

Hypoxia and sulphide as structuring factors in a macrozoobenthic community on the Baltic Sea shore: colonisation studies and tolerance experiments

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ABSTRACT: Colonisation by macrobenthos after defaunation due to anoxia and sulphide accumulation was studied in 2 field experiments, performed at shallow sites in the southwestern Baltic Sea. In the first experiment (Wismar Bight) an area was initially covered with dark foil which caused azoic anoxic sediments with high sulphide concentrations (up to 3.4 mmol l⁻¹ at 2 cm depth). After foil removal sulphide concentrations in the upper sediment layer decreased, but at 10 cm depth high concentrations of 1.65 mmol l⁻¹ sulphide remained even after 69 d. Within 3 d, adults of species living in the upper sediment layer, e.g. the ostracod *Cyprideis torosa*, appeared as first immigrants. After 1 mo the density, species composition, diversity and evenness of the macrobenthic community in the experimental area were not significantly different from the reference area. In the second experiment (Hiddensee Island) the colonisation of an area defaunated by a thick cover of decaying algae *Fucus vesiculosus* was investigated. After removal of the algal mat, recovery of the experimental area (decrease of sulphide concentrations, colonisation pattern of macrofauna, development of community parameters, recovery time) was similar to that described for the first colonisation experiment. Laboratory tolerance experiments revealed that species such as *C. torosa* that returned first to the experimental areas also showed highest survival rates under hypoxia and sulphide. In contrast, the amphipod *Corophium volutator*, the most sensitive species to hypoxia and sulphide, was one of the last animals to reach both experimental areas. The macrobenthic community consists mainly of deposit feeding species with a high tolerance for temporary hypoxic conditions and frequent exposure to sulphide. The few less tolerant species have the capacity to produce large populations within short time periods (e.g. the oligochaete *Paranais litoralis*) and/or have a high mobility (e.g. *C. volutator*). At these shallow sites in the Baltic Sea a combined set of abiotic and biotic factors seems to favour rapid recovery of a stress-preconditioned macrobenthos from recurring small-scale hypoxic and sulphidic periods which dominate the ecosystem as structuring factors.

KEY WORDS: Macrozoobenthos · Hypoxia · Sulphide · Colonisation · Tolerance experiments · *Cyprideis torosa*

INTRODUCTION

The shallow coastal regions of the Baltic Sea are well known for their varying abiotic parameters (Kosler 1968). Here, the benthic community is exposed to large fluctuations in water depth, temperature, salinity and oxygen concentrations.

High sulphide concentrations have previously been reported mainly from deep basins of the Baltic Sea (e.g. Leppäkoski 1969, 1971, Ehrhardt & Wenck 1984). However in recent decades, due to eutrophication, even the shallow areas of the Baltic have become increasingly exposed to hypoxic conditions combined with high concentrations of toxic sulphide (e.g. Prena 1994). The importance of sulphide as a prominent distributional factor for benthic species has been dis-

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cussed in recent literature (Vismann 1991, 1992, Giere 1992, Thiermann et al. 1996, Vopel et al. 1996).

This study investigates the influence of hypoxia and high sulphide concentrations on the macrobenthic community of shallow coastal sites in the southwestern Baltic Sea (Wismar Bay and Hiddensee Island). Here, in periods when there is stagnant water, small sediment patches under accumulating algae or cyanobacterial mats frequently become anoxic and highly sulphidic (authors' unpubl. data).

In 2 field experiments, recovery and colonisation of sediment patches with macrozoobenthos were studied after defaunation due to hypoxic and sulphidic conditions created by artificial foil coverage and by a decaying algae mat. Field data were supported by laboratory experiments assessing the resistance to hypoxic and different sulphidic conditions of the 6 dominant macrobenthic species.

MATERIAL AND METHODS

Field experiments. Recovery and colonisation after foil coverage: Located in the shallow eulittoral (<0.5 m water depth) of Wismar Bay, Germany (southwestern Baltic Sea: 54°N, 11°30'E), the study site was fitted with a platform so that the reference and the experimental areas could be reached without causing sediment disturbance. To achieve defaunation before starting the colonisation experiment, about 4 m² were covered with dark PVC foil for more than 1 mo. The experiment lasted from April to November 1993. At the beginning of the experiment the foil was removed from the sediment and measurements of chemico-physical parameters and samples for macrofauna were taken—first at daily, later at weekly and finally at monthly intervals. For studying the pattern of colonisation by macrozoobenthos 3 experimental areas (each about 1 m²) were established. One experimental area could be populated unconstrainedly via the water column and the sediment. The second area could be colonised only via the water column, because of a plexiglass barrier that reached 20 cm into the sediment and was flush with the sediment surface. The third area could be colonised only through the sediment because of a plexiglass barrier in the water column that enclosed this area. For comparison, an untreated reference area adjacent to the experimental areas (about 2 m distance) was investigated for the same time period.

Recovery and colonisation after algae coverage: The study site was located in the shallow eulittoral of Fährinsel, an islet near (300 m) Hiddensee Island, Germany (southern Baltic Sea: 54°30'N, 13°08'E). At the study site 2 platforms were built to enable sam-

pling without sediment disturbance. In this experiment an area of about 20 m² was covered naturally by a thick (15 cm) mat of *Fucus vesiculosus*, that had accumulated on the sediment surface, about 1 mo prior to the start of the experiment. The colonisation experiment lasted from May to the end of September 1995. At the beginning an experimental area of about 4 m² was established by removing the algae cover from the sediment. Here, the experimental area, which was still surrounded by a 3 m wide belt of decaying algae mat, could be colonised unconstrainedly via the water column and through the sediment. Measurements of chemico-physical parameters and samples for macrofauna were taken at the intervals given below. For comparison, an undisturbed area adjacent to the algae mat (about 10 m from the experimental area) was investigated for the same time period.

Chemico-physical parameters: Water temperature was determined with a thermistor probe. For salinity measurements a hand-held refractometer was used. The pH of the overlying water was recorded with an insertion electrode (Ingold) connected to a Knick pH meter. For granulometry, 2 sediment cores were taken from the experimental and the reference area and sliced into 0–1, 1–2, 2–4, 4–6, 6–8, 8–10, and 10–15 cm horizons. The particulate organic matter (POM) was computed as ash-free dry weight (2 h at 550°C). The median particle diameter (MD) and sorting coefficient were determined according to Giere et al. (1988). Sulphide was measured by extracting sediment pore water from 2, 5 and 10 cm depth with hand-made samplers (after Howes et al. 1985). For each depth 2 samples were fixed immediately in vials containing 2 ml zinc acetate and 0.5 ml sodium hydroxide. Subsequently, total sulphide concentrations were determined photometrically according to the methylene blue method of Gilboa-Garber (1971) modified by Howarth et al. (1983). In this paper, the term sulphide always refers to total reduced sulphur, i.e. undissociated H₂S, HS⁻ and S²⁻.

