (2.5–3.0 phi) with a mud content of < 5% (FLEMMING AND DAVIS [1994]) and a water content of 20 % (W/W).

### *Environmental parameters*

The time-course of some relevant abiotic parameters was monitored during and after the winter of 1995/96. Between December 30, 1995, and February 18, 1997, temperatures of the bottom water and of the sediment were measured at vertical intervals of 2 cm with a digital probe. Salinity of ice, bottom water and pore water (sucked with a pore water lance) was measured with a hand refractometer. Total organic carbon (TOC) of the sediment was determined with a Ströhlein Coulomat 702-LI at 2 cm intervals down to 10 cm depth, after removal of carbonates with diluted HCl. Water content and porosity of the sediment were determined from wet weight and dry weight of a known volume of sediment after freeze-drying, and concentrations of chlorophyll *a* (an estimate of living algal biomass) and phaeopigments (an estimate of degraded plant material) of the top 2 cm sediment were determined according to STAL et al. [1984]. In addition, the thickness of the visible oxidized layer was monitored during the study period not only at Station 63 but also at 9–16 other sites covering the entire Gröninger Plate (see FLEMMING AND BARTHOLOMÄ [1993]). For this purpose 10 cores were taken and the thickness of the visible oxidized layer was measured (KOGGE [1993]).

### *Meiofaunal sampling*

Four sediment cores (inner diameter 2.6 cm, 10 cm long) were taken at low tide. On February 15, 1996, we took 4 additional cores from an area covered with ice which was about 18 cm thick. The same number of cores was taken simultaneously from an adjacent area without ice. The cores were sliced at 2-cm intervals, which was appropriate for sandy sediments of the same area (NEIRA AND RACKEMANN [1996]) to examine the vertical distribution of the meiofauna. The samples were treated with a 6 % water solution of magnesium chloride to promote tissue relaxation and then preserved with a 4 % formaldehyde solution containing Rose Bengal (0.5 g dm$^{-3}$). The sediment was sieved once through a 500-µm mesh with tap water to exclude macrofauna and larger particles. The sediment that passed the sieve was resuspended in a 500-cm$^3$ cylinder, and the meiofauna was poured over a 40-µm sieve by successive shaking, decanting and sieving. Thus, meiofauna was defined as metazoans that passed through a 500-µm mesh sieve and were retained on a 40-µm sieve. All meiofauna were counted and identified to major taxa under a dissecting microscope.

## Results

### *Environmental conditions*

Freezing temperatures began to be noticeable in early December 1995, and during our first field observation on December 30, 1995, a layer of ice had already formed. The thickness of the ice ranged from several centimetres to over one meter. The tidal currents moved the ice floes back and forth over the flats and through the channels. Water temperatures around 0 °C characterized the three first months of 1996. In addition, although with values above 0 °C, low temperatures continued until late May (around 10 °C). Between June and late August the temperature increased to 20 °C. Then it began to decrease rapidly. Fig. 1 shows the course of the temperatures of the sediment down to 15 cm depth. The spatial distribution of the temperatures represented by isolines clearly revealed the differences between the winter of 1995/96 and the winter of 1996/97. Temperatures below 0 °C were recorded until March 1996 down to 15 cm depth, and temperatures below 10 °C were still dominant in May 1996. On the contrary, the cold period in winter 1996/97 was very short with values under 0 °C in January 1997. The greatest temporal variability of the temperature was found in the upper 2 cm, the least in 15 cm depth. During the entire cold season the vertical differences within the sediment were very low (0.9 °C). By contrast, a difference of 7 °C between surface sediment (2 cm) and the depth (15 cm) was re-

