

Succession in marine benthic habitats and fauna in response to oxygen deficiency: analysed by sediment profile-imaging and by grab samples

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ABSTRACT: This study shows, for the first time, *in situ* images of changes in marine benthic habitats in response to oxygen deficiency. Tight coupling is demonstrated between gradual degradation of benthic habitat and faunal behaviour, species richness, abundance and biomass. The critical oxygen level that forced changes in the benthic faunal successional stages was ~10% that of air saturation (~0.7 ml O₂ l⁻¹). Before this critical saturation level was reached, tube-building polychaetes their tubes extended higher into the water column, the width of the sub-oxic sediment layer decreased, and vertical animal burrows (formerly oxidised and brown in colour) became sulphidic and black. Over a 10 mo hypoxic period (June 1997 to April 1998) in the Gullmarsfjord (Swedish west coast), benthic community successional stages declined from equilibrium to virtually azoic conditions. As normoxic conditions returned, pioneering stages gradually recolonised the area.

KEY WORDS: REMOTS · SPI · Hypoxia · Anoxia · *Melinna cristata*

INTRODUCTION

Riverine inputs of nitrogen in many temperate regions have increased greatly since pre-industrial times, e.g. in the North Sea by 6- to 20-fold (Howarth et al. 1996). In addition to this and other nutrient inputs, organic enrichment of sediments in coastal areas is increasing worldwide (Rosenberg 1985, Nixon 1995). In stratified and partly enclosed waters, areas with low oxygen concentrations critical for marine bottom-living animals are expanding, which has a negative impact on fisheries (Caddy 1993, Diaz & Rosenberg 1995). In areas where benthic fauna has been reduced or even eliminated, sediment chemistry, including nutrient fluxes, is changing significantly, with consequences for the ecosystem (Aller 1988).

Structural changes in soft-bottom benthic communities resulting from organic enrichment have been modelled by Pearson & Rosenberg (1978), who demonstrated how species-abundance-biomass (SAB) curves and faunal distributions in the sediment change along

a gradient from excess organic input to 'normal' conditions (Fig. 1). This generalised successional model has also been shown to hold for physical disturbance (Rhoads & Germano 1986) and to apply generally to disturbed sublittoral benthic communities (Heip 1995).

Since the pioneering work of Rhoads & Cande (1971) and Rhoads & Germano (1982), sediment-profile imaging, SPI, (Fig. 1) has proved useful in demonstrating benthic habitat changes connected with physical disturbance (Rhoads & Germano 1986, Rumohr & Schomann 1992), organic enrichment (O'Connor et al. 1989), low salinities (Bonsdorff et al. 1996), and low oxygen concentrations (Schaffner et al. 1992, Nilsson & Rosenberg 1997). The effects of oxygen deficiency on the behaviour of benthic fauna at the sediment surface (Dethlefsen & von Westernhagen 1983, Stachowitsch 1984) and the presence of sulphur bacteria (Rosenberg & Diaz 1993, Rumohr 1993) have also been documented by *in situ* photography. One advantage of SPI over traditional grab sampling methods is that the organism-sediment relationship is lost in grab samples when the sediment sample is processed (Rhoads & Germano 1982).

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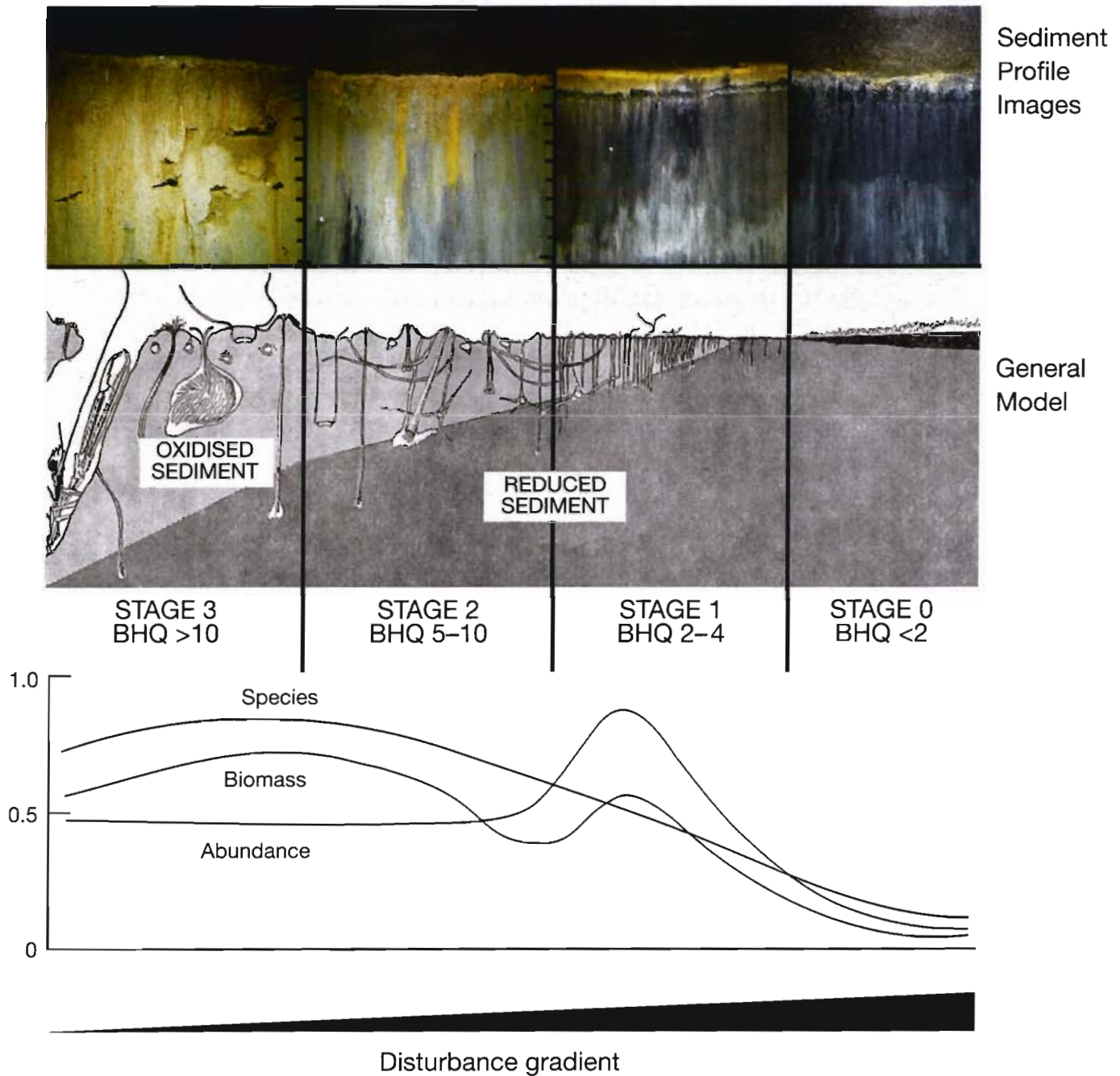


