

# Recovery of marine benthic habitats and fauna in a Swedish fjord following improved oxygen conditions

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**ABSTRACT:** The Gullmarsfjord on the Swedish west coast has a sill at 40 m and a maximum depth of 118 m. The stagnant bottom water is usually renewed with oxygen-rich water each spring. In 1997 this did not occur, and the fauna was eliminated at depths below about 100 m and severely reduced between 80 and 100 m depth. In spring 1998, the whole fjord was re-oxygenated and the succession of the benthic fauna was studied at 5 stations over a 2 yr period. Simultaneously, the benthic habitat quality (BHQ) was assessed by analysing sediment redox conditions and faunal burrow structures in sediment profile images. Succession of the benthic fauna is described as increases in number of species, abundance and biomass. Conspicuous colonisers below 100 m depth were the polychaete *Capitella capitata* and the heart urchins *Echinocardium cordatum* and *E. flavescens*. Return to pre-oxygen stressed conditions was slowest at the deepest stations. By using a multivariate technique (multi-dimensional scaling) we show that the benthic communities at all depths more or less returned to the same faunal composition as during pre-disturbed conditions. The pioneering and mature benthic faunal Successional Stages I and III were predictable but not the intermediate Stage II. The path of recovery of the benthic community succession did not retrace the path of degradation. The sedimentary habitats and redox conditions were similarly restored over the 2 yr period as analysed by the BHQ index.

**KEY WORDS:** Sediment profile imaging · SPI · Hypoxia · Benthos · Faunal succession · *Capitella*

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## INTRODUCTION

The pioneering papers by Petersen (1913), Molander (1928) and Thorson (1957) documented that benthic macrofaunal species may be long-lived, and that the benthic community structure is tightly coupled to the sedimentary habitat. Later, successional models were developed showing that the structure of benthic communities changes in a predictable way in relation to environmental disturbance, e.g. organic enrichment (Pearson & Rosenberg 1978), physical disturbance (Rhoads & Germano 1982) and sediment toxicity (Swartz et al. 1985). Multivariate analysis has been useful in analysing disturbances of benthic communities (Warwick & Clark 1993, Rumohr & Karakassis 1999), but has also shown that different faunal groups may respond differently to enrichment and toxicity

(Peterson et al. 1996). The models depicted the faunal distribution along a gradient of disturbance as a continuum, but for pedagogic reasons different successional stages were distinguished according to the degree of disturbance. Along an environmental gradient from severely disturbed to undisturbed conditions, the successional stages may be classified as Successional Stages (SS) 0 (grossly disturbed), I (pioneer/disturbed community), II (intermediate community), and III (undisturbed/'climax' community). Pearson & Rosenberg (1976, 1978) showed in parallel studies from Scotland, where environmental disturbance increased, and Sweden, where the conditions improved after pollution abatement, that the benthic community structure was similar under similar degrees of disturbance even when the succession of these communities changed in different directions.

In the Gullmarsfjord on the Swedish Skagerrak coast (Fig. 1), the impact of declining oxygen concentrations

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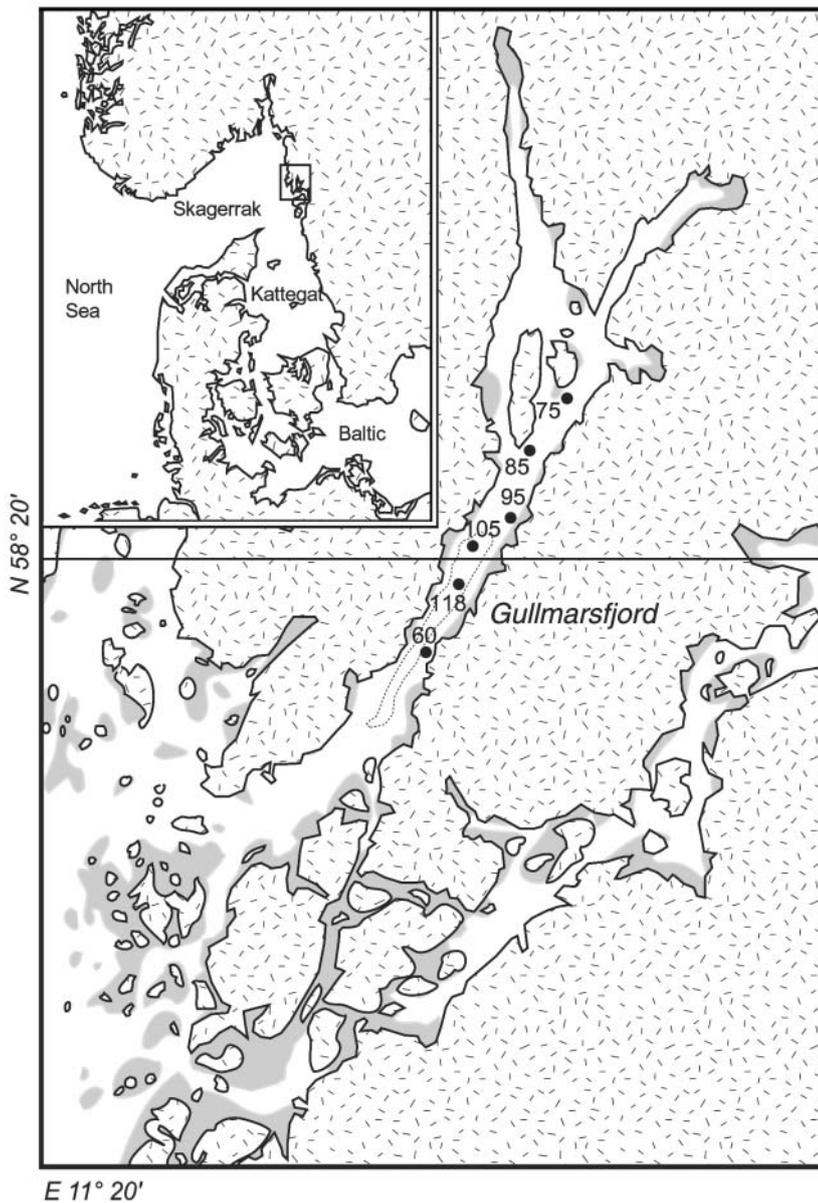