Macrofauna: For faunal analysis, 4 replicate sediment cores were taken in each experimental area with plexiglass tubes and subdivided into 0–1, 1–2, 2–4, 4–6, 6–8, 8–10, and 10–15 cm fractions. The animals were extracted by sieving (500 µm mesh size), fixed in buffered formaldehyde solution (final concentration 5 to 10 vol%), sorted quantitatively and identified under a dissecting microscope. Specimens of the gastropod *Hydrobia* spp. and the ostracod *Cyprideis torosa* (≥ larval stage VI; Heip 1976) retained by the 0.5 mm meshes were considered here as adults. Community parameters such as species diversity (Shannon-Wiener Index) and evenness were calculated according to Gray (1984).

Tolerance experiments. Survival times under hypoxic and sulphidic conditions of the 6 most abundant macrobenthic species [*Cyprideis torosa*, *Hydrobia ventrosa*, *Hediste (Nereis) diversicolor*, *Heterochaeta costata* (*Tubifex costatus*), *Paranais litoralis*, *Corophium volutator*] were measured in tolerance experiments (2 to 4 replicates). Animals (adult specimens only, except for juvenile *H. diversicolor*) were collected from the field (Wismar Bight) by sieving the upper sediment layer through a 500 µm sieve and kept in aerated aquaria with natural sediment and seawater (12 to 14‰ S, 16°C). For each experiment animals were placed in 60 ml (*H. diversicolor* in 250 ml) jars and exposed (without sediment but small glass beads) to 4 different treatments: (1) *Normoxia (control)* – artificial seawater (14‰) buffered with 10 mmol l⁻¹ HEPES (pH: 7.8) and aerated continuously; (2) *Hypoxia* – same seawater but bubbled with pure nitrogen for 1 h before inserting the animals; (3) *Hypoxia plus low sulphide concentrations* and (4) *Hypoxia plus high sulphide concentrations* (Table 1) – bubbled with nitrogen for 1 h plus subsequent addition of sulphide stock solution (100 mmol l⁻¹, pH: 7.9).

After insertion of animals, jars were closed and placed in a 1 l container which was cooled (16°C) and percolated with nitrogen to prevent aeration. Jars were checked every couple of hours under the dissecting microscope and live individuals counted. Mortality assessment (see 'Discussion') of the animals was based on failure of tactile response to the glass beads after stirring them up in their incubation jar. Hence, 'mortality' in these experiments refers both to moribund and dead animals. Oxygen content, sulphide concentrations and pH of the incubation media were measured at the beginning (after inserting the animals into the jars) and the end of each experimental run. In all cases, oxygen concentration, measured with a sulphide-insensitive polarographic electrode (Orbisphere, Gießen, Germany), stayed below its detection limit of 1 µmol l⁻¹ O₂ (= hypoxia). After determination of oxygen concentration in the incubation medium for hypoxic treatments the medium was again bubbled with nitrogen before closing the jars. Sulphide measurements were performed with the same colorimetric method as described for field studies. Over the experimental time the sulphide concentrations in the jars decreased by less than 10% of the initial value.

Statistical analysis. The data are presented as mean values with their standard deviation. For the field data (animal density, number of species, diversity, evenness), the non-parametric Mann-Whitney *U*-test at the

Table 1. Conditions of the tolerance experiments. Sulphide concentrations and pH values are given as mean values (n = 4 to 8) with standard deviations

Species	No. of animals/treatment	pH	Low sulphide (µmol l ⁻¹)	High sulphide (µmol l ⁻¹)	No. of experimental runs
<i>Cyprideis torosa</i>	20	8.1 ± 0.1	1019 ± 81	1802 ± 190	4
<i>Hydrobia ventrosa</i>	12	7.9 ± 0.2	289 ± 47	566 ± 87	3
<i>Hediste diversicolor</i>	4	8.4 ± 0.1	367 ± 65	978 ± 207	3
<i>Heterochaeta costata</i>	10	8.0 ± 1.2	552 ± 126	1956 ± 132	2
<i>Paranais litoralis</i>	12	8.1 ± 0.1	49 ± 11	143 ± 26	2
<i>Corophium volutator</i>	20	7.7 ± 0.2	35 ± 13	87 ± 11	2

0.05 level was used to test the differences between the experimental and the reference areas over time. For the tolerance data, the same test at the 0.05 level was used to test the significance of the influence of hypoxia and hydrogen sulphide on survival time (LT₅₀) of the animals. Statistics were used only on data of experiments repeated 3 or more times.

RESULTS

Recovery and colonisation after foil coverage

Chemico-physical parameters

The study site (Wismar Bight) was continually subjected to large fluctuations of water depth, temperature and salinity (Fig. 1). In May the experimental and reference areas fell dry twice for 3 to 4 d. The pH values in the water ranged between 7.9 and 8.3.

Significant differences in content of POM in the upper horizons of the 2 areas were not found. POM varied between 4% (0–1 cm depth, reference area) and 2% (0–1 cm depth, experimental areas). Deeper sediments of all areas contained 1% POM. MD in the experimental area ranged from 179 to 187 µm in the 0–4 cm horizons corresponding to fine sand. In deeper sediment layers MD increased up to 742 µm. In the reference area MD was in the same size class, ranging from 154 to 238 µm in the upper 0–4 cm. The sorting coefficient of both areas varied between 1.4 and 2.2 (= poorly sorted sediments).

Coverage with foil caused azoic sediments with high sulphide concentrations (3.39 mmol l⁻¹ at 2 cm depth) in all experimental areas (Fig. 2). This contrasted to the reference area which had not more than 140 µmol l⁻¹ sulphide at 2 cm depth. The experimental areas were anoxic throughout, while in the reference area oxygen penetrated down to 1.5 mm sediment depth (J. Rethmeier pers. comm.); beneath this depth the sediment was anoxic as well. After 69 d of recovery, 230 µmol l⁻¹

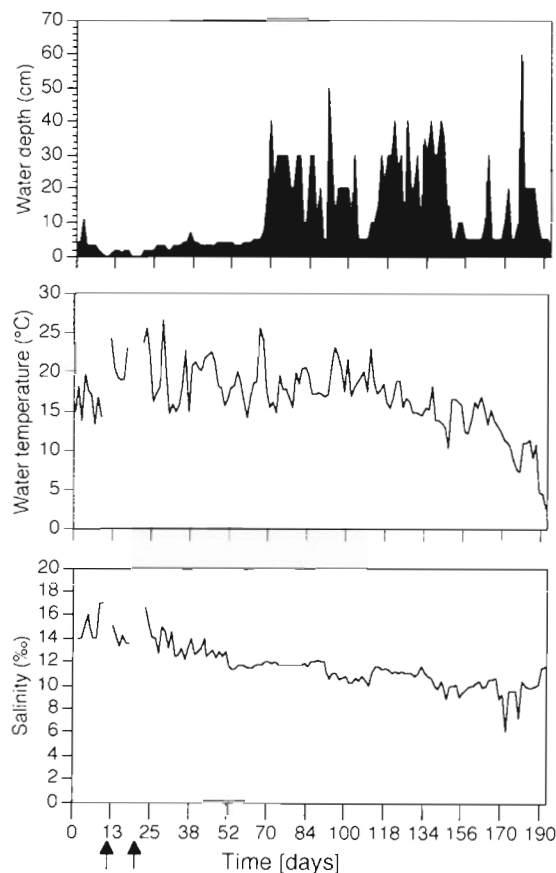


Fig. 1. Chemico-physical parameters at the study site in Wismar Bight over the experimental time from April to November 1993. Arrows indicate dry periods (water depth = 0 cm)