Fig. 1. Distribution of benthic infaunal successional stages along gradient of increasing environmental disturbance (from left to right) (after Pearson & Rosenberg 1978), and associated benthic-habitat quality (BHQ) index (Nilsson & Rosenberg 1997). Sediment-profile images assigned to successional stage are shown above the general model (colours digitally enhanced); oxidised sediment is rust-brown, and reduced sediment grey or black. Bottom graph illustrates generalised changes in species, abundance, and biomass (after Pearson & Rosenberg 1978)

To summarise *in situ* data concerning the benthic habitat, Rhoads & Germano (1986) developed an organism-sediment index (OSI), which is calculated from the SPIs combined with measurements of dissolved oxygen over the bottom sediment. In addition to oxygen recordings, their index is based on the mean ap-

parent depth of the redox potential discontinuity (RPD; Fenchel & Riedl 1970), subjective assessment of the faunal successional stages (similar to the example in our Fig. 1), and the presence or absence of sedimentary methane. The index ranges between -10 and +11. In a recent paper, Nilsson & Rosenberg (1997) sug-

gested another method for assessing successional stages of the benthic habitat, whereby surface and sub-surface structures together with the mean depth of the apparent RPD are assessed and summarised as a benthic-habitat quality (BHQ) index, ranging between 0 and 15 (Table 1). The BHQ index is related to the faunal successional stages in Fig. 1, and we will demonstrate in our study that it is correlated with SAB curves.

This study analyses *in situ* SPIs of infaunal behaviour in relation to benthic-habitat responses to declining and low oxygen concentrations over a 10 mo period. These analyses are compared with changes in SAB parameters obtained from grab samples taken every second month during the same 10 mo period. The study was carried out at 6 stations (60 to 118 m bottom depth) in the deeper parts of the Gullmarsfjord on the Swedish west coast (Fig. 2), where salinity is ~34.5 psu and temperature 4 to 8°C. Sediments are similar at all stations, being composed predominantly of clay with ~3% organic carbon and 0.3% nitrogen. The Gullmarsfjord has a sill at 40 m and a maximum depth of 118 m. The stagnant bottom water is usually renewed with cold, oxygen-rich deep water annually each spring. In 1997, however, this bottom-water exchange failed to occur, and dissolved oxygen content continued to decrease to <10% saturation at depths >80 m

Table 1. Calculation of the benthic-habitat quality (BHQ) index from sediment-profile images ($BHQ = \sum A + \sum B + C$, where A = surface structures, B = sub-surface structures, and C = mean sediment depth of apparent redox potential discontinuity, RPD. BHQ values vary between 0 and 15, and BHQ index corresponds to various successional stages in Fig. 1

Faunal and sediment structures		BHQ
A: Surface structures		
	Faecal pellets	1
	Tubes ≤ 2 mm diam. ^a	1
or	Tubes > 2 mm diam. ^b	2
	Feeding pit or mound	2
B: Sub-surface structures		
	Infauna	1
	Burrows # 1-3	1
or	Burrows # >3	2
	Oxic void at ≤ 5 cm depth	1
or	Oxic void at > 5 cm depth	2
C: Mean depth of apparent RPD		
	0 cm	0
	0.1-1.0 cm	1
	1.1-2.0 cm	2
	2.1-3.5 cm	3
	3.6-5.0 cm	4
	5 cm	5

^ae.g. *Euchone* sp., *Polydora* sp.
^be.g. *Melinna* sp. Terebellidae sp., Ampharetidae sp., *Rhodine* sp.

(Fig. 3). It was not until January 1998 that a slight increase in oxygen saturation was recorded, followed by a major exchange of bottom water in the spring.

MATERIAL AND METHODS

Beginning in June 1997, 3 replicate SPIs and 3 grab samples were collected bi-monthly from the same single stations at each of 6 depths (60, 75, 85, 95, 105 and 118 m; Fig. 2) until April 1998. The 2 shallow stations were used as reference stations, since oxygen saturation here was comparatively high (generally >30%; Fig. 3). These stations were compared with 4 stations between 85 and 118 m which had lower oxygen saturations and exhibited increasing effects on sediment and fauna with increasing depth. At the beginning of the study in June 1997, the fauna appeared to be relatively unaffected by low oxygen concentrations down to 95 m depth, whereas at the deeper stations, where oxygen saturation had been <10% for several months, the fauna had been affected (see second subsection of 'Results'). *In situ* SPIs were taken through a prism (30 × 22 cm; Rosenberg & Diaz 1993) penetrating ~12 cm into the sediment. The contrast of the colours was digitally enhanced in Adobe Photoshop 4.0; the depth of the mean apparent RPD was analysed in NIH image 1.6. From each image, a BHQ index was calculated. This index parameterises sediment structures, sub-surface structures, and the apparent depth of the RPD (Table 1), and is related to the faunal successional stages of the Pearson-Rosenberg model (Fig. 1; and Nilsson & Rosenberg 1997). The lengths of *Melinna cristata* tubes above the sediment surface were digitally measured in the SPIs, a total of 119 tubes in 65 images. In images containing several visible tubes close to the prism, a maximum of 2 randomly chosen tubes were measured in each image. Macrofauna was collected with a 0.1 m² Smith-McIntyre grab (1 mm sieve), and biomass is given as formalin wet weight.