Fig. 1. Stations sampled in the Gullmarsfjord, west Sweden. Stations are numbered according to depth. Depth contour is 100 m

in the bottom water on benthic communities at different depths was investigated from June 1997 to April 1998 (Nilsson & Rosenberg 2000). This decline in oxygen concentrations was an unusual event as the bottom water normally is exchanged once a year in winter or spring, but this water renewal did not occur during 1997. Instead the oxygen concentrations showed a temporal decline with depth. The benthic communities were more or less unaffected at 60 and 75 m (oxygen saturations remained >15%), significantly reduced at 85 and 95 m after oxygen saturation declined <10%, and severely affected at 105 and 118 m, where the

fauna finally was eliminated. In Nilsson & Rosenberg's study, the benthic habitat quality, e.g. redox conditions in the sediment, was assessed by analysing sediment profile images. At stations affected by hypoxia, the oxidised part of the sediment decreased, the reduced part increased, and the top sediment was finally disintegrated. At the studied depths, salinity is ~34.5 psu, temperature between 4 and 8°C and sediment is predominantly mud.

In early 1998, the bottom water of the Gullmarsfjord was re-oxygenated, and for most of the period up to April 2000, the bottom oxygen saturations were >20% (Fig. 2), i.e. above critical concentrations for at least most benthic infaunal species (Diaz & Rosenberg 1995). Thus, this was an opportunity to study the succession of benthic communities from different initial successional stages. The questions are: Are the benthic successional models predictable, and are the paths of recovery and degradation similar? How long will it take to restore the sediment and to obtain a depth of redox potential discontinuity (RPD) similar to pre-hypoxic conditions? Models by Baden et al. (1990) and Gray (1992) have suggested that distribution of benthic fauna and sediment redox conditions change in relation to gradients of oxygen concentrations in a similar way as described in the Pearson-Rosenberg (1978) model.

In the present investigation, we used *in situ* sediment profile imaging (SPI) to digitally analyse biogenic structures and redox profiles of the sediments. This technique was developed by Rhoads & Cande (1971) and has been

used to demonstrate changes in benthic habitats related to, e.g., organic enrichment (O'Connor et al. 1989) and physical disturbance (Rhoads & Germano 1986). Nilsson & Rosenberg (1997) used the SPI technique to develop a benthic habitat quality (BHQ) index, which in a recent study (Nilsson & Rosenberg 2000) in the Gullmarsfjord correlated significantly with each of the variables species numbers, abundance and biomass. The BHQ index was used to assign the sedimentary quality and biogenic structures to the 4 different benthic successional stages (SS 0 to SS III) described above (Nilsson & Rosenberg 2000).

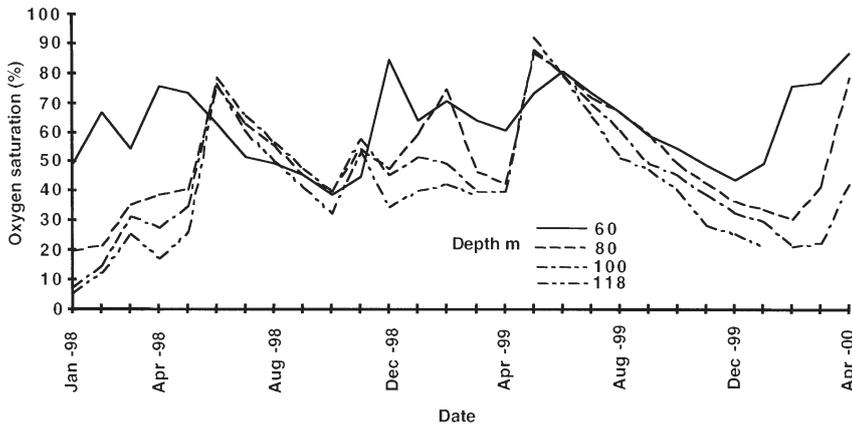


Fig. 2. Temporal changes in oxygen saturations (%) from January 1998 to April 2000 at depths between 60 and 118 m measured by the Winkler method in the water on a depth transect at the deepest part of the Gullmarsfjord (data from the Gullmarsfjord Control Programme). The Water Quality Association of the Bohus Coast

## MATERIALS AND METHODS

This study included 6 stations numbered after their depths: 60, 75, 85, 95, 105 and 118 m. Sampling dates were April, June, August and October 1998; January, April, August and October 1999; and April 2000. Three SPIs were taken at each station, and 3 samples were taken with a 0.1 m<sup>2</sup> Smith-McIntyre grab at the same stations and sampling times, except at 60 m where only SPIs were analysed. SPIs were taken *in situ* through a prism (30 × 22 cm; Rosenberg & Diaz 1993) penetrating about 12 cm into the sediment. Cameras used were a Nikon 801 (with ISO 100 color-positive film, E6-developed) up to April 1999 and thereafter a digital CCD camera (Canon Power Shot Pro 70). Contrasts in the colours were digitally enhanced in Adobe Photoshop 5.5, which allowed accurate assessment of the depth of the apparent redox potential discontinuity (aRPD) measured as the shift between oxidised yellowish top sediment and reduced black sediment below (Rosenberg et al. 2001). The BHQ index was calculated from each image. This index parameterises sediment structures, sub-surface structures, and the depth of the aRPD (Nilsson & Rosenberg 1997). The BHQ index varies between 0 and 15 and is related to the benthic fauna successional stages of the Pearson-Rosenberg model (Nilsson & Rosenberg 2000), where BHQ < 2 relates to SS 0, BHQ = 2–4 to SS I, BHQ = 5–10 to SS II, and BHQ > 10 to SS III. The Smith-McIntyre grab took samples down to ~17 cm depth in the sediment at all stations; the sediment was sieved on 1 mm

mesh and preserved in 4% buffered formalin. Numerical similarity between macrofaunal samples was analysed by multi-dimensional scaling (MDS) based on Bray-Curtis similarity index after  $\sqrt{x}$  transformation (Clark & Warwick 1994). Correlations between BHQ index and number of species, abundance and biomass were analysed by simple linear correlation [ $\log(x+10)$ ]. Biomass is formalin wet weight. Carbon (C) and nitrogen (N) of the top of the sediment were analysed at the same time in 2 replicate deep-frozen samples from each station in April 1999 and 2000 in a Carlo Elba elemental analyser. Loss of ignition was analysed on 4 replicates of the top 1 cm of the sediments from April 2000 after drying at 80°C to constant weight and subsequent burning at

500°C for 5 h. Statistical analysis in differences as percent C and N between sampling times was made by ANOVA.

