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Deterioration of soft-bottom benthos along the Swedish Skagerrak coast

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Abstract

Oxygen deficiency in the near-bottom water associated with eutrophication has been shown to have negative impacts on marine benthos in many Scandinavian waters. In the present study, the benthic fauna and the sedimentary habitat have been studied between 7 and 34 m depth; at 14 stations in three Swedish fjords in four different years, and at 12 stations along the Swedish coast in three different years. Ignition loss of the top sediment indicated generally enriched conditions. The benthic fauna showed temporal declines in number of species, numerical abundance and biomass, particularly since the first samplings in 1976 at the fjord stations, and in 1987 at the coastal stations. Benthic macrofauna was lacking at some stations and very low numbers were recorded in several samples. Highest quantities were recorded at the deepest fjord and coastal stations. Multivariate analysis showed that the faunal composition changed with time. Analysis of sediment profile images classified the benthic habitat as disturbed with a thin vertical depth distribution of the apparent redox potential discontinuity. It is the first time reductions in benthic fauna have been shown to occur in relatively shallow waters over large coastal areas at the Swedish Skagerrak coast. The cause of the deterioration of the fauna is suggested to be low oxygen concentrations at the bottom in association with detached vegetation, leading to organic enrichment and locally even to anoxic sediment conditions.

Keywords: Eutrophication; Oxygen deficiency; Drift algae; Sediment profile imagery (SPI)

1. Introduction

Eutrophication is one of the greatest threats to the marine coastal environment. Eutrophication-induced hypoxia or anoxia has over the last decades been spreading in many coastal parts of the world (Diaz and Rosenberg, 1995; Cloern, 2001), in some enclosed seas such as the Baltic Sea (Bonsdorff et al., 1997; Karlson et al., 2002), and even in open sea areas in the Gulf of Mexico (Rabalais et al., 2001). The impact on the benthic fauna is often severe, and Karlson et al. (2002) estimated that the loss in benthic

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faunal biomass due to hypoxia/anoxia in Scandinavian waters including the Baltic Sea could be in the order of 3 million metric tonnes. Such great losses will have significant negative effects on the benthic biodiversity and on the functioning of the ecosystem, including energy transfer to higher trophic levels (Pearson and Rosenberg, 1992).

In Scandinavian waters, in the microtidal Kattegat and the Skagerrak, the input of nutrients has increased in the order of 6 times for nitrogen and 10 times for phosphorus over the last ~100 y (Rosenberg et al., 1996). As a result, the winter concentrations of nitrogen and phosphorus have increased in the Kattegat and along the Skagerrak coast during the 1971-1990 period (Andersson, 1996). From the early 1950s or 1960s up to 1984 the oxygen concentrations in the bottom water declined significantly at 12 sites in Swedish Skagerrak fjordic and coastal bottom waters (Rosenberg, 1990), which probably was associated with increasing eutrophication over that period. Similarly, Johannessen and Dahl (1996) calculated that for 31 stations sampled along the Norwegian Skagerrak coast since 1927, significant declines in oxygen concentrations had occurred at all analysed depths (10 m, 30 m and bottom water). In the bottom water, a marked decline occurred at the beginning of the 1970s and several stations turned hypoxic or even anoxic. The authors attributed these changes to increased eutrophication. Their long-term analysis was, however, questioned by Gray and Abdullah (1996), who suggested that observations of changes before 1972 could be attributed to sampling errors.

Stratified open coastal bottom areas of the SE Kattegat have also experienced intermittent hypoxia in many years from 1980 onwards, with negative impacts on the benthic fauna (Josefson and Jensen, 1992; Rosenberg et al., 1992). This was probably related to an increased sedimentation of phytodetritus, due to an estimated doubling of primary production from the 1950s to early 1993 (Richardson and Heilmann, 1995). Josefson et al. (1993) found that the benthic faunal biomass and abundance at five offshore stations in the Kattegat, sampled between 1973 and 1988, were best correlated with river run-off that occurred 1 or 2 y prior to sampling the fauna. Thus, already the results by Josefson et al. (1993) suggest a coupling between climate, river run-off, nutrient input, sedimentation of phytoplankton, and benthic community structure. Climatic factors have been shown to have large-scale impacts on marine ecosystems, e.g. in the North Sea (Edwards et al., 2002), and it is likely that climate changes modify the intensity of the impact of eutrophication.

The Swedish Skagerrak coast faces the North Sea. The coastal water is stratified with brackish (~25 psu) water generally occurring down to between 10 and 20 m, where a halocline separates the surface water from the deeper oceanic water (~34 psu) below. No large rivers enter the area of investigation. Analysis of benthic fauna is frequently used to assess the environmental quality and to detect changes related to various disturbances (Pearson and Rosenberg, 1978), because most macrobenthic infauna is long-lived and rather stationary.

The aim of the present study is to re-visit three fjords studied in 1976 by Josefson and Rosenberg (1988), here called the ‘fjord study’, and to assess possible long-term changes of the benthic macrofauna along the Swedish west coast. The fjords studied in the present investigation were the Åbyfjord (four Å-stations), the Ellösfjord (four E-stations) and the Stigfjord (six S-stations) (Fig. 1). In addition, twelve stations were sampled north of the fjords during three different years; here referred to as the ‘coastal study’. We hypothesise that (1) the fauna at the protected fjord stations was poor also in the period after 1976, and (2) the fauna at the semi-protected coastal stations was also negatively impacted by large-scale eutrophication along the Swedish west coast. One consequence of eutrophication could be enrichment of the bottoms by sedimenting micro- and macroalgae and associated development of oxygen deficiency.

As a complement to sampling the fauna, the sedimentary habitat was studied by analysing sediment profile images (SPIs). SPI has proved to be useful for assessment of benthic environmental quality in several fjords on the Swedish Skagerrak coast. Based on structures on the sediment surface and in the sediment in combination with the mean depth of the apparent redox potential discontinuity (aRPD) in the images, a benthic habitat quality (BHQ) index was developed (Nilsson and Rosenberg, 1997), which has been shown to correlate significantly with characteristics of the benthic fauna: number of species, abundance