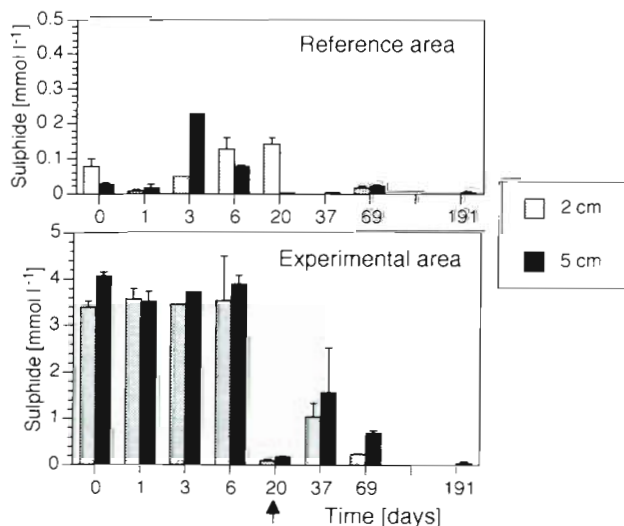


Fig. 2. Mean sulphide concentrations ($n = 3$) over the experimental time at 2 and 5 cm sediment depth in the reference and experimental areas in Wismar Bight. Arrow indicates dry period (water depth = 0 cm)

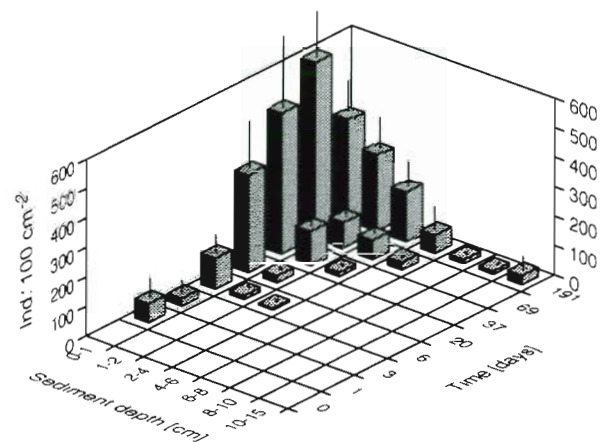


Fig. 3. Mean ($n = 4$) abundance and vertical distribution of total macrofauna over time in the experimental area after foil cover in Wismar Bight. Note non-linear time scale

sulphide were recorded at 2 cm sediment depth, while at 10 cm depth high concentrations (1.65 mmol l^{-1} sulphide, data not shown) were measured in all experimental areas. At the end of the experiment (after 191 d), reference and experimental areas had similar sulphide concentrations of $60 \text{ } \mu\text{mol l}^{-1}$.

Macrofauna

The macrobenthos of the study site consisted of 10, mainly deposit feeding species, which were abundant in the reference area throughout the experimental time. Dominating species were the ostracod *Cyprideis torosa*, the oligochaete *Paranais litoralis*, the gastropod *Hydrobia ventrosa* and the polychaete *Hediste (Nereis) diversicolor*. The bivalve *Cerastoderma edule*, the gastropod *Hydrobia ulvae*, the polychaetes *Manayunkia aestuarina*, *Streblospio benedicti* (shrubsolei) and *Polydora ciliata*, and the oligochaete *Nais elinguis* occurred only at low densities.

Colonisation via water column and sediment

The first colonisers of this experimental area were mainly adult immigrants settling in the upper sediment layer (Fig. 3). After 20 d from the onset of the colonisation experiment, abundance and number of species, diversity and evenness in the experimental area were still lower, but no longer significantly different from the reference area (Figs. 4 & 5). There were no pronounced seasonal variations during the experimental period in the reference area. After 69 d the total biomass reached the values found in the reference area.

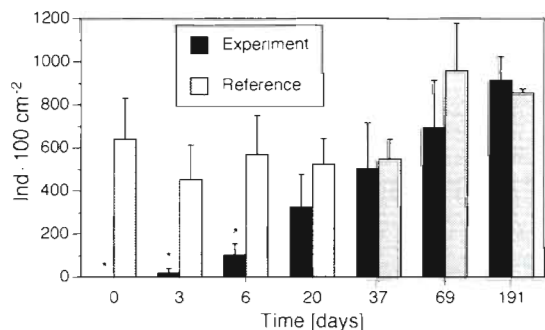


Fig. 4. Mean macrofauna density ($n = 4$) in the experimental and the reference area over experimental time in 'Wismar Bight'. Note non-linear time scale. *Significant differences ($p \leq 0.05$) between experimental and reference areas

Densities and vertical distribution of the 6 most abundant species in the experimental area over time are shown in Fig. 6. The ostracod *Cyprideis torosa* was one of the first species to appear on the experimental area after 1 d with a high abundance (25 ± 10 ind. 100 cm^{-2}), already comparable to densities in the reference area (33 ± 12 ind. 100 cm^{-2}). At this time, 3.56 mmol l^{-1} sulphide was still being measured at 2 cm depth. First specimens of the gastropod *Hydrobia* spp. were also found on the first day in the experimental area. On the study site *Hydrobia* spp. occurred as

the 2 species *H. ventrosa* and *H. ulvae*, in a proportion of 98 to 2. They will be referred to here jointly as *Hydrobia* spp. The polychaete *Hediste diversicolor* was represented by postlarval stages (body length less than 1 cm) and small juveniles (1 to 2 cm) only. They first appeared after 1 wk. An abundance comparable to the reference area was reached after 1 mo. The new settlers populated the sediment only in the upper 4 cm, while in the reference area they occurred down to 15 cm. Also, the tubificid oligochaete *Heterochaeta costata* (*Tubifex costatus*) showed a deeper vertical distribution in the reference area. In the experimental area it appeared in the upper sediment layer after 3 wk. The nauid oligochaete *Paranais litoralis* was found after 3 d in low abundances; 'normal' densities (as in the reference area) were reached within 3 wk. One of the last species colonising the experimental area was the amphipod *Corophium volutator*. First adults were found after 2 mo.