## RESULTS

### Sediment and sediment profile imaging

Percent fines (<16 µm) of the sediment was ≥94% at all stations except Stn 95, where the sediment had coarser particles (Table 1). In April 1999, means of C varied between 3.7 and 4.2% with higher values at the deep stations (Table 1). In April 2000, the mean content of C had declined significantly (ANOVA,  $p < 0.05$ ) at all stations to between 3.2 and 4.0%. Similarly, a significant (ANOVA,  $p < 0.05$ ) decline was recorded for mean N, ranging between 0.32 and 0.35% in 1999 to between 0.26 and 0.33% 1 yr later. The mean loss of ignition was >10% dry weight at all stations, except at Stn 95 where it was 7.8%.

Table 1. Depth and position of the benthic stations in the Gullmarsfjord, west Sweden. Mean percent C, N, loss of ignition (LI), and percent fine sediment (FS; <16 µm) in the top cm of the sediment in April 1999 and 2000

Stn (depth, m)	Position		C		N		LI 2000	FS 2000
	N	E	1999	2000	1999	2000		
75	58° 22.7'	11° 36.6'	3.7	3.6	0.34	0.31	10.5	96
85	58° 21.7'	11° 35.2'	3.8	3.6	0.34	0.30	10.8	98
95	58° 20.4'	11° 34.7'	3.7	3.2	0.32	0.26	7.8	76
105	58° 15.0'	11° 26.8'	4.2	4.0	0.35	0.33	11.2	95
118	58° 19.4'	11° 32.7'	4.2	3.9	0.35	0.31	12.4	94

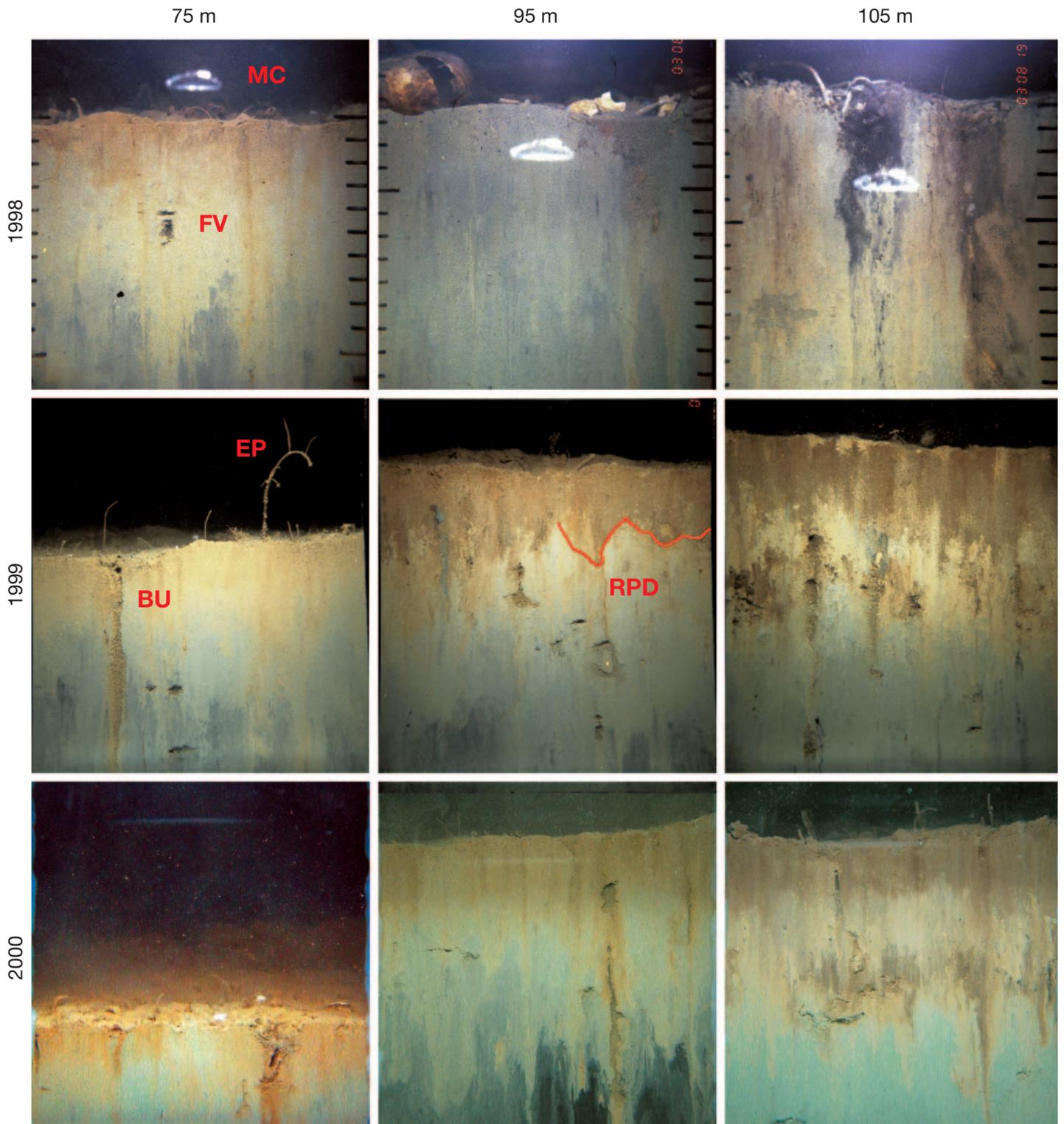


Fig. 3. Sediment profile images from April 1998, 1999 and 2000 at 75, 95 and 105 m depth in the Gullmarsfjord. Scales on the sides of images from 1998 are in centimetre intervals. BU: burrow; FV: feeding void; RPD: redox potential discontinuity; EP, MC: tubes that appear to be *Euchone papillosa* and *Melinna cristata* tubes, respectively. Halo is an artifact (reflection of flash); colours in images are computer enhanced