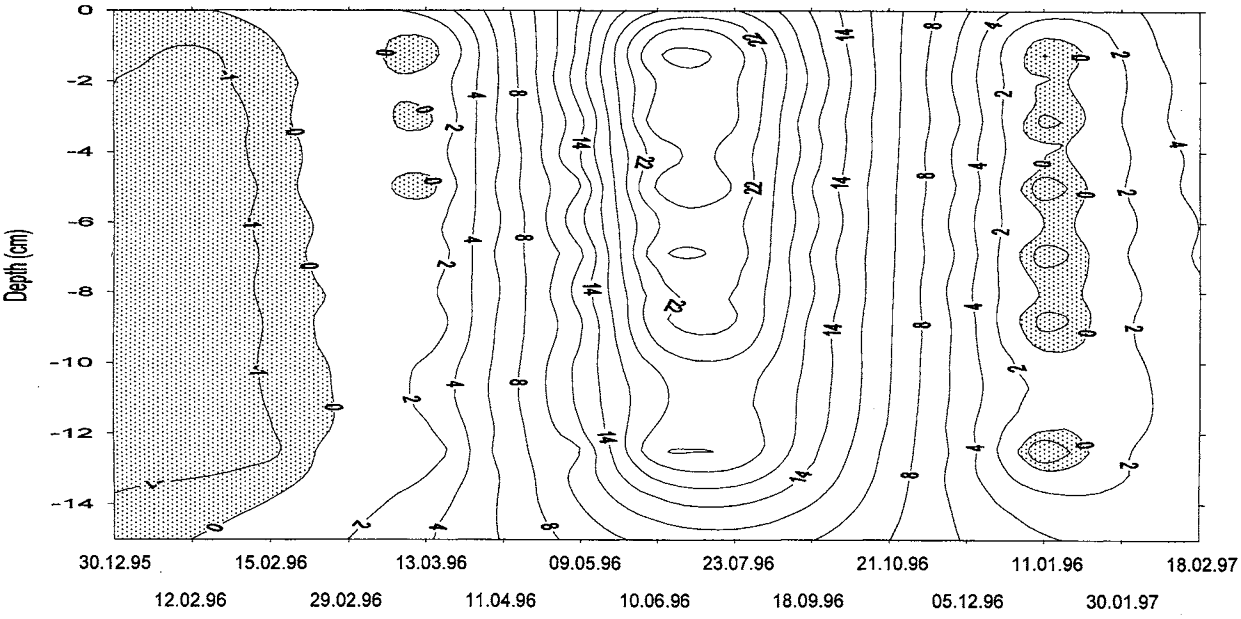

Fig. 1: Course of the sediment temperatures down to 15 cm depth at the study site. Isolines are in °C

corded in summer. This suggests that in summer organisms avoid unfavourable temperatures by migration, while in winter migrations are temporarily prevented by freezing. Thus, low and uniform temperatures are decisive factors, enhanced by changes in salinity, oxygen and sulfide. The course of the salinity and the temperature of the bottom water (measured during low tide) are shown in Fig. 2. The salinity varied locally and temporally due to precipitation, ice formation, ice-melting, and evaporation during the winter months and later. In general the salinity fluctuated between 30 and 36. Particularly on February 18, 1997, strong rain reduced the salinity temporally to 30. This situation was dissipated quickly by mixing during the next flood (32). In winter 1995/96, we measured ice salinities of 6.5 1 cm above and of 1 30 cm above the sediment surface. The salinity in deeper sediments hardly showed fluctuations. Water content and porosity, which were determined at 2-cm intervals down to 10 cm depth, remained rather constant during the whole study period with values of 20 % and 0.4, respectively. Only in February was there an increase in the top 2 cm which we attributed to the erosion effect of the ice, making the sediment loose.

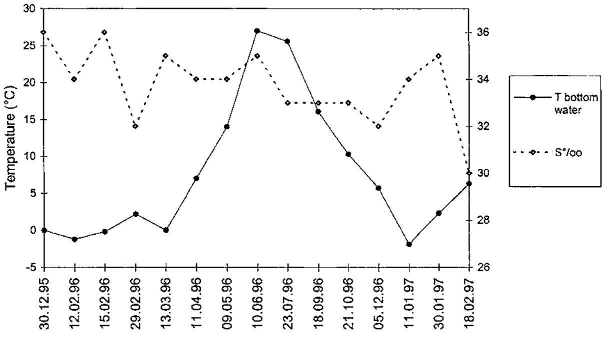

Fig. 2: Course of salinity and temperature of the bottom water measured at low tide at the study site

As shown in Fig. 3, the course of the thickness (±SD) of the visible oxidized layer, measured between March 1996 and February 1997 revealed a clear seasonality. The maximal mean thickness, 2.9 cm, was observed in March 1996. In July 1996 it attained only 0.9 cm. Maximal absolute values of 9 cm were measured in March 1996 in the westernmost part of the Gröninger Plate. Minimal values of 1 mm were measured not only in summer but occasionally also in winter which were related to depressions left by ice floes after melting.