Statistical analyses were made of changes in mean number of species, total abundance, total biomass, and BHQ indices before and after minimum oxygen saturation (November/December 1997) occurred. The statistical test was a nested 3-way analysis of variances (ANOVA), with 'station' and 'before/after' as fixed factors and 'time' as a nested factor in station and before/after. Multiple comparisons of means were performed using the Student-Newman-Keuls (SNK) procedure. Homogeneity of variances was examined with Cochran's C-test, and gross heterogeneity was removed by log(x+1) transformation. Numerical similarity between macrofauna samples was analysed by multi-dimensional scaling (MDS) based on the Bray-

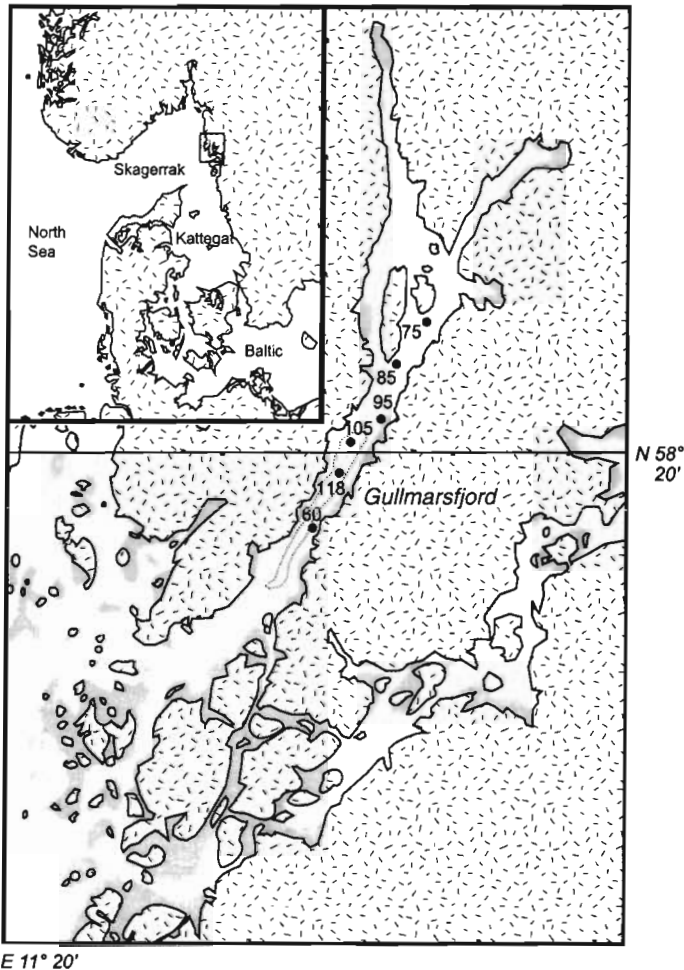


Fig. 2. Location of stations in Gullmarsfjord; numbers are depths at sampling sites

Curtis similarity index after \sqrt{V} transformation (Clark & Warwick 1994). Correlations between BHQ index and number of species, total abundance, and biomass were analysed by simple linear correlation [$\log(x+1)$].

RESULTS

Sediment-profile imaging

Fig. 4 shows the sediment habitat-succession in response to low oxygen saturations as SPIs from sites at depths of 75, 85 and 95 m (Fig. 4). At 60 and 75 m, the upper, rust-brown, sub-oxic layer extended deeper than 3 cm below the sediment surface during the entire

period. At 85 and 95 m, SPIs from stations in June through October 1997 were similar in appearance to that at 75 m as far as RPD, feeding voids and deep vertical-burrow structures. However, at 85 and 95 m, worm tubes extended several centimetres higher into the water column. The contents of the grab samples suggest that these tubes contained *Melinna cristata*. This species constructs clay tubes that can extend 20 cm vertically into the sediment as indicated in many of the images in Fig. 4. The lengths of the tubes above the sediment in the SPIs were measured and were related to the prevailing oxygen saturations (Fig. 3). At saturations $>25\%$ maximum tube lengths were ≤ 1.7 cm (Fig. 5). At saturations $\leq 15\%$ tube lengths were variable, maximum lengths generally increasing with declining oxygen saturation. A maximum tube length of ~ 9 cm was recorded at $\sim 7\%$ oxygen saturation. At 75 m, elongated tubes above the sediment surface were also seen in December 1997 (Fig. 4), but 2 mo later, as oxygen saturation improved, these appeared to have returned to their normal length. It appears that *M. cristata* can extend its tube higher into the water column, probably by lengthening it; it can probably also cut off the top of its tube. The SPIs from December 1997 and February 1998 at 85 and 95 m show *M. cristata* tubes bent and collapsed on the surface, and a worm that appears to be dead is visible in the 95 m image of December (Fig. 4). Presumably the tubes collapse after the worms die, since worm density thereafter declined in the grab samples (see below). The burrows now appeared black and re-