SPIs from April 1998, 1999 and 2000 are shown for Stns 75, 95 and 105 in Fig. 3. In 1998, the sediment at Stn 75 appeared undisturbed. Tubes were seen on the sediment surface, the largest probably being *Melinna cristata* tubes. The upper 2 to 3 cm of the sediment was oxidised, with several burrows extending down below this depth and 1 void. At Stn 95, the SPI showed fragments of sea urchin tests and polychaete tubes. The sediment appeared reduced to the surface on the left side, and a pit on the right indicated recent activity. The sediment at Stn 105 appeared reduced, with black fragments of tubes, reduced old burrow structures, and 1 anoxic, black void.

In 1999, several tubes that appeared to be those of *Euchone papillosa* extended several centimetres up into the water at Stn 75 (Fig. 3). The branches of 1 tube in the front of the image are suggested to be constructed by the crustacean *Dyopodos monacanthus* (Mattson & Cedhagen 1989). Three voids, and 1 long burrow extending >9 cm into the sediment were also present. At Stn 95, the upper ~1 cm was reworked and the aRPD was at 2 to 3 cm depth. One tube and several burrows and voids were present in the image. At Stn 105, the upper 2 to 3 cm was oxidised, with several burrows and voids deeper down in the sediment.

In 2000, the penetration of the prism was poor at Stn 75, resulting from mechanical failure. The thin tubes protruding above the surface (Fig. 3) appeared to

be *Euchone papillosa* and the larger *Melinna cristata*. Burrows penetrated down below the lower part of the image. At Stn 95, the upper ~3 cm of the sediment was oxidised in the image, and some small tubes were present on the surface. The large burrow on the right penetrated >12 cm down in the sediment. Some voids were also present. At Stn 105, the upper 2 to 3 cm of the sediment was oxidised, and some tubes protruded into the water. One large burrow >15 cm long and some smaller ones were noted in the sediment.

The mean depth of the aRPD measured in the SPIs over the sampling period varied around 5 cm on Stn 60 and between 3 and 4 cm at Stn 75 (Fig. 4). At the deeper stations, aRPD showed a general increase over the whole period from values ~1, and reached values similar to that at Stn 75 in April 1999.

The mean values of the BHQ index were  $\geq 10$  at Stns 60 and 75 over the whole study. At the deeper stations, BHQ indices increased from means of <5 in April 1998 to >10 for Stns 85 and 95 two years later. At that time, in April 2000, the mean BHQ indices at Stns 105 and 118 were 9.7 and 8.0, respectively.

### Species, abundance and biomass

The 5 dominant species recorded at each station for samplings in April 1998, 1999 and 2000 are listed in Table 2. Dominant species at Stn 75 during the whole

Table 2. Mean abundance (ind.  $m^{-2}$ ) of 5 dominant species, and total abundance and number of species at each station in the Gullmarsfjord in April 1998, 1999 and 2000

Taxon	75 m			85 m			95 m			105 m			118 m		
	1998	1999	2000	1998	1999	2000	1998	1999	2000	1998	1999	2000	1998	1999	2000
<i>Abra nitida</i>	477	210	293	0	0	7	0	97	53	0	7	30	33	10	147
<i>Amphiteis gunneri</i>	50	50	53	0	60	123	0	70	143	0	0	17	0	0	3
<i>Amphiura filiformis</i>	107	187	240	0	0	0	0	0	0	0	0	0	3	3	3
<i>Anobothrus gracilis</i>	77	80	113	13	33	107	3	43	37	0	0	23	0	0	13
<i>Capitella capitata</i>	0	0	0	43	0	0	407	0	0	960	0	0	1300	0	0
<i>Chaetozone setosa</i>	13	7	73	17	87	70	0	207	107	0	0	0	0	0	13
<i>Chlamys septemradiatus</i>	0	13	13	0	3	23	0	13	0	0	0	57	0	0	0
<i>Echinocardium cordatum</i>	13	13	20	0	30	0	0	0	0	0	200	13	0	220	3
<i>Echinocardium flavescens</i>	27	20	17	0	0	3	0	73	13	0	390	30	0	173	13
<i>Euchone papillosa</i>	10	23	17	0	177	63	0	33	0	0	0	17	0	3	0
<i>Heteromastus filiformis</i>	790	330	190	13	23	10	3	173	100	3	0	0	0	17	13
<i>Lipobranchus jeffreysi</i>	0	0	13	0	160	147	0	13	7	0	3	0	0	3	0
<i>Maldane sarsi</i>	323	217	110	3	13	0	0	0	0	0	0	0	0	0	0
<i>Melinna cristata</i>	230	113	123	207	167	150	63	80	113	0	0	23	3	0	10
<i>Myriochele oculata</i>	67	167	117	0	0	3	0	133	43	0	0	17	0	0	0
<i>Mysella bidentata</i>	47	190	193	0	0	3	0	7	3	0	0	0	0	0	3
<i>Nemertini spp.</i>	117	10	43	180	13	13	320	47	7	0	7	0	0	0	7
<i>Nereimyra sp.</i>	33	7	3	233	220	87	7	10	7	0	63	153	0	57	180
<i>Nuculoma tenuis</i>	317	3	3	0	23	17	0	7	7	0	0	0	0	0	7
<i>Ophelina acuminata</i>	0	0	27	0	90	153	0	30	97	0	0	183	0	0	83
<i>Scalibregma inflatum</i>	3	7	160	0	320	60	0	117	87	0	17	10	0	10	27
<i>Spiophanes kroyeri</i>	413	237	177	0	0	3	0	30	53	0	0	10	0	3	27
<i>Thyasira equalis</i>	97	43	143	143	153	70	0	7	60	0	10	113	3	10	143
<i>Thyasira sarsi</i>	67	63	53	120	143	53	87	613	180	0	70	377	0	117	663
<b>Total abundance</b>	3623	2230	2680	1007	1780	1390	910	1947	1210	963	833	1270	1343	690	1573
<b>Total no. of species (0.3 m<sup>-2</sup>)</b>	51	48	52	14	27	35	13	42	26	2	19	33	5	24	39