Colonisation via the water column

This experimental area showed the same sequence of species as described above. The ostracod *Cyprideis torosa* (28 ± 28 ind. 100 cm^{-2}) and the mudsnails *Hydrobia* spp. (5 ± 10 ind. 100 cm^{-2}) were the first species to occur, both being found after 1 and 2 d, respectively; the oligochaete *Paranais litoralis* appeared next, after 20 d. Even after 69 d of colonisation, the spectrum of species was limited to: *C. torosa* (70 ± 26 ind. 100 cm^{-2}), *Hydrobia* spp. (75 ± 60 ind. 100 cm^{-2}), *P. litoralis* (224 ± 101 ind. 100 cm^{-2}), juvenile *Hediste diversicolor* (8 ± 10 ind. 100 cm^{-2}) and *Corophium volutator* (6 ± 9 ind. 100 cm^{-2}). Thus, diversity (1.15) and evenness (0.71) remained significantly below values of the reference area.

Colonisation through the sediment

Also in this experimental area, *Cyprideis torosa* was the first species to appear (10 ± 12 ind. 100 cm^{-2} , second day of colonisation phase). Even after 69 d, the density of the reference area was not reached. After 20 d all endobenthic annelids were found, i.e. *Paranais litoralis* (51 ± 40 ind. 100 cm^{-2}), *Nais elinguis* (5 ± 10 ind. 100 cm^{-2}), *Heterochaeta costata* (10 ± 10 ind. 100 cm^{-2}) and *Hediste diversicolor* (5 ± 10 ind. 100 cm^{-2}). *Hydrobia* spp. occurred after 37 d in low density only (14 ± 10 ind. 100 cm^{-2}). After 69 d diversity (0.97) and evenness (0.7) were still significantly below the values for the reference area.

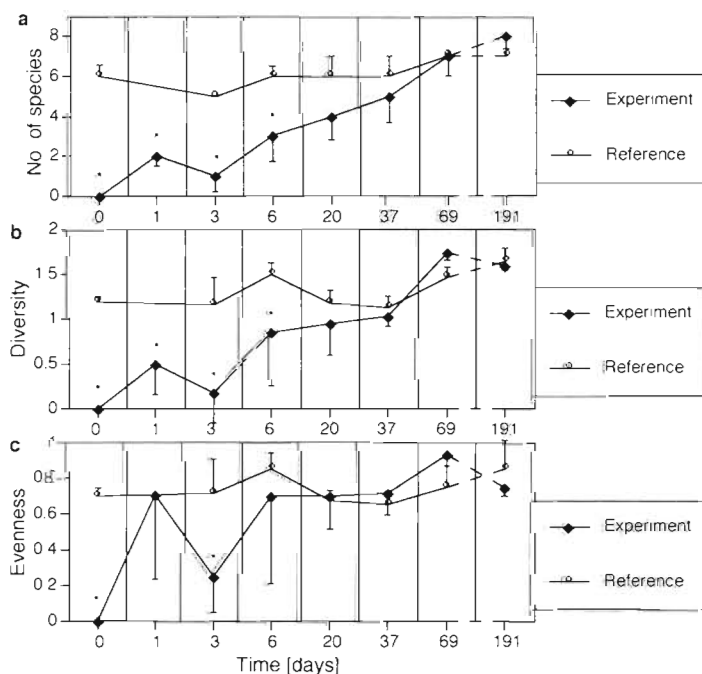


Fig. 5. (a) Number of species, (b) diversity and (c) evenness ($n = 4$) of the macrobenthic community in the experimental and the reference area over experimental time in Wismar Bight. Note non-linear time scale. *Significant differences ($p \leq 0.05$) between experimental and reference areas