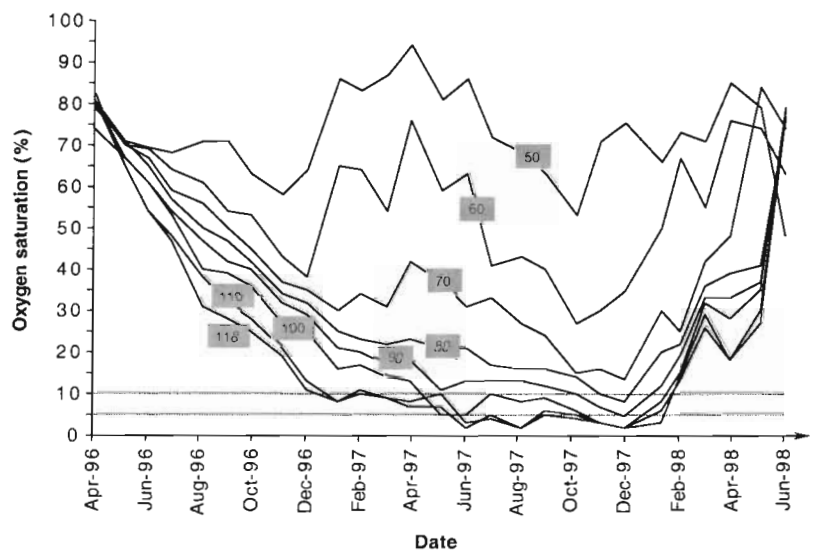


Fig. 3. Temporal changes in oxygen saturation (%; Winkler analysis) from April 1996 to June 1998 at depths between 50 and 118 m (bottom) measured in water at the deepest part of Gullmarsfjord, west Sweden

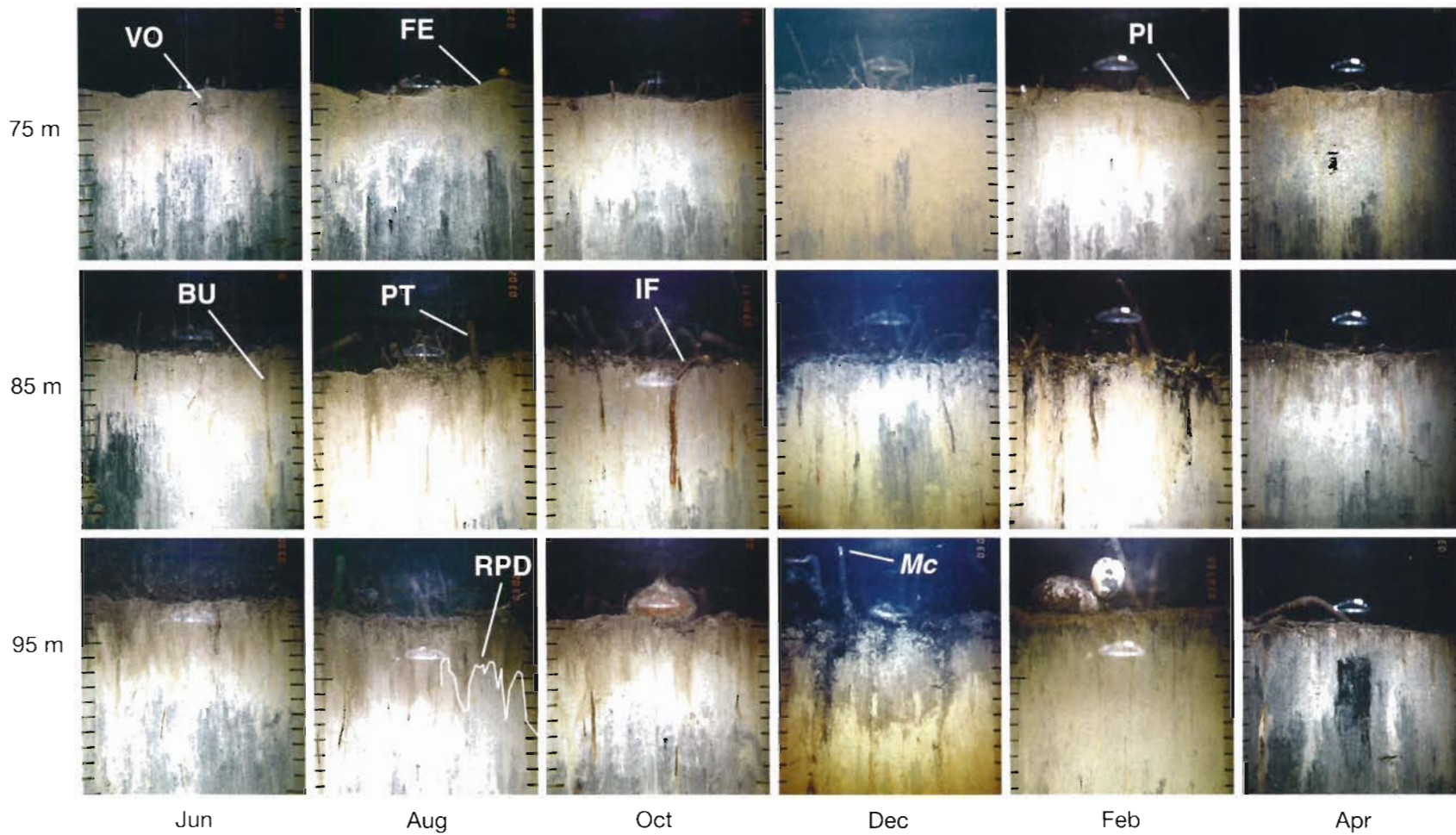


Fig. 4. Sediment-profile images (SPIs) from June 1997 through April 1998 at 75, 85 and 95 m depth in Gullmarsfjord. Scales on left in centimetre intervals. BU: burrow; FE: fecal pellets; IF: infauna; Mc: body part of what appears to be a dead *Melinna cristata*; PT: polychaete tube; RPD: redox potential discontinuity; VO: feeding void. Halo is an artefact (reflection); colours in images are computer-enhanced; those for December appear slightly different because of the addition of anti-freezing liquid to prism