period, and found in numbers  $>100$  ind.  $m^{-2}$ , were the bivalve *Abra nitida*, the polychaetes *Maldane sarsi*, *Melinna cristata*, *Heteromastus filiformis* and *Spiophanes kröyeri*, and the brittle star *Amphiura filiformis*. At Stns 85 and 95, *M. cristata* and the bivalve *Thyasira sarsi* were abundant over the whole period. The following polychaetes had increased in numbers by the last 2 sampling periods: *Amphicteis gunneri*, *Chaetozone setosa*, *Ophelina acuminata* and *Scalibregma inflatum*. At the deep stations (Stns 105 and 118), which had no macrofauna in February 1998, *Capitella capitata* was the initial coloniser in April 1998. In the following 2 yr conspicuous species were the heart urchins *Echinocardium cordatum* and *E. flavescens*, the bivalves *T. sarsi* and *T. equalis*, and the

polychaete *Nereimyra* sp. On the last sampling date, the polychaetes *O. acuminata*, *Anobothrus gracilis* and *M. cristata* were found.

The greatest number of species over the sampling period was generally found at Stn 75 (Fig. 4). At the other stations there was a general and gradual increase in numbers, except at Stn 95, where the numbers reached 29 species per  $0.3 m^2$  in August 1999, but declined to 20 species in April 2000. The abundance was generally highest at Stn 75, but showed great variation over time. Abundance at the other stations was also variable over time, with peaks in August 1999 at Stns 85 and 95. In April 2000, the abundance at all stations except Stn 75 was similar, with means between 121 and 157 ind. per  $0.1 m^2$ . On most sampling

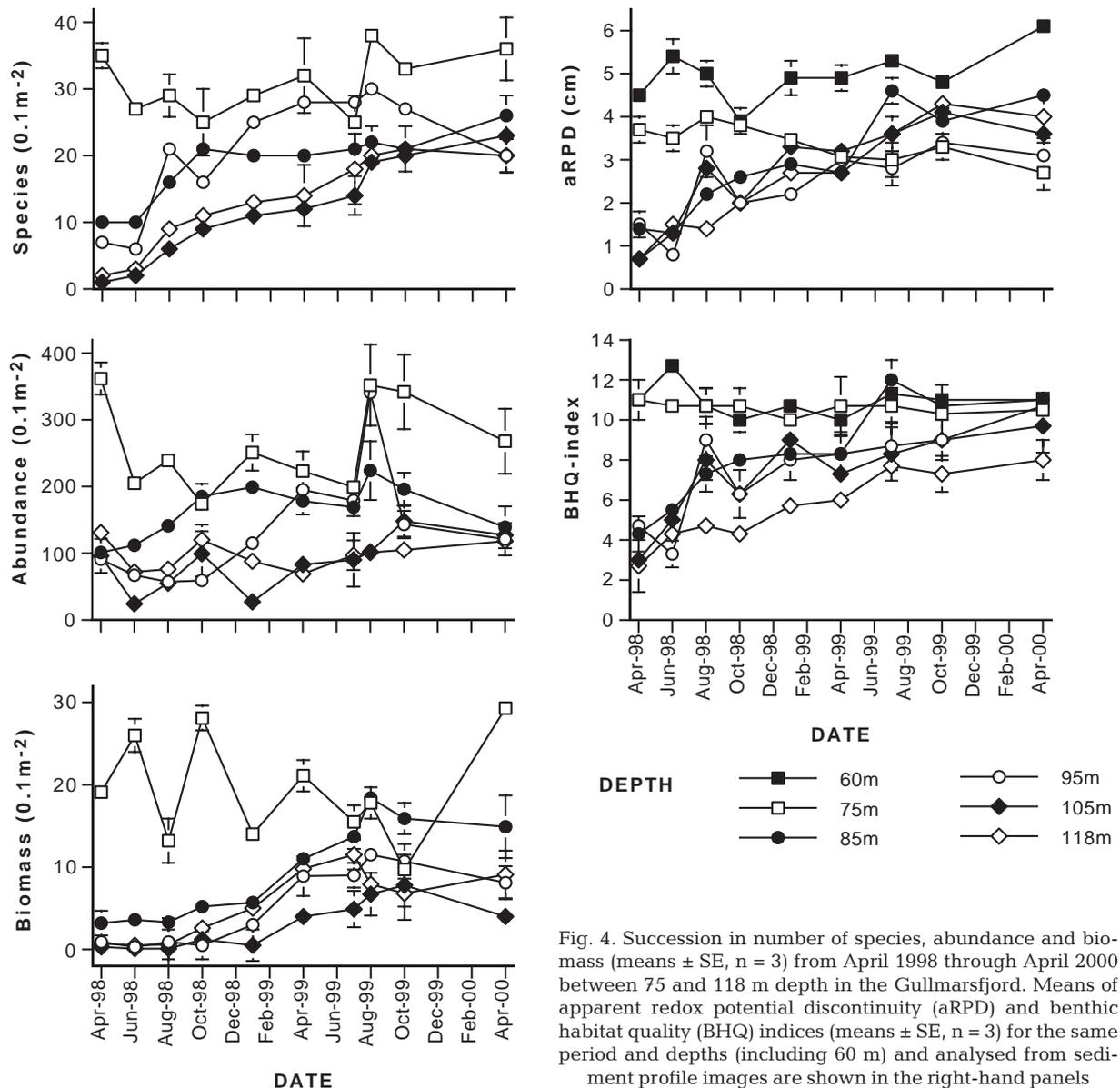


Fig. 4. Succession in number of species, abundance and biomass (means  $\pm$  SE,  $n = 3$ ) from April 1998 through April 2000 between 75 and 118 m depth in the Gullmarsfjord. Means of apparent redox potential discontinuity (aRPD) and benthic habitat quality (BHQ) indices (means  $\pm$  SE,  $n = 3$ ) for the same period and depths (including 60 m) and analysed from sediment profile images are shown in the right-hand panels

occasions, biomass was highest at Stn 75, but varied between sampling dates. At the other stations, the recovery in biomass was minor during 1998, but increased after this, particularly at Stn 85. Temporal changes in the logarithm of number of species, abundance and biomass were significantly ( $p = 0.001$ ) correlated with the BHQ indices (correlation coefficients of  $r = 0.81, 0.56$  and  $0.71$ , respectively).