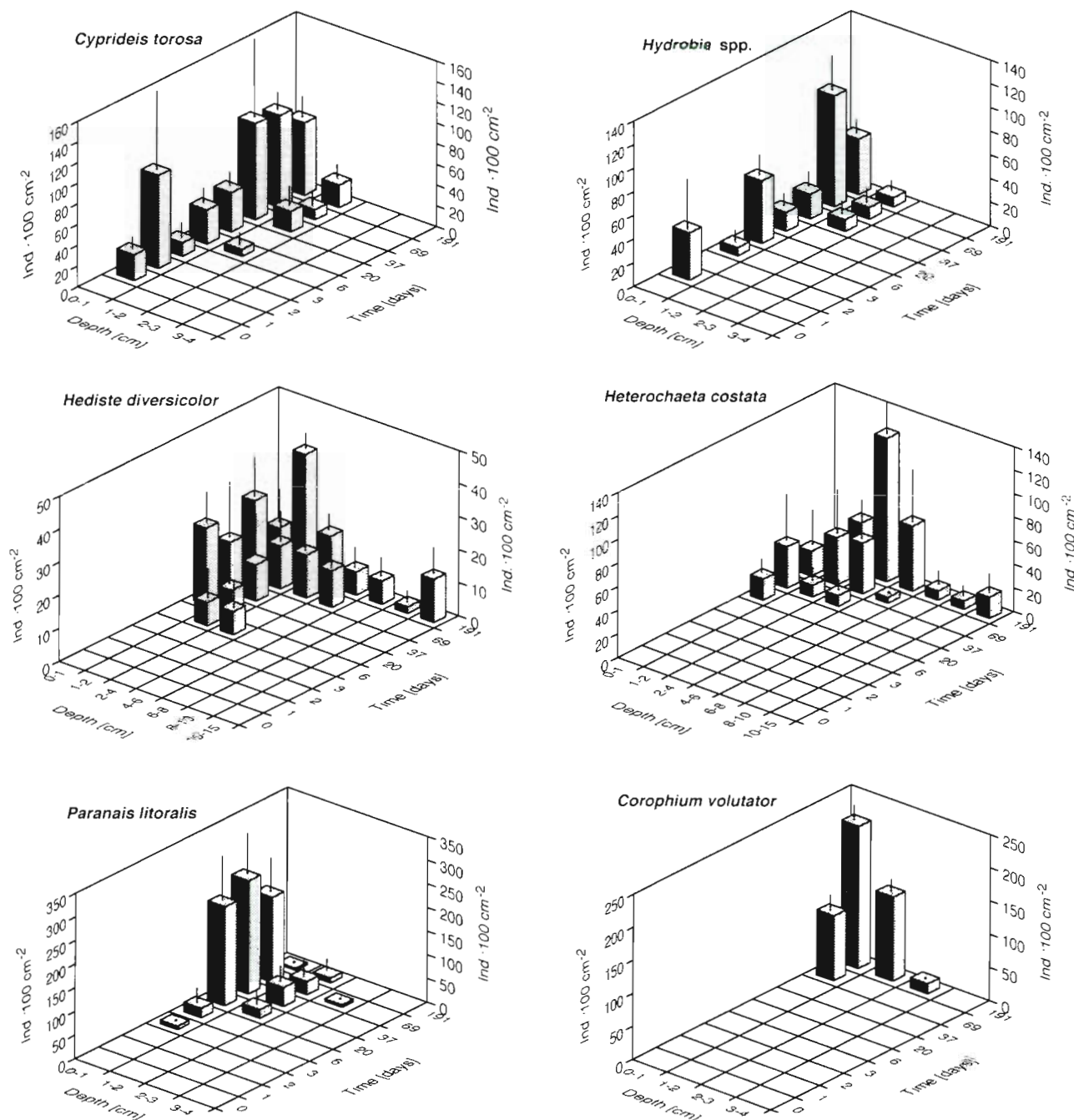


Fig. 6. *Cyprideis torosa*, *Hydrobia* spp., *Hediste diversicolor*, *Heterochaeta costata*, *Paranais litoralis*, *Corophium volutator*. Mean abundance ($n = 4$) and vertical distribution in the experimental area over time in Wismar Bight. Note non-linear time scale

Recovery and colonisation after algae coverage

Chemico-physical parameters

This experiment at Hiddensee Island was influenced neither by dry periods nor by extreme temperatures. Depth of overlying water ranged between 12 and

30 cm over the experimental time. Water temperature varied from 18°C at the experimental start in May to 9°C in September. Fluctuations of the overlying water in salinity ($9.7 \pm 1.1\text{‰}$, $n = 11$) and pH values (7.58 ± 0.41 , $n = 11$) were not substantial.

Content of POM in the upper horizons (0–2 cm) differed markedly between experimental and reference

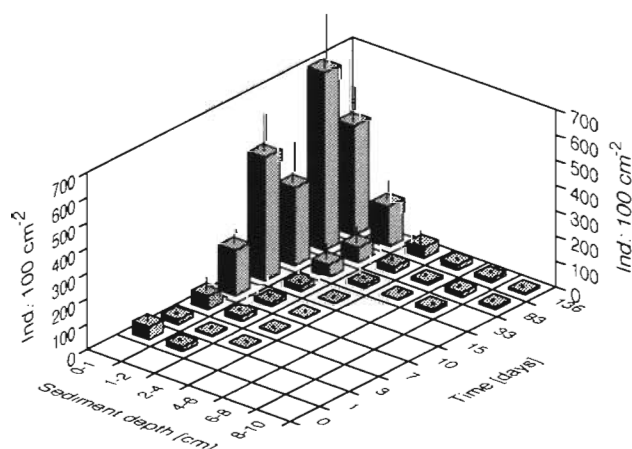


Fig. 7. Numerical abundance and vertical distribution of total macrofauna ($n = 4$) over time in the experimental area after algae cover near Hiddensee Island. Note non-linear time scale

area. In the experimental area, 5.3% was found, while the reference area contained only 1.5% organic material. The MDs of both areas were similar, with 279 μm in the experimental and 292 μm in the reference area. The sorting coefficient differed between 0.93 and 1.22, which in both cases signifies poorly sorted sediments.

In the experimental area the algae cover caused sediments free of macrofauna with high sulphide concentrations (2.75 mmol l^{-1}) at 5 cm sediment depth. This contrasted to the reference area with sulphide concentrations (up to 25 $\mu\text{mol l}^{-1}$) only in 10 cm sediment depth. During the recovery time sulphide concentrations decreased slowly but with no regularity in the experimental area (5 cm sediment depth) (Day 5: 1.4 mmol l^{-1} ; Day 7: 0.73 mmol l^{-1} ; Day 15: 0.33 mmol l^{-1} ; day 33: 1.5 mmol l^{-1}). After 83 d of recovery no marked differences in sulphide concentrations were recorded between the reference (11 $\mu\text{mol l}^{-1}$) and experimental (14 $\mu\text{mol l}^{-1}$) area.

Macrofauna

The macrobenthic community near Hiddensee Island consisted of 10 species. The dominating species were the ostracod *Cyprideis torosa*, the oligochaete *Paranais litoralis*, the gastropod *Hydrobia ventrosa* and the polychaete *Hediste diversicolor*. The polychaetes *Streblospio benedicti* (*shrubsoli*) and *Manayunkia aestuarina*, the mudsnail *H. ulvae*, the oligochaetes *Heterochaeta costata* and *Nais elinguis* and chironomid larvae occurred only at low densities.

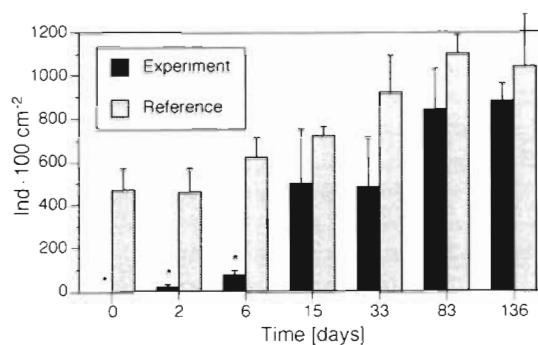


Fig. 8. Mean macrofauna density ($n = 4$) in the experimental and the reference area over experimental time near Hiddensee Island. Note non-linear time scale. *Significant differences ($p \leq 0.05$) between experimental and reference areas

Colonisation both via water column and the sediment

The first colonisers of the experimental area were adult immigrants settling at the upper sediment layer (Fig. 7). After 15 d, animal density, number of species, diversity and evenness in the experimental area were not significantly different from the reference area (Figs. 8 & 9).

Cyprideis torosa was one of the first species to appear on the experimental area. After 1 d it occurred

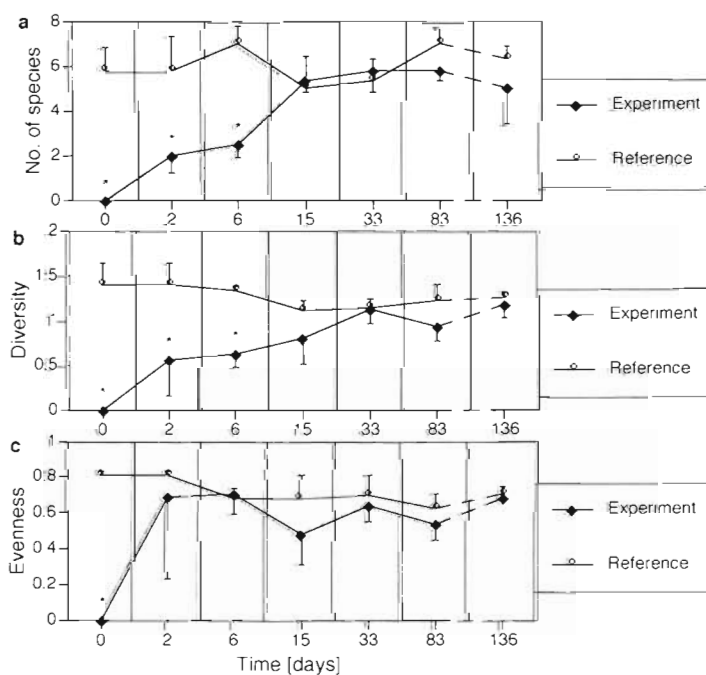


Fig. 9. (a) Number of species, (b) diversity and (c) evenness ($n = 4$) of the macrobenthic community in the experimental and the reference areas over experimental time near Hiddensee Island. Note non-linear time scale. *Significant differences ($p \leq 0.05$) between experimental and reference areas