The changes in the Chl *a* and phaeopigment concentrations of the top 2 cm at Station 63 are shown in Fig. 4. Chl *a* ranged between 0.3 and 1.2 $\mu g \cdot g^{-1}$ DW, the phaeopigments between 0.3 and 3.8 $\mu g \cdot g^{-1}$ DW. Although we found some Coscinodiscus cells (not quantified) apparently recently deposited (citoplasma stained with Rose Bengal), probably most of Chl *a* was degraded to phaeopigment as indicated by the increase noted in late February 1996. In April and May the pigment content decreased to a minimum. From June to October 1996 an increase occurred again. Vertical profiles (down to 10 cm) showed a characteristic pattern of a content diminishing with depth, except in May when there was a slight increase at 4 cm depth.

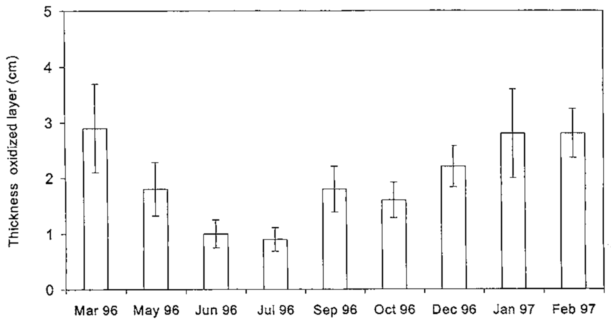

Fig. 3: Mean thickness (± SD) of the visible oxidized layer at the Gröninger Plate. Each value represents 10 measurements at 9-16 sites covering the entire Gröninger Plate

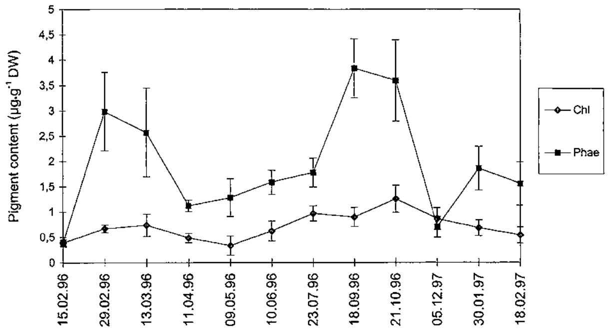

Fig. 4: Mean pigment content (± SD) in the top 2-cm sediment layer at the study site ($\mu g \cdot g^{-1}$ DW, *n* = 4)

The total organic carbon at Station 63 during the study period ranged between 0.06 % and 0.8 % DW (Fig. 5), which corresponded with the generally observed organic content of sandy tidal flats. Until July 1996 the carbon content did not exceed 0.1 % DW in the uppermost sediment layer (2 cm) which appeared to be rather low at this time. Already in September 1996 we found about 0.2% DW of total organic carbon which continued into October. A steep increase to 0,8 % was recorded in February 1997 ($n = 4$). This value does not reflect the pigment data of Fig. 4. We attribute it to the frequently observed foam depositions on the flats. Normally, the carbon content decreased with depth down to 4 cm and then increased slightly down to the depth of 10 cm.