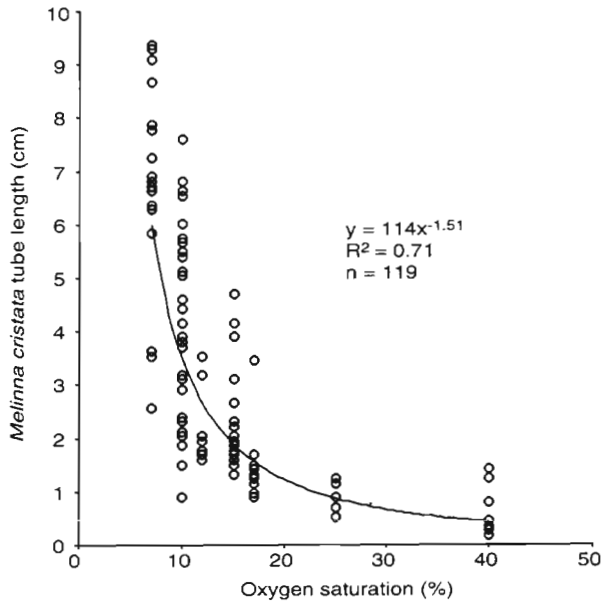


Fig. 5. *Melinna cristata*. Lengths of tubes above sediment surface, measured from SPIs. Lengths are presented as a function of estimated oxygen saturations in Fig. 3 at the time images were taken. Each data point represents individual measurement of 1 tube, and curve is the best-fit power function

duced, as did the sediment surface, resulting in a narrower sub-oxic zone. At 95 m, in October 1997, a live heart sea-urchin, probably *Brissopsis lyrifera*, had emerged onto the sediment surface (Fig. 4). Later, in February, 2 dead sea-urchins were visible in an image from the same depth (Fig. 4). In June 1997 at 105 m depth, the mean apparent RPD was ~3 cm, but the sediment turned black in August 1997. No RPD was observed at 118 m before April 1998, when a recently sedimented, spring phytoplankton-bloom was visible in the top layer at depths >85 m.

Species, abundance and biomass

The 5 dominant species at all stations from the beginning and end of the survey are listed in Table 2. Among the dominants at the 2 shallow stations were the polychaetes *Heteromastus filiformis*, *Melinna cristata* and *Spiophanes krøyeri*, the bivalves *Abra nitida*, *Thyasira equalis* and *T. sarsi*, and the brittle stars *Amphiura chiajei* and *A. filiformis*. *M. cristata* and *T. equalis* appeared to be among the organisms most tolerant to low oxygen concentrations: they survived at 95 m until April 1998 (Table 2) and occurred sparsely at 105 m depth even after 6 mo of exposure to oxygen saturations of <10%. The polychaete *Capitella capitata* was the dominant coloniser of deeper bottoms in spring 1998, while the nemertean *Hubrechtella dubia* colonised 85 and 95 m depths.

At 60 and 75 m depth there was comparatively little temporal change in the number of species and abundance, except for some recruitment during summer and autumn (Fig. 6). At 85 and 95 m, however, a decrease in both species richness and abundance occurred between October and December 1997. This decline coincided with a further drop in oxygen saturation to <10%. Thus, the critical oxygen saturation for survival of most benthic animals seems to be ~10%. At the 2 deepest stations, such critical oxygen concentrations were present before the first sampling in June 1997 (Fig. 3). Biomass largely followed patterns similar to species and abundance, but with low values being recorded at 95 m as early as mid-1997. No macrofauna was found at 118 m between August 1997 and February 1998, nor at 105 m in December 1997 and February 1998.

Significant interactions between station and occurrence of the oxygen minimum were observed in total

Table 2. Mean abundance (ind. m⁻²) of 5 dominant species at each station (depth) in Gullmarsfjord in June 1997 and April 1998

Taxa	60 m		75 m		85 m		95 m		105 m		118 m	
	Jun 97	Apr 98	Jun 97	Apr 98	Jun 97	Apr 98	Jun 97	Apr 98	Jun 97	Apr 98	Jun 97	Apr 98
<i>Abra nitida</i>	77	80	420	477	27		10					3
<i>Amphicteis gunneri</i>		17	13	50	33		103					
<i>Amphiura chiajei</i>	293	410	77	43								
<i>Amphiura filiformis</i>	323	367	97	107	7							
<i>Capitella capitata</i>	10					43	407		960			1300
<i>Heteromastus filiformis</i>	600	450	470	790	187	13	3	17	3	20		
<i>Maldane sarsi</i>	3		53	323		3						
<i>Melinna cristata</i>	100	287	127	230	170	207	263	63	87			3
<i>Hubrechtella dubia</i>	53	73	7	117		180		320			3	
<i>Nereimyra</i> spp.		3	27	53	93	233	80	10	13			
<i>Nuculoma tenuis</i>	133	153		317	27		113		63			
<i>Pholoe</i> spp.	267	313	90	77	17	3	23	3				
<i>Scalibregma inflatum</i>	27	13	3	3	100		23					
<i>Spiophanes krøyeri</i>	13	23	147	413	593		173					
<i>Thyasira equalis</i> + <i>T. sarsi</i>	157	347	90	163	190	263	187	87	123			3