at the remarkable density of 39 ± 15.5 ind. 100 cm^{-2} increasing to maximal values of 569 ± 171 ind. 100 cm^{-2} after 83 d (reference area: 541 ± 141 ind. 100 cm^{-2}). Also on the first day, first (adult) specimens of the mudsnail *Hydrobia* spp. were found. At this study site *Hydrobia* spp. occurred as the 2 species *H. ventrosa* and *H. ulvae* in a proportion of 90 to 10. The polychaete *Hediste diversicolor* was represented by postlarval stages and small juveniles, which appeared only sporadically within the first month. The oligo-

chaete *Paranais litoralis* was found after 2 d in low abundances; densities comparable to the reference site were reached after 15 d (22 ± 20 ind. 100 cm^{-2}). The tubificid oligochaete *Heterochaeta costata* appeared at the surface of the experimental area after 1 d; after 15 d it was found also in deeper sediment layers (down to 4 cm). After 33 d its vertical distribution corresponded to that in the reference area (down to 10 cm). As in Wismar Bight one of the last species appearing in the experimental area was the amphi-

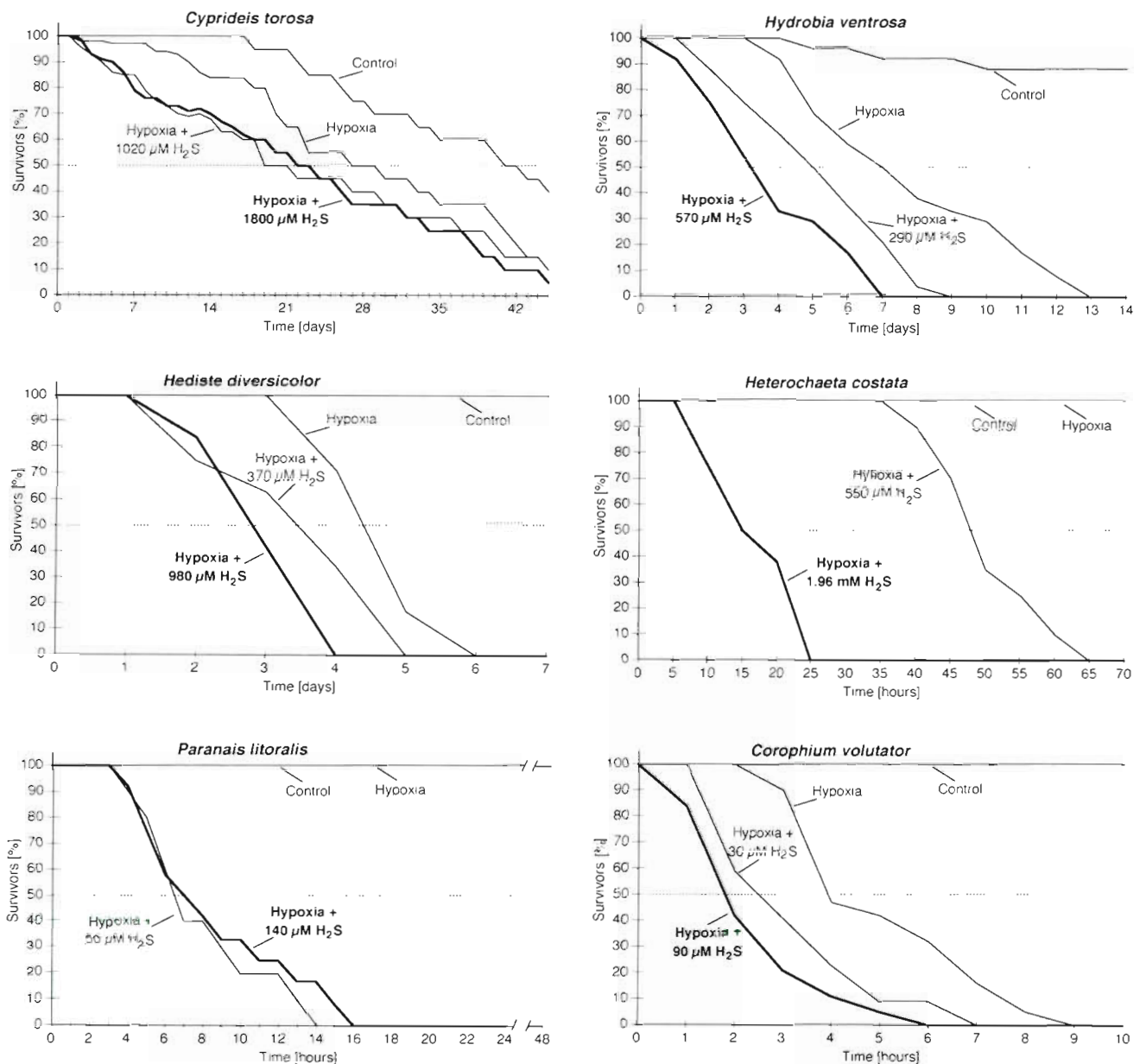


Fig. 10. *Cyprideis torosa*, *Hydrobia ventrosa*, *Hediste diversicolor*, *Heterochaeta costata*, *Paranais litoralis*, *Corophium volutator*. Surviving animals (%) as a function of time when exposed to hypoxia and hypoxia plus sulphide. Note different time scales

pod *Corophium volutator*. A few adults (3 ± 2 ind. 100 cm^{-2}) were found after 1 mo, but they were absent again after 83 d.

In the experimental area the densities of colonising macrozoobenthic species never exceeded values in the reference area.