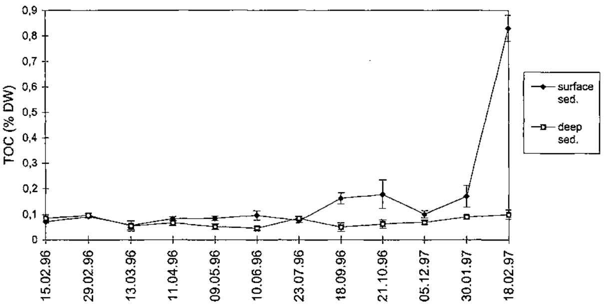

Fig. 5: Mean total organic carbon, TOC (± SD) in the top 2-cm and 10-cm sediment layers at the study site (% DW, $n = 4$)

The ice caused considerable mechanical disturbance. Drifting ice left long dragging traces on the surface with a depth of sometimes several centimetres. Due to repeated back and forth movements most of the ice floes became rounded with a diameter of several metres. Depressions left by lifted or melted ice floes converted the tidal flat to a pitted landscape. Most of the ice floes turned dark because sediment was attached to the surface or frozen into the ice. Some ice floes showed repeated layers of sediment-free and sediment-containing ice at their bases. In February 1996, samples ($n = 10$) were taken at different distances from the bottom with a cut-off syringe. For instance, ice samples 40 cm above the bottom contained 0.5 g sediment per 30 cm$^3$, samples taken near the bottom amounted to 1.5 g per 30 cm$^3$. This sediment consisted of mud (< 63 µm) with an organic carbon content of over 1 % DW, i.e. almost by a factor 10 higher than that measured in the top 2-cm sediment layer in February 1996. This suggests that not only large amounts of muddy sediment were transported by drifting ice, but also enormous quantities of organic matter. Such aspects should be considered in future studies in order to determine the amount of organic matter transported by ice.

### *Meiobenthos*

a. Sediment without an ice cover:

Mean meiofaunal densities in the top 2-cm layer ranged from 1,776 ± SD 104 to 8,509 ± SD 826 ind.·10 cm$^{-2}$ (Fig. 6). The total meiofaunal abundance was relatively low until late April, 1996, with about 2,000 ind. · 10 cm$^{-2}$. A slight increase occurred between February 15 and February 29, 1996. In June we found the highest number of individuals (see above). In July the number diminished rapidly to 3,039 ± SD 301 ind. · 10 cm$^{-2}$. Until October 1996 it increased again, but decreased in December 1996. Abundances found in January and February 1997 were similar to those found in January 1996, i.e., values around 2,000 ind. · 10 cm$^{-2}$. In terms of abundance, nematodes were the dominant taxonomic group during the whole period of investigation, followed by nauplii (harpacticoids, MARTÍNEZ [pers. comm.]) and adult harpacticoid copepods; gastropods showed the lowest dominance (Table 1). The temporal patterns of the major meiofaunal groups (groups which were present at least in 50 % of all sampling dates) are shown in Fig. 7. Minor meiofauna-taxa, i.e. those that showed less than 50 % of presence were Gastropoda, Gnathostomulida, Hydrozoa, Rotifera, Bivalvia, Gastrotricha and Polychaeta. The nematodes were consistently the most abundant metazoans with a minimum of around 2,000 ind. · 10 cm$^{-2}$ in February both in the years 1996 and 1997 and a maximum of 5,313 ± SD 544 ind. · 10 cm$^{-2}$ in June 1996. The nauplii and the harpacticoid copepods began to be numerically important in May, reaching a maximum in July when their share amounted to 42 %. During sampling dates such as February 15, 1996, February 29, 1996, April 11, 1996, and January 30, 1997, other taxa ranged second, namely tardigrades, ostracods, and gnathostomulids. However, if copepods and nauplii are added, harpacticoids were the second dominant taxon.

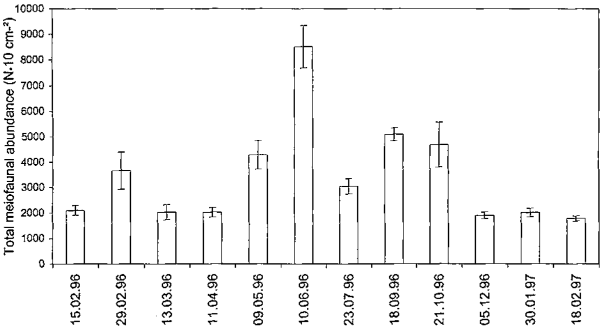

Fig. 6: Mean total meiofaunal abundances (± SD) in the top 2-cm sediment layer at the study site during the sampling period (N · 10 cm$^{-2}$, $n = 4$)