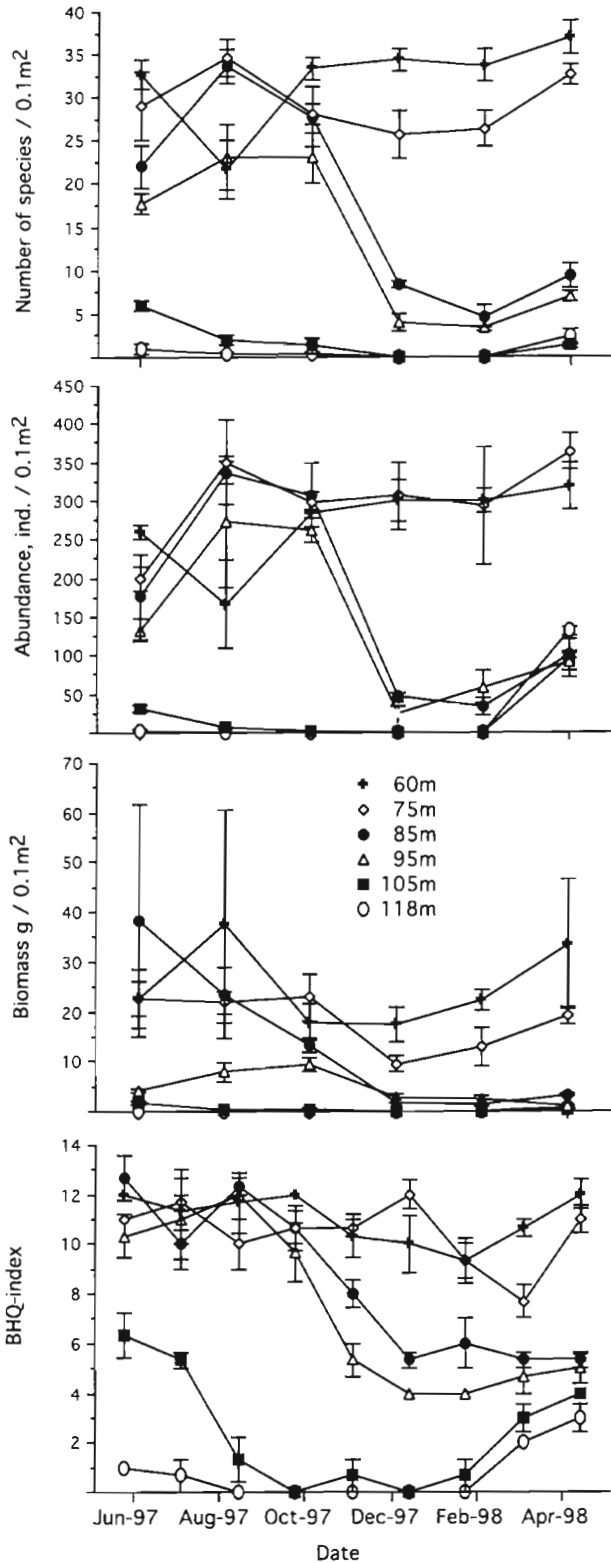


Fig. 6. Succession in number of species, abundance and biomass (means \pm SE; $n = 3$) of benthic macrofauna from June 1997 through April 1998 at various depths between 60 and 118 m. Benthic-habitat quality (BHQ) index (means \pm SE; $n = 3$) for same period is shown in bottom graph

abundance (ANOVA, $F_{5,24} = 7.34$, $p < 0.01$), number of species (ANOVA, $F_{5,24} = 13.65$, $p < 0.01$) and total biomass (ANOVA, $F_{5,24} = 11.45$, $p < 0.01$). No significant (SNK, $p > 0.01$) temporal changes in mean total abundance, number of species and total biomass were observed at 118, 105, 75, or 60 m. However, at 95 and 85 m significantly (SNK, $p < 0.01$) lower total abundance, number of species and total biomass were recorded after the oxygen minimum level had been reached.

Successional changes

Fig. 7 presents the successional changes in the benthic communities as ordination of samples by MDS. Groups (Roman numerals) correspond to the successional stages of the Pearson-Rosenberg (1978) model (Fig. 1). The different stages are allocated according to the BHQ index. The MDS plot reveals similar faunal composition throughout the 10 mo period at 60 and 75 m (Stage III). The 85 and 95 m stations were included in Stage III grouping through October 1997, but then 'moved' into Stage II with a subsequent reduction in successional stage. In June 1997, the fauna at 105 m also belonged to Stage II, but later moved into a separate stage (Stage 0) with further simplification of community composition. The oppor-

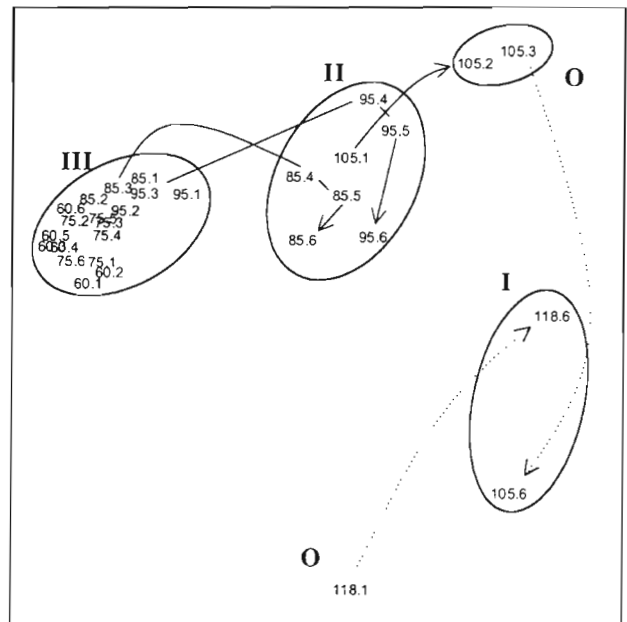


Fig. 7. Benthic faunal similarities shown as multi-dimensional scaling (MDS; stress = 0.09) at different depths (first 2 digits) and sampling occasions (last digit) (e.g. 60.1 = 60 m at first sampling occasion; June 1997). 0 to III: successional stages corresponding to Pearson-Rosenberg model (see Fig. 1)

tunicate polychaete *Capitella capitata* was the initial and dominant coloniser in April 1998 at the 2 deep stations when oxygen had increased to >20% saturation (Stage I).