Tolerance experiments

Corresponding to their colonisation pattern, the tolerance (% survivors) of 6 species to hypoxia and hypoxia plus sulphide was investigated (Fig. 10). The most resistant species of the assemblage was the ostracod *Cyprideis torosa*. Under hypoxia, its 'mean lethal time' (LT_{50} rate, $n = 4$) was about 4 wk (27 ± 2 d). Under hypoxia plus 1.8 mmol l^{-1} sulphide this species still survived for 3 wk (22 ± 7 d). No significant differences in survival time were found between hypoxic treatments and different sulphide concentrations. In the first days of the incubations the ostracods kept their mobility at all treatments. The mudsnail *Hydrobia ventrosa* survived hypoxic conditions for approximately 1 wk; the addition of $570 \text{ } \mu\text{mol l}^{-1}$ sulphide reduced its LT_{50} rate significantly to 3 d (75 ± 4 h, $n = 3$). Juvenile specimens (body length 1.7 ± 0.3 cm, $n = 16$) of the polychaete *Hediste diversicolor* showed a LT_{50} rate of about 4 d (105 ± 10 h, $n = 3$) for hypoxia and survived 1 mmol l^{-1} sulphide for 3 d (72 ± 6 h, $n = 3$). Here, no significant differences in mortality rate were found between exposure to solely hypoxic and hypoxic plus sulphidic conditions. Postlarval *H. diversicolor* (body length 0.7 ± 0.2 cm, $n = 16$) showed less tolerance to hypoxia and sulphide. They survived (LT_{50} rate) hypoxic conditions for 14 h and hypoxia plus $270 \text{ } \mu\text{mol l}^{-1}$ sulphide for 10 h (1 experimental run, data not shown). The tubificid oligochaete *Hete-*

rochaeta costata was not affected by hypoxic conditions for at least 3 d. In contrast, the addition of sulphide (1.96 mmol l^{-1}) caused mortality after 1 d (Fig. 6). The naidid oligochaete *Paranais litoralis* survived hypoxia at least for 2 d without any mortality, but low doses of $50 \text{ } \mu\text{mol l}^{-1}$ sulphide reduced its survival time to 7 ± 2 h ($n = 4$). The most sensitive species to hypoxia and sulphide was the amphipod *Corophium volutator*. Under hypoxic conditions it survived (LT_{50} rate) for 4 h; when $90 \text{ } \mu\text{mol l}^{-1}$ sulphide was present, *C. volutator* survived for only 2 h. Average LT_{50} rates compiled for all species tested under hypoxia plus sulphide are summarized in Fig. 11.

DISCUSSION

Colonisation experiments in the field

Adverse ecological conditions delayed the consortium of species returning to the experimental areas:

- Anoxia and high sulphide concentrations even at the sediment surface,
- Strong variations of abiotic parameters and dry periods in one experiment,
- A considerable organic enrichment after algal coverage.

Nevertheless, both experimental areas were repopulated by macrofauna in a highly comparable pattern. As soon as 1 mo later the disturbed areas were not significantly different from their reference areas (identical species composition, diversity and abundance). Regular inhabitants of these Baltic shore habitats are euryoecious, opportunistic species, well adapted to extreme ecological conditions by their high 'recolonisation potential'.

Which factors were responsible for this high resilience of the ecosystem? Presumably, colonisation was facilitated by the small size of the defaunated areas. This can be deduced from other small-scale colonisation studies where faunal abundance and species number increased inversely to the size of the experimental area (Smith & Brumsickle 1989). Bonsdorff & Österman (1985) also attributed rapid colonisation to a short immigration distance.

Colonisation of the disturbed areas was accomplished mainly by adult immigrants from the surrounding populations, both via the water column and through the sediment. Many recolonisation studies documented postlarval and adult dispersal as the primary route of early colonisation (Dauer & Simon 1976a, Pearson & Rosenberg 1978, Smith &

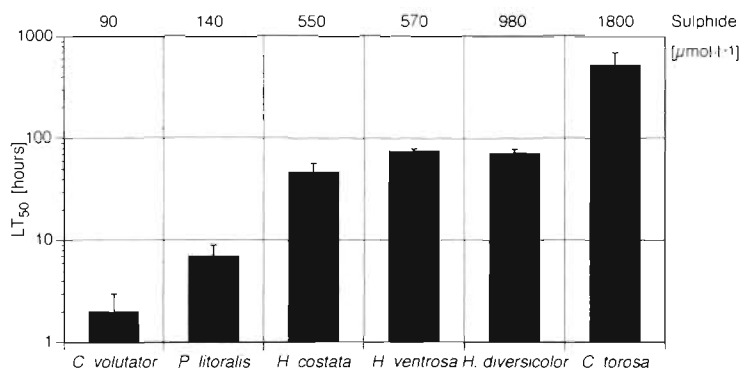


Fig. 11 *Cyprideis torosa*, *Hydrobia ventrosa*, *Hediste diversicolor*, *Heterochaeta costata*, *Paranais litoralis*, *Corophium volutator*. Comparison of mean survival rates (LT_{50}) at hypoxia and different sulphide exposure. For further details see Table 1

Brumsickle 1989). Although the process is certainly also taxon-specific, Santos & Simon (1980) assumed that small areas (on the scale of cm²) become predominantly repopulated by adults entering laterally from the nearby sediments. Another factor controlling colonisation pathways (via planktonic larvae or benthic stages) seems to be water depth and exposure to currents. A strongly mixed water column with agitation and resuspension of sediment, as occurring frequently in the shallow Baltic areas investigated here, may substantially contribute to the colonisation rate by drift of 'tychoplanktonic' benthos or 'hyperbenthos'. There was evidence of this pathway of colonisation in the first experiment, although it could not be quantitatively evaluated due to intermittent dry periods in the area.

The early colonisation of adult specimens of *Hydrobia* spp. is probably based on their high dispersal capacity through drift by adhering to the surface film of the water (Siegismund & Hylleberg 1987) and on their high physiological tolerance (see below). Norkko & Bonsdorff (1996) described *Hydrobia* spp. as the macrobenthic species dominating the recovery process. Similarly, the regular presence of *Paranais litoralis* in shores with frequent 'sulphide conditions' is most likely based on its ability to escape adverse oxygen/sulphide conditions by drifting in the overlying water. Moreover, as in other nauid species, possible mass mortality can be quickly compensated by its asexual multiplication through paratomy (budding off zooids; Giere & Pfannkuche 1982). In contrast, the burrowing annelids *Hediste diversicolor* and *Heterochaeta costata* colonised the experimental area through the sediment only.

Corophium volutator, another endobenthic species, became progressively inhibited from burrowing at higher concentrations of hydrogen sulphide. Hence, its survival seems solely based on avoidance and escape reactions. More than in all the other species encountered at the study site, its colonisation ability is based on its high mobility despite its physiological sensitivity to hypoxia and sulphide (see below).

Consequently, the rapid colonisation in our study can be assigned to a combination of biotic adaptations and physically favorable factors: a consortium of few species well adapted to frequent small-scale disturbance, a favourable season for population development, an area small enough for immediate colonisation by adults, and a hydrographic regime favoring suspension and drift.