| Taxa | Presence % | Dominance % |
|---|---|---|
| Nematoda | 100.0 | 78.0 |
| Copepoda | 100.0 | 7.6 |
| Nauplii | 91.6 | 10.7 |
| Tardigarda | 91.6 | 1.0 |
| Ostracoda | 91.6 | 0.6 |
| Turbellaria | 66.6 | 0.5 |
| Polychaeta | 50.0 | 0.4 |
| Bivalvia | 41.5 | 0.7 |
| Gastrotricha | 33.3 | 0.05 |
| Rotifera | 25.0 | 0.13 |
| Hydrozoa | 16.6 | 0.05 |
| Gastropoda | 8.3 | 0.01 |
| Gnathostomulida | 8.3 | 0.2 |

Table 1: Presence (% of all samples) and dominance (% of total abundance) of the meiofauna-taxa at the study site during the sampling period

An obviously late new spatfall of macrozoobenthic species was revealed when only in June a high number of bivalves and polychaetes appeared as temporal meiofauna, especially the bivalves *Cerastoderma edule*, *Mya arenaria* and the polychaetes *Pygospio elegans*, *Scoloplos sp.* and *Heteromastus filiformis*. Likewise, the gastropod *Hydrobia ulvae* was found in May as temporal meiofauna, although in low numbers.

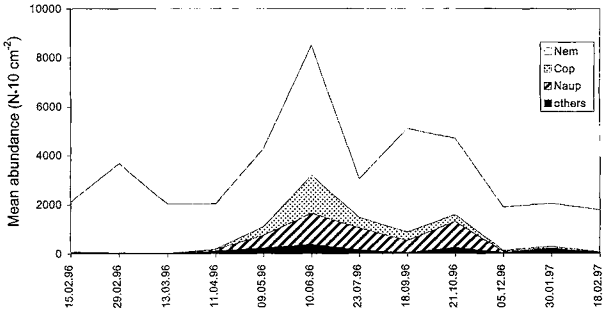

Fig. 7. Abundances of the major meiofauna groups (present during over 50 % of all sampling dates) at the study site. NEM = Nematoda, Cop = Copepoda (adults + copepodids), Naup = Nauplii. Others: Turbellaria, Ostracoda, Tardigrada, Gnathostomulida, Gastropoda, Hydrozoa, Rotifera, Bivalvia, Gastrotricha, Polychaeta. The latter 7 taca were represent during 50 % or less of all sampling dates.

b. Sediment with ice cover:

Sampling on February 15, 1996, at an ice-covered site of the same study area revealed that between 0 and 10 cm depth the total meiofauna (97 % nematodes) was numerically not significantly reduced, but differently distributed with depth. In fact, in the top 2-cm layer we found only 552 ± SD 36 ind. · 10 cm$^{-2}$, but 1,295 ind. · 10 cm$^{-2}$ in 4 cm depth (Fig. 8). Other meiofaunal groups found both in sediments with ice cover and without ice were copepods, tardigrades ostracods, gastrotriches, although together representing less than 7 % of the meiofauna in the top 2 cm (as indicated by arrow in Fig. 8).

Qualitative sampling of the lower part of ice floes showed variable results. After thawing, some samples did not contain meiofauna and some did. In those containing animals, we found nematodes, copepods, and turbellarians.