BHQ index and correlations with number of species, abundance and biomass

We used the SPIs to assess benthic-habitat quality with the BHQ index (which parameterises animal and sediment structures) and the depth of the mean apparent RPD observed in the images (Table 1). The mean BHQ index was high (>10) at the 2 shallow stations, except for samples taken in March 1998 (Fig. 6). At the 2 stations at intermediate depths, similar high BHQ indices were observed until December 1997, followed by a decline. At the 2 deepest stations, significantly lower BHQ indices were observed as early as in June 1997. In March and April 1998, however, the low BHQ index at the 2 deepest stations increased in parallel to an improvement in the habitat as a response to re-oxygenation of the bottom water to >20% saturation. A significant interaction (ANOVA, $F_{5,36} = 4.65$, $p < 0.01$) between station and before/after the oxygen minimum was observed in the BHQ indices. No significant (SNK, $p > 0.01$) temporal changes in mean BHQ indices were observed at 118, 105, 75, or 60 m. However, at 95 and 85 m significantly (SNK, $p < 0.01$) lower BHQ indices were measured after the oxygen minimum level had

been reached. Temporal changes in the BHQ indices at the various depths in the Gullmarsfjord were correlated to those of the faunal parameters (Fig. 6). Significant relationships between the BHQ index and the logarithm of species richness, abundance, and biomass were observed (correlation coefficients of $r = 0.96$, 0.88 and 0.94 , respectively). Thus, the benthic habitat and faunal community succession were correlated, and mirrored the bioturbating activity of the fauna and its response to hypoxia. We used the successional stages in Fig. 7 to calculate mean species richness, abundance and biomass at each stage during the temporal changes in the Gullmarsfjord. Based on these means, Fig. 8 shows SAB curves and accompanying BHQ indices during the oxygen-disturbance event. The curves are drawn to scale according to the Pearson-Rosenberg model in Fig. 1. It is notable that Successional Stage II was low, indicative of a rather strong disturbance through the low oxygen concentrations in the Gullmarsfjord.

DISCUSSION

The colours in the SPIs reflect animal vertical distribution and activity (particularly irrigation effects) on biogeochemical processes and the vertical distribution of the RPD. The brown colour of the sediment surface is indicative of the presence of Fe^{+III} , and below this is the sulphidic, reduced area (Lyle 1983). Dissolved oxygen usually penetrates only a few millimetres into muddy sediment (Revsbech et al. 1980, Gundersen & Jørgensen 1990), and in the sub-oxic zone NO^{-III} , Mn^{+IV} and Fe^{+III} act as oxidising agents (Aller 1988, Santschi et al. 1990). Burrowing, irrigation and feeding activity of animals oxidise a 3-dimensional matrix throughout the reduced layer. The burrow walls are important sites for nitrification-denitrification processes in the sediment, since these require a juxtaposition of oxic and anoxic micro-habitats (Jenkins & Kemp 1984). Thus, a reduction in richness and abundance of the fauna and their associated biogenic structures will presumably increase the flux of inorganic nitrogen to the water column and enhance primary production. In the present study, the sub-oxidised layer was compressed both from below and from the surface, as can be seen in the images from December and February at 85 and 95 m depth (Fig. 4). Thus, irrigation of the sediment had been reduced, which affected the benthic-pelagic coupling including the flux of nutrients.

We have shown for the first time how the benthic habitat and the infauna change *in situ* with changing oxygen concentrations. Tubes of *Melinna cristata* increased in height above the surface as oxygen content decreased, and then finally collapsed; except at 75 m

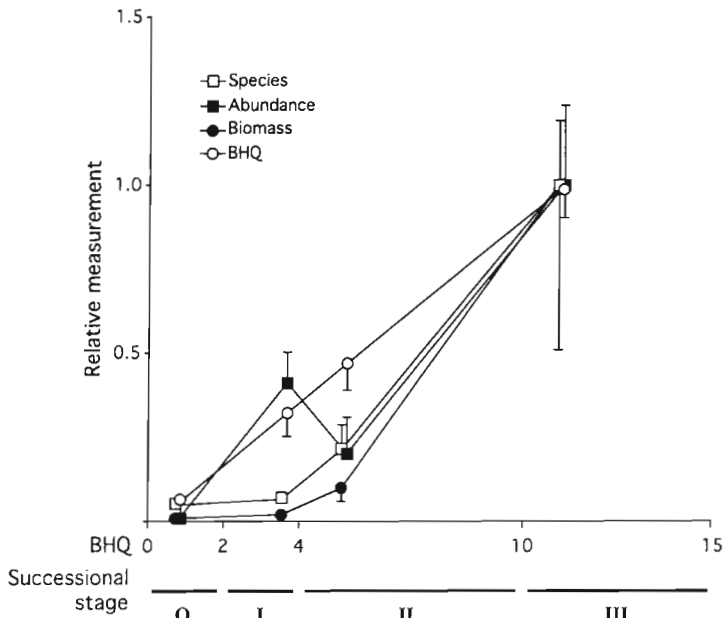


Fig. 8. Succession in number of species, total abundance and biomass (means \pm SD) in Gullmarsfjord between June 1977 and April 1998 based on MDS plot and BHQ index. Curves drawn to scale according to Pearson-Rosenberg model (Fig. 1)