**Benthic community recovery pattern**

Benthic community succession following re-oxygenation of the bottom water in the Gullmarsfjord is illustrated using a multivariate statistical analysis (Fig. 5). No. 1 represents the 3 replicate samples taken in April 1998 when colonisation was first observed, No. 2 the second sampling date, etc., according to the dates given in Fig. 4. At the reference station (Stn 75), no apparent directional change was observed, but there was a tendency for the replicates to be close to each other. At Stn 85, the fauna for the first 2 dates was similar; the faunal composition

changed at Sampling Time 3, was similar over Samplings 4 through 9, and then changed somewhat more at Sampling Time 10. At Stn 95, successive changes were apparent between the first 5 sampling dates; subsequently, the faunal composition was comparatively more similar. Stns 105 and 118 showed a progressive change to the end of the sampling. The faunal composition was rather similar at the 2 first samplings, with a subsequent larger change at the third and fourth samplings, with a gradual change during the following samplings up to the final sampling date. (Note that the scales are not comparable between the station plots in Fig. 5.) For comparison of faunal succession between stations, we combined the average faunal composition on each sampling date into 1 graph (bottom, right-hand panel in Fig. 5), which indicates that the faunal composition at Stn 75 was similar over the whole 2 yr period, and that the fauna changed to a minor degree at Stn 85, and to a higher degree at Stn 95. The comparatively greatest change occurred at Stns 105 and 118, and the faunal composition during recovery at these stations was similar.

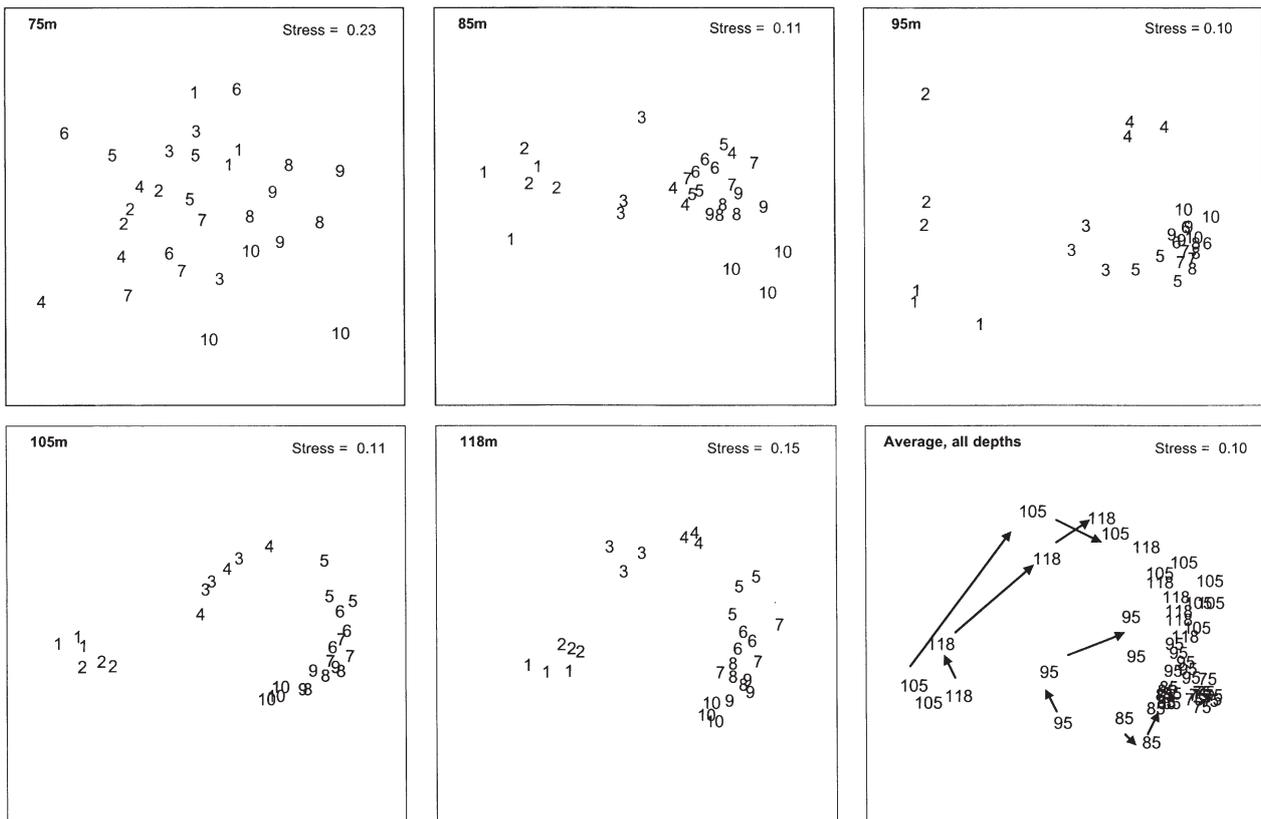


Fig. 5. Multi-dimensional scaling (MDS) showing the changes in benthic community structure from April 1998 through April 2000 ( $n = 10$ ) at the depths 75, 85, 95, 105 and 118 m. 1 is the first sampling date, 2 the second sampling date, etc., each with 3 replicates. In the bottom, right-hand panel, means of the fauna for all depths are combined and arrows indicate the temporal recovery. Scales are not comparable between plots