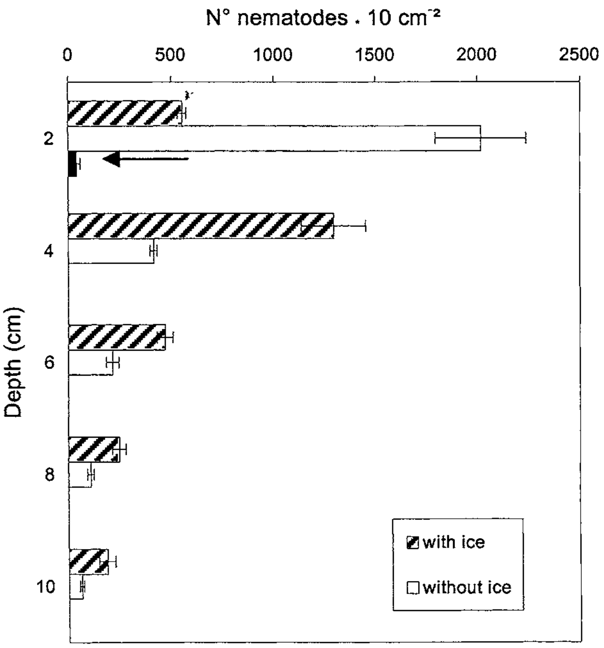

Fig. 8: Mean vertical distribution (± SD) of nematodes, with and without ice cover on 15 February 1996 at the study site. Arrow shows the mean abundance of other meiofauna (Copepoda, Tardigrada, Ostracoda and Gastrotricha) in an area with ice ($n = 4$)

## Discussion

### *Ice winter influences on abiotic parameters*

On intertidal flats ice began to form when the air temperature fell below the freezing point of sea water (–1.6 °C at a salinity of 29.5, and –1,8 °C at 34). This may occur within 2–3 days, because the uncovered tidal flats show a higher heat radiation than the water masses and because during low tide the wind cools down the bottom through evaporation of water (Eisma [1983]). In late December 1995, when the temperature of the air was lower than that of the seawater, the temperature in the surface sand dropped several degrees below that of flooding seawater. At this stage, the pore water within the sediment froze and a thin glaze of ice formed on the sediment surface (situation observed on 30 December 1995). During low tide at night the cooling may have been more severe since heat is lost upward contributing to the freezing. The net result of such a long period of low temperatures was the formation of an ice cover which became locally over one metre thick with maxima of 3 m. The temperature difference between the surface water (overlying water) and the 15 cm depth level within the sediment amounted to 4 °C in the winter months of December 1995 and March 1996. Reichert and Dörjes [1980] found a difference of 8.8 °C in Crildumersiel during the ice winter of 1978/79. The mean temperature difference within the sediment (2 and 15 cm) during the winter months amounted to 0.9 °C, in summer it amounted to 7 °C. The depth of the frozen bottom depends on the time of inundation (Reichert and Dörjes [1980]). At the Gröninger Plate, during January and mid-February 1996, easterly winds dominated and extended the low water periods. This allowed not only the formation of a thick ice layer but also the freezing of the sediment. The same occurred in January 1997, when we measured temperatures of –2.4 °C even at a depth of 30 cm.

Besides changes of temperatures, ice formation and ice movement have consequences relevant to sediment organisms. During freezing, salt is released leaving the sea ice with a salinity from 3 to 10 (Taylor and McCann [1983, own obs.]). At the same time the salinity of the surrounding sea water may increase dramatically. In fact, we measured absolute salinities of over 36, even 39 was recorded (G. Liebezeit [pers. comm.]). Other important influences are the physical perturbation and the transport of sediment. Sediment can accumulate on or within sea ice. Waves and currents wash considerable amounts of sediment onto the top of ice floes trapped on the tidal flats (Gilbert [1983]). At low tide, a several mm thick layer of fine sediment with its interstitial water may freeze to the bottom of the ice. This may repeat itself, interrupted by periods of floating, leading to sediment-containing layers within the ice. After melting, sediments may be deposited at places where other sediment characteristics are typical. Preferably fine sediment seems to be translocated by such a process (Rosen [1979, own obs.]). Since the organic material is predominantly associated to fine particles, the transport of sediment means at the same time transport of organic carbon. It may be that the content of organic carbon and pigments at the study site was affected by such events. We observed that the horizontal movement of ice floes eroded the top of the sediment down to the anoxic layer, particularly on January 30, 1997, after a short ice period of one and a half week. We found holes of several centimetres in the sediment produced by ice floes, where the oxidized horizon was thinner than in the adjacent sediment.