An often discussed aspect in benthic colonisation studies is the sequence of species re-appearing in a disturbed area. Generalized successional patterns in benthic soft-bottom systems have been inferred (Bonsdorff 1980): initial colonisation with dominance of

opportunists arriving early, multiplying their population stock rapidly, and expanding their habitat due to a high dispersive capacity (Dauer & Simon 1976b, Pearson & Rosenberg 1978, Bonsdorff 1980, Arntz & Rumohr 1982, Chesney 1985). In most soft-bottom communities polychaetes, through high mobility and/or with an opportunistic life history, are the most rapid colonists and are regarded as typical pioneer species (Simon & Dauer 1977, Bonsdorff 1980, Diaz & Rosenberg 1995).

However, in the present experimental study a clear sequence of colonising species corresponding to this contention was not recognizable. Apparently, in an area characterized by fluctuating ecofactors, the inhabitants have to be highly 'stress-tolerant' and stress-preconditioned to meet the frequent environmental impairments. Consequently, a transition from mostly *r*-selected pioneer species to *K*-selected specialists cannot develop (Diaz & Rosenberg 1995) and the opportunistic coenosis of both study sites remains in an early successional stage (Boesch & Rabalais 1991). This ecological situation and the small size of the experimental areas do not allow for deduction of general successional rules as described before.

Large and complex field experiments like the ones presented here can rarely be conducted in sufficient replicates to meet statistical requirements. This inherent shortcoming is to some extent compensated here by the close match of the colonisation data and sequence between the 2 field experiments and, additionally, with those of the tolerance tests (see below). The validity of our results is confirmed also by the closely corresponding 'sequence of disappearance' under the impact of induced hypoxia and hydrogen sulphide (authors' unpubl. experimental data).

Tolerance experiments

The sequence of colonising species in our study matches their tolerance to hypoxic and sulphidic conditions. The species appearing first in all experimental areas, e.g. *Cyprideis torosa*, were the ones with highest survival time under hypoxic and sulphidic conditions. In contrast, sensitive species like the amphipod *Corophium volutator* were not found on the experimental areas before conditions had markedly improved.

Although LT₅₀ experiments with their debatable criteria for mortality are ecologically problematical, in this case the close match with the field experiments is striking and confirms their ecological validity. Under natural conditions, a differentiation between paralysed, moribund or dead specimens is often redundant since these animals, regardless of such differences in condition, will be outcompeted or devoured.

Cyprideis torosa is known for its occurrence in extreme biotopes and its marked resistance to salinity changes and high temperatures (Arndt 1973). In addition, we can now document high survival rates under hypoxia and sulphide. The physiological basis of this high tolerance and the adaptational flexibility of *C. torosa* to hypoxia and sulphide was investigated by Jahn et al. (1996). In experiments its (low) mortality rate was presumably more influenced by starvation (indicated by the tolerance curve in the normoxic controls; Fig. 10) than by tolerance of hypoxia and sulphide (see similar arguments for *Capitella capitata*; Diaz & Rosenberg 1995). This means that *in situ* survival rates of *C. torosa* could be, in fact, even higher. The ostracod *C. torosa* can survive the adverse conditions of the study area by its high physiological tolerance combined with its mobility which it retains under sulphidic conditions.

The high tolerance of *Hydrobia ventrosa* to hypoxia and sulphide found in our laboratory experiments exceeds survival rates obtained by Lassen & Kristensen (1978) who tested mudsnails from biotopes with anaerobic sediment and dense growth of purple sulphur bacteria.

The polychaete *Hediste (Nereis) diversicolor* is known as an euryhaline species from areas with high variations in abiotic parameters (e.g. salinity). It seems well adapted to eutrophic waters (Cognetti 1982, Arndt 1989). Our laboratory data proved that the high tolerance to hypoxia and sulphide of juvenile *H. diversicolor* paralleled that of adults. Supportive data on adults have been presented by Theede et al. (1969) who, additionally, found the resistance to vary according to conditions in the respective 'home habitats'. When exposed to a combination of salinity changes and hypoxia plus sulphide (Theede et al. 1973, Vismann 1990) *H. diversicolor* was found the best adapted among various nereid species.

The oligochaete *Heterochaeta costata* lives predominantly in deeper sediment layers, but, unlike *Hediste diversicolor*, without building a permanent tube. Thus this species is directly exposed to considerable sulphide concentrations. In this respect it corresponds to the other common marine macrobenthic tubificid, *Tubificoides benedii*, that also occurs in deeper layers where sulphide is present in high concentrations (e.g. Pearson & Rosenberg 1978, Dubilier et al. 1995, Thiermann et al. 1996). In both tubificids, tolerance experiments for sulphide and hypoxia (Dubilier 1993, present study) underlined their adaptation to an endobenthic life under these extreme conditions.

The hardness of the aforementioned tubificid oligochaetes is not paralleled by the nauidid oligochaete *Paranais litoralis*. Although this mostly epibenthic and frequently suprabenthic species survived hypoxia for

longer without any mortality, its survival time dropped drastically after exposure to sulphide.

The amphipod *Corophium volutator* was most sensitive to hypoxia and sulphide judging from both the field colonisation and tolerance experiments. A pronounced sensitivity of *C. volutator* to sulphide has also been described by Meadows et al. (1981) who showed that it avoided sediments containing more than $50 \mu\text{mol l}^{-1}$ sulphide.

Our tolerance experiments confirmed the general rule that sulphide combined with hypoxia is more toxic than hypoxia alone (Diaz & Rosenberg 1995). On the other hand, they underline a possible discrepancy between opportunistic species and *r*-strategists. The biological properties of *Corophium volutator* and of the previously discussed nauidid species demonstrate that species well capable of an effective colonisation, and consequently often termed opportunistic or pioneering, do not necessarily represent *r*-strategists. Physiological sensitivity and, in *C. volutator*, a low reproductive potential (brood protection), contradicting the concept of opportunistic species, can well occur among colonisers.

Conclusions

The rapid colonisation of the defaunated experimental areas on the Baltic shore by macrozoobenthos is influenced by an interacting combination of biotic properties and favourable abiotic conditions. Well adapted to frequent disturbances of chemico-physical factors, a limited number of euryoecious species are highly tolerant to hypoxia and high sulphide concentrations that occur repeatedly under natural conditions, and/or the species possess the potential of high mobility, effective dispersal or rapid asexual reproduction. Usually the sediment patches which become defaunated (mostly covered by algae or cyanobacterial mats during warm periods and minimal water exchange) remain small with intermittent normally populated areas of high recruitment potential. Moreover, the variable currents in a shallow water system usually limit the duration of 'sulphide conditions' to brief periods, allowing for quick recolonisation (Diaz & Rosenberg 1995). The colonisation process, completed in the present experiments within 1 mo, closely reflects our data from tolerance experiments to hypoxia and sulphide exposure. This proves that in shallow coastal sites of the Baltic Sea these ecological stressors structure the macrozoobenthic coenosis. Here, oxygen deficiency and sulphide repeatedly dominate the ecosystem without long-lasting devastation of the stress-preconditioned and well-adapted macrobenthic community.

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