depth, where they seemed to recover. *M. cristata* can probably lengthen and shorten its tube in response to variations in the ambient oxygen micro-climate. Long tube structures will induce turbulence in the near-bottom water layer, which may increase the oxygen supply to the viscous sublayer next to the sediment surface (Eckman & Nowell 1984, Gundersen & Jørgensen 1990). Other infaunal species have also demonstrated changes in positioning of tubes or burrow structures in response to critical oxygen concentrations; e.g. the polychaete *Pectinaria koreni* pushes its tube above the sediment surface (Nilsson & Rosenberg 1994), and the amphipod *Corophium volutator* extends its burrow higher above the mud surface (Eriksson & Weeks 1994). Similarly, under conditions of oxygen deficiency, the polychaete *Malacoceros fuliginosa* has been observed to stretch its body from the sediment surface high up into the overlying water (Tyson & Pearson 1991), and the brittle stars *Amphiura chiajei* (Stachowitsch 1984) and *Ophiura albida* (Baden et al. 1990), to aggregate in elevated regions of sediment, where presumably the oxygen concentration is somewhat greater than in surrounding, flatter areas.

Elimination of macrofauna from the deepest bottoms (118 m) of the Gullmarsfjord as a result of low oxygen concentrations has been demonstrated on an earlier occasion: in the winter of 1979/1980 by Josefson & Widbom (1988), who recorded some of the last survivors as *Heteromastus filiformis*, *Thyasira equalis*, *T. sarsi*, and *Melinna cristata*, i.e. the same species that we found to be most tolerant to hypoxia in the present investigation. We suggest that the 3 last-mentioned species should be added to the list of species resistant to severe hypoxia (summarised by Diaz & Rosenberg 1995). Infaunal dominants in the present study and in that of Josefson & Widbom (1988) were the same and consistent over the depths investigated (Table 2). Oxygen concentrations in the deeper part of the Gullmarsfjord show a clear seasonal trend, with annually rather low (<2 ml O₂ l⁻¹) concentrations (O. Lindahl pers. comm.); however such low concentrations for such a long period as in 1997/1998 have never been reported before. Our results suggest that the populations are pre-conditioned to hypoxia. As the oxygen conditions improved, the cosmopolitan opportunistic coloniser *Capitella capitata* was the first to appear in the deeper defaunated sediment; this was also the case in 1980 (Josefson & Widbom 1988). The present study of long-term hypoxia indicates a critical oxygen saturation for survival of ~10% (=0.7 ml O₂ l⁻¹), since at about this saturation great reductions in density and species richness occurred at 85 and 95 m depth at the end of 1997. This critical value is slightly lower than that reported for predominantly coastal areas, but higher than reported for upwelling areas (Diaz & Rosenberg 1995)

in which species have become adapted to permanently low oxygen concentrations for long periods.

The MDS (Fig. 7) shows the benthic community succession in relation to changing oxygen concentrations over time. Should oxygen saturations over the coming years remain rather high, say with minimum saturations of >25%, it is likely that the community structure at all depths would return to the original equilibrium stage as shown for Stage III in Fig. 7. This type of community was also found at 118 m in 1977 to 1979 by Josefson & Widbom (1988). The recovery of benthic fauna was studied previously in an inner branch of the Gullmarsfjord. In these heavily enriched and defaunated sediments, recovery to an equilibrium stage took 5 to 8 yr following pollution abatement (Rosenberg 1976). We suggest that the recovery is quicker in the deep part of the Gullmarsfjord because the sediment there is less organically enriched.

The changes in the benthic community showed clear similarities to the Pearson-Rosenberg model (Fig. 1), but hypoxia had a rather sudden and strong negative effect at the 2 intermediate depths in the Gullmarsfjord. As a result, the SAB curves were low in relation to the BHQ index (Fig. 8). The 'buffering capacity' of the sediment in conditions of low oxygen concentration may arise from the fact that diminishment of the RPD layer is a slow process compared to the rather abrupt effects of decreased oxygen content on fauna.

Correlations have been demonstrated between the SAB curves and the BHQ index; thus changes in benthic habitat quality closely parallel changes in faunal community succession. The strongest correlation was for number of species and the BHQ index. This would be expected, since the species curve increases rather smoothly from Seral Stage 0 to III (Fig. 1). In their pioneering study with SPI, Rhoads & Germano (1982) also found that species richness generally corresponded to that inferred from *in situ* photos. In contrast, abundance and biomass may show peaks ('peaks of opportunists': Pearson & Rosenberg 1978) in Seral Stage I, which would reduce the correlation. The OSI developed by Rhoads & Germano (1986) has been used in some studies to map habitat-quality (Rhoads & Germano 1986), to assess physical disturbances and organic enrichment (Valente et al. 1992), and to evaluate the effects of mariculture (O'Connor et al. 1989). In the 2 latter studies, low values of apparent RPD were correlated with low OSIs. Similarly, Nilsson & Rosenberg (1997) found that the distribution of RPD corresponded well with benthic successional stages. One difference between the OSI and the BHQ index is that in the former the successional stages are determined by examining the images by eye whereas in the BHQ index, different structures in the images are scored and their summary relates to a particular seral stage (Fig. 1).

The variables in the BHQ index seem to constitute an accurate description of a benthic habitat that reflects the successional stages of a benthic community. In this and a related study (Nilsson & Rosenberg 1997), such correspondence has been demonstrated for coastal, oxygen-stressed areas, but the BHQ index is likely to be useful also in other areas where the Pearson-Rosenberg succession model is applicable. From a benthic study in New Jersey, USA, Grizzle & Penniman (1991) concluded that SPI data are as useful as traditional data in delimiting the spatial extent of benthos effected by pollution. Thus, the BHQ index is useful as a cost-effective sediment-habitat classification and in disturbance-impact assessment.

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