The annual course of the situation of the oxidized horizon showed a clear seasonality with minimal mean values in summer. Considering that the Gröninger Plate is a sandy tidal flat, a mean winter value of 2.8 cm is very thin for this time as indicated by previous observations (DÖRJES [1978], MICHAELIS [1987], KOLBE [1991], MICHAELIS ET AL., [1992]). Comparable measurements on the Gröninger Plate from 1992/93 (KOGGE [1993]) resulted in 3.3 cm in March, 1.4 cm in June, 2.9 cm in December of 1992 and 1.4 cm in July 1993. This supports assumptions of a generally decreasing oxidized layer (MICHAELIS [1987]). The most extreme situation is found in the black spots where the values decrease to zero (HÖPNER AND MICHAELIS [1994], NEIRA AND RACKEMANN [1996], HÖPNER AND OELSCHLÄGER [1997]). Since the situation of the visible oxidized horizon is an indicator of the state of the sediment, it should be incorporated in future long-term monitoring programmes as a standard environmental parameter.

### *Ice winter influences on algae and meiobenthos*

According to EISMA [1988] and ASMUS ET AL. [1994] the microphytobenthos living on tidal flats is predominantly composed by benthic diatoms and is one of the principal sources of primary productivity. Since during the study period we practically found no macroalgae, we used the pigment content (Chl *a*) as an indirect indicator to quantify the biomass of intertidal microphytobenthos (CARIOU-LE GALL AND BLANCHARD [1995]). The course of Chl *a* in the study area suggests that the microphytobenthos was not or only slightly affected during the ice period. The Chl *a* content was similar in both winter periods, at about 0.5 $\mu g \cdot g^{-1}$ DW, with an increase in summer. The highest values attaining 1.3 $\mu g \cdot g^{-1}$ DW were recorded in October 1996. In the months of July, September and October 1994, NEIRA AND RACKEMANN [1996] recorded concentrations of Chl *a* of 1.1, 2.2, 1,6 $\mu g \cdot g^{-1}$ DW at Station 61 (about 500 m away, similar sediment typ), respectively. For the phaeopigments the corresponding concentrations were 8.3, 11 and 15 $\mu g \cdot g^{-1}$ DW, respectively. On the tidal flats back of the island of Baltrum, we found 2.4 and 1.5 $\mu g \cdot g^{-1}$ of Chl *a* in the top 2 cm in July and September 1994, respectively. The high content of phaeopigment in the cold period was not surprising. In fact, it was reported that large amounts of the cold-water planktonic diatom *Coscinodiscus concinnus* formed a bloom in early 1996 which after decaying deposited on the bottom (ELBRÄCHTER [1996], NIESEL [1997]). We suppose that this bloom influenced the phaeopigments data of Fig. 4. Chl *a* degrades in a relatively short time, whereas its tetrapyrrole derivatives or phaeopigments degrade more slowly (SUN et al. [1993]). In this way an increasing phaeopigment content may occur on the tidal flat.

Long periods of low temperatures and ice-formation may alter the infaunal community on at least short time scales. Noteworthy is that frost periods in the Wadden Sea generally are accompanied by easterly winds so that temperature effects are intensified by extended low water periods. The consequences range from even lower temperatures to drying up, oxygen depletion (REICHERT AND DÖRJES [1980]) and sulphide increase (BUHR [1981], BEUKEMA [1990]). In fact, pore water sulphide determinations in the study area revealed concentrations as high as 0.6 $mmol \cdot dm^{-3}$ in January and February 1996, which is highly toxic for most aerobic organisms. By March 1996 sulfide concentrations had decreased to 0.05 $mmol \cdot m^{-3}$ (HÖPNER AND OELSCHLÄGER [1997]).