## DISCUSSION

### Comparison with other studies

Molander (1928, 1963) has contributed most to the knowledge of distribution of different benthic communities in the Gullmarsfjord. His investigations during the years 1923 through 1926 formed the basis for his classification of 10 separate associations and several more sub-communities (facies). In the deeper part (72 to 118 m) of the fjord, i.e. approximately the same depth interval as sampled in the present study, he characterised the community as a *Melinna cristata-Nucula tenuis* assemblage. Molander (1928) found 42 species at 3 stations (3 replicates of 0.1 m<sup>2</sup> each); this seems to be lower than that in the present study, but a comparison is difficult as different grabs and sorting techniques were used. For the 3 stations he listed, average densities (given as ind. m<sup>-2</sup>) of the dominant species were as follows: *M. cristata* 72, *Nuculoma tenuis* 193, *Abra nitida* 118, and *Thyasira* spp. 110. The same taxa were among the dominant species in the present study also (Table 2), except for *N. tenuis* which was present as shells only.

The response of benthic fauna to hypoxia was studied at the deepest station at 118 m in the Gullmarsfjord by Josefson & Widbom (1988) in 1977 to 1981. During the winter 1979/1980, oxygen concentration declined to a minimum of 0.21 ml l<sup>-1</sup>, and the macrobenthos was eliminated. Later in 1980, *Capitella capitata* and *Heteromastus filiformis* colonised the area, but the recovery was halted by a new decline in oxygen concentration later that year. Gustafsson & Nordberg (2001) found major changes in foraminiferan species composition between 1927 and 1994 towards species more tolerant to hypoxia. In many parts of the world, e.g. in Japan (Tsutsumi 1987), species of the genera *Capitella* are rapid colonisers following cessation of hypoxia and are frequently associated with organic enrichment (e.g. Pearson & Rosenberg 1978, Weston 1990).

In the innermost part of the Gullmarsfjord, the Saltkällefjord, outlets from a sulphite pulp mill enriched the bottoms up to 1966 to such an extent that the fauna was eliminated in the inner area of that fjord, due to oxygen deficiency in the bottom water and hydrogen sulphide in the sediment (Bagge 1969, Leppäkoski 1975). Leppäkoski (1975) described how the benthic faunal communities changed in time and space, or as he called it, moved as 'migrating communities' from the inner part to the outer part of the fjord along with increasing pollution. Following the discontinuation of the pulp mill in 1966, the first colonisers, *Capitella capitata* and *Malacoceros (Scolelepis) fuliginosus*, did not appear until 1969 on the most enriched bottoms (Rosenberg 1972). Thus it took about 3 yr for

the top sediment to recover to an extent that made it suitable for macrofaunal life. The benthic community succession documented here contributed to the development of the Pearson-Rosenberg model, and once initiated the recolonisation of different species and increases in their densities were rapid. After 5 to 8 yr, depending on the area of the fjord, the faunal structure was considered as having returned to pre-pollution levels and resembled that described 40 yr earlier (Rosenberg 1976). The longer time for recovery compared to the present study was due to the severe organic enrichment of the sediment. Recovery to a community structure that is normal to a particular habitat depends on several environmental factors, e.g. severity of the hypoxia (Llansó 1992), salinity, temperature, current regimes, latitude, etc. Recovery is generally more rapid in shallow waters than in deeper waters (Diaz & Rosenberg 1995). An exception to this was, however, the benthic faunal recovery rate in one of the largest lagoons in the western Mediterranean, the Orbetello lagoon in Italy. This lagoon was affected by anoxic crises in 1992 and 1993, with resultant drastic reductions in benthic fauna and fish mortality. In 1999, 6 yr after anoxia, a clear recovery was observed, but opportunistic species still dominated (Lardicci et al. 2001). The reason for this slow recovery is suggested as being due to the lagoon being enclosed, with poor water interchange with the sea.

### Recovery of the benthic fauna

The significant reduction in mean C and N of the top sediment between April 1999 and April 2000 could have been a result of increased mineralisation related to increased maturity of the benthic communities and associated increased bioturbation rates. The amount of phytodetritus settling on the bottom was, however, probably much greater in 1999 compared to 2000, as the accumulated primary production in the Gullmarsfjord between early January and mid-April in each of these years was calculated as 74.0 g C m<sup>-2</sup> (n = 7) in 1999 and 18.6 (n = 10) g C m<sup>-2</sup> in 2000 (O. Lindahl pers. comm.). Thus, the differences in primary production were most probably coupled to differences in organic matter content of the sediment. The greatest difference in sediment properties between stations was at Stn 95, where organic matter was slightly lower and sediment slightly coarser than at the other stations, probably because this station was situated on the slope of the deep basin.

All investigated stations had similar salinity and temperature and fairly similar sediment-grain sizes; therefore, the ecological factors that would have had the greatest impact on the succession in the benthic communities are the difference and the temporal change in

oxygen concentrations at different depths in 1997 to early 1998. During the time of the present and a previous study (Nilsson & Rosenberg 2000), covering the 35 mo period from June 1997 to April 2000, oxygen was recorded every month and the fauna and SPI were sampled a total of 15 times, i.e. on average almost every second month. This time series, and the dynamic faunal changes occurring over that period, allowed, probably for the first time, a test of the predictability of the Pearson-Rosenberg successional model in relation to increased hypoxia followed by improved oxygen conditions, i.e. will benthic communities that are disturbed to different degrees by hypoxia return to pre-disturbed conditions?