A markedly low meiofaunal abundance, particularly of nematodes in the top 2 cm, was recorded on February 15, 1996, in samples taken under an ice cover as compared to sediment without ice cover. However, adding the abundances in the whole sediment core of 10 cm (Fig. 8), the figures with and without ice were almost equal. This suggests that some nematodes migrated downward, which is revealed by the abundance maximum in

2–4 cm depth under the ice. It is known that nematodes differ in their tolerance to low temperatures (LORENZEN [1968], GERLACH AND SCHRAGE [1971], FARKE et al. [1985]). Mechanical effects might have contributed locally to the reduction of nematodes by sweeping the sediment surface. Probably the near surface and surface-dwelling taxa were more susceptible to the direct and indirect effects caused by the ice cover than those living deeper in the sediment. This pattern would be consistent with observations from shallow water environments (DAUER [1984], SCHAFFNER et al. [1987], TAMAKI [1987]). Such winter migration of meiofaunal animals into deeper sediment layers in order to avoid changing conditions has been observed earlier (GIERE [1993]).

On the other hand, we found living copepods, nematodes, ostracods as well as tardigrades, in ice samples and in the top 2 cm. Some species of copepods, such as *Tisbe furcata*, are able to migrate into the sea-ice during the winter months (GRAINGER [1991]). It is known that copepods have developed diverse strategies to compensate for extreme environmental temperatures and to exploit the ice (GRAINGER [1991], BERGMANS et al. [1991]). The presence of living nematodes, copepods, turbellarians and ostracods in ice samples is well known from polar regions. Within about 5.5 cm$^3$ of sediment obtained from the subsurface of an ice floe (10 x 10 cm, 0.5 cm thick) which after thawing gave 80 cm$^3$ of water, D. BLOME [pers. comm.] found 51 nematodes, 3 copepods and 4 turbellarians.

As FARKE et al. [1985] we believe that most of the meiofaunal organisms inhabiting the tidal flats are hardly adapted to cope with ice and that most of them were simply embedded randomly into the ice. However, there are species more sensitive than others to ice effects. In fact, in the same area increasing dominances of the nematodes *Oncholaimellus calvadosicus* (29 %), *Viscosia rustica* (15 %), and *Innocuonema tentabundum* (12 %) were recorded in February 1996 by D. BLOME [pers. comm.] while in 1995 the corresponding figures were 13 %, 9 %, and 1 %, respectively. However, in general there were no significant other changes in nematode species composition owing to the ice winter. On the other hand, the macrofauna suffered large mortalities (C. VON BERNEM [pers. comm; own obs.]) or even in some cases disappearance until August 1996, e.g. *Cerastoderma edule*, *Mya arenaria*, *Nephtys hombergii*, *Lanice conchilega*, *Harmothoe sp.* The meiofauna seemed to overcome the stress better. A rich spatfall of several bivalve and polychaete species occurred in late spring and summer in the East-Frisian Wadden area. This was well expressed by the abundant temporal meiofauna we found from late June 1996. ZIEGELMEIER [1964, 1970] reported that dramatic reductions in benthic abundances due to very cold winters are followed by unusual mass occurrences of various benthic invertebrates. Similar observations have been made by other authors in different areas of the Wadden Sea (MEIXNER [1979], RACHOR [1980], BEUKEMA [1982]). The mass recolonization of distinct benthic fauna has been attributed to favourable habitat conditions and the absence of predators allowing the settlement of new larvae (BUHR [1981]). Drifting ice eroded the uppermost sediment layers transporting large amounts of fine sediment, meiofauna, microphytobenthos, and organic matter. After thawing, the sediment and transported organisms may have been released in other areas with different sedimentary characteristics. We assume that only in some areas, where an ice cover prevailed for an extremely long time, loss of buried macro- and meiofauna due to oxygen depletion and increasing sulfide, may have occurred (BUHR [1981]).

HÖPNER AND OELSCHLÄGER [1997] included effects of the ice winter in the steps of a hypothetical cascade scheme which tried to explain the black area event of summer 1996. They supposed that the injury to infaunal organisms contributed to a stock of dead biomass which served as a reductant and produced the unprecendentedly high pore water sulphide concentrations (see also BUHR [1981]). The biomass amounts needed for such effects can be provided neither by the meiofauna nor by epibenthic algae but rather by macroorganisms or by the *Coscinodiscus* biomass and lipids discussed elsewhere (BECKER [1996], ELBRÄCHTER [1996], NIESEL [1997]).

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