We used a multivariate analysis to show the successional changes during this 35 mo period (Fig. 6). Data from June 1997 to April 1998 are from Nilsson & Rosenberg (2000). Each number represents the mean from 1 sampling date. In June 1997, the benthic community structures at Stns 75, 85 and 95 grouped into an octagonal in Fig. 6, here named the 'climax' community, equal to SS III. The faunal composition at Stn 75 remained unchanged throughout this study, demonstrating its usefulness as a reference station. In the pre-

vious study (Nilsson & Rosenberg 2000), the 60 m station was also used as a reference for faunal changes, and both stations had a similar faunal composition. The means of the BHQ indices were >10 for the whole period. The faunal composition at Stn 85 (as illustrated in the MDS-plot: Fig. 6, Loop 'A'), moved away from the 'climax' stage during hypoxia, but returned gradually back to the climax stage at the end of this survey. Means of the BHQ indices at the 3 last samplings were between 10.7 and 12.0. The change in faunal structure at Stn 95 followed a similar but wider loop ('B') and had also returned to the 'climax' stage by the last sampling date. The wider loop for Stn 95 compared to Stn 85 demonstrates that the faunal structure during the succession had a greater dissimilarity with the 'climax' community than that at Stn 85. At the last sampling, the mean BHQ index at Stn 95 had increased to >10. The benthic fauna at Stns 105 and 118 was already reduced due to hypoxic conditions when sampling began in June 1997, and later that year the fauna was first eliminated at Stn 105 and subsequently at Stn 118. The recovery phases, indicated by Loop 'C', were similar for the benthos at these 2 stations, and the faunal structure changed dramatically during the early part

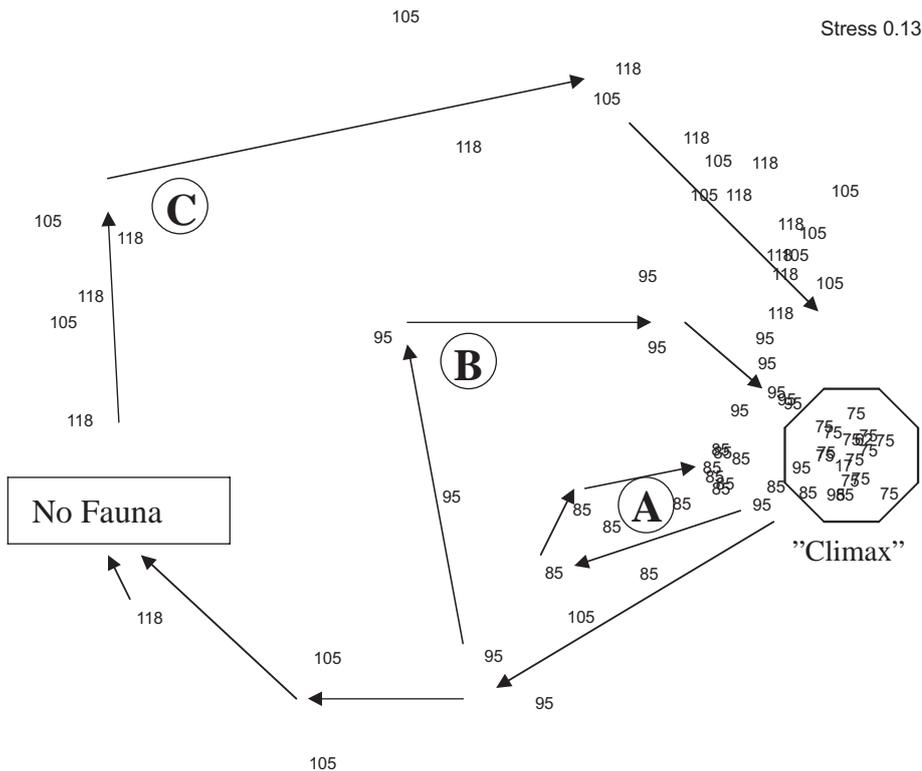


Fig. 6. Multi-dimensional scaling (MDS) showing benthic faunal succession as means of all stations (numbered according to depth) for all sampling dates between April 1997 and April 2000 combined ( $n = 15$ ). The octagonal is the 'climax' (Successional Stage III) or reference (Stn 75) benthic community. The succession during hypoxia and the recovery phase are shown as solid lines. The successional loops in the MDS plot for the different stations are marked A (Stn 95), B (Stn 105) and C (Stn 118). Data for the period April 1997 to April 1998 are from Nilsson & Rosenberg (2000)

of recovery. At the end of this study, the community structure at these 2 stations approached but did not reach the 'climax' stage, with mean BHQ indices of 9.7 and 8.0, respectively. This suggests that the benthic faunal composition in the Gullmarsfjord at depths from 75 m down to the deepest basin at 118 m was fairly similar. This is probably also true for 60 m, as the fauna at that station was similar to that of Stn 75 over a 10 mo period in 1997 and 1998 (Nilsson & Rosenberg 2000). The distance between the most widely separated stations is about 11 km and the bottom area below 60 m depth is close to 14 km<sup>2</sup> (Svansson 1984).

From the multivariate analysis we conclude that the benthic fauna succession followed the Pearson-Rosenberg successional model. During the phase of decreasing oxygen concentrations, the benthic communities affected by hypoxia changed from SS III to lower successional stages. The communities at Stns 85 and 95 returned to SS III, and those at the

deeper stations were close to this stage and would probably have reached it later. Thus, SS III is clearly identified by the model, as are SS 0 and SS I, the latter with the typical initial coloniser *Capitella capitata*. The intermediate community, SS II, had however a different faunal composition between Stns 85 and 95 and Stns 105/118 combined. Thus, the recovery path was not the same as the degradation path, i.e. the benthic system did not show a hysteretic recovery pattern (Westman 1978). However, the communities showed a great resiliency and elasticity. Recovery of benthic fauna following cessation of a fish farm and improved oxygen conditions in Greece generally followed the Pearson-Rosenberg model, but the early stages of succession were affected by the heavy organic enrichment of the sediment (Karakassis et al. 1999). Resiliency of benthic communities following the cessation of hypoxia is dependent on the constituent species, which have different life-cycles, reproduction periods and patterns of larval dispersal (Boesch & Rosenberg 1981, Llansó 1992). Elasticity means rapid recovery, which is promoted by the presence of undisturbed communities in the vicinity. Such communities can provide colonising larvae. Immigration of adults may also be important for some species, e.g. *Amphiura filiformis* (Rosenberg et al. 1997). The present study does not, however, support the classification by Molander (1928, 1963), whereby several community types exist in the deeper parts of the Gullmarsfjord; rather, the faunal composition recorded suggests only one community-type is present when oxygen concentrations are high enough to meet the fauna's requirements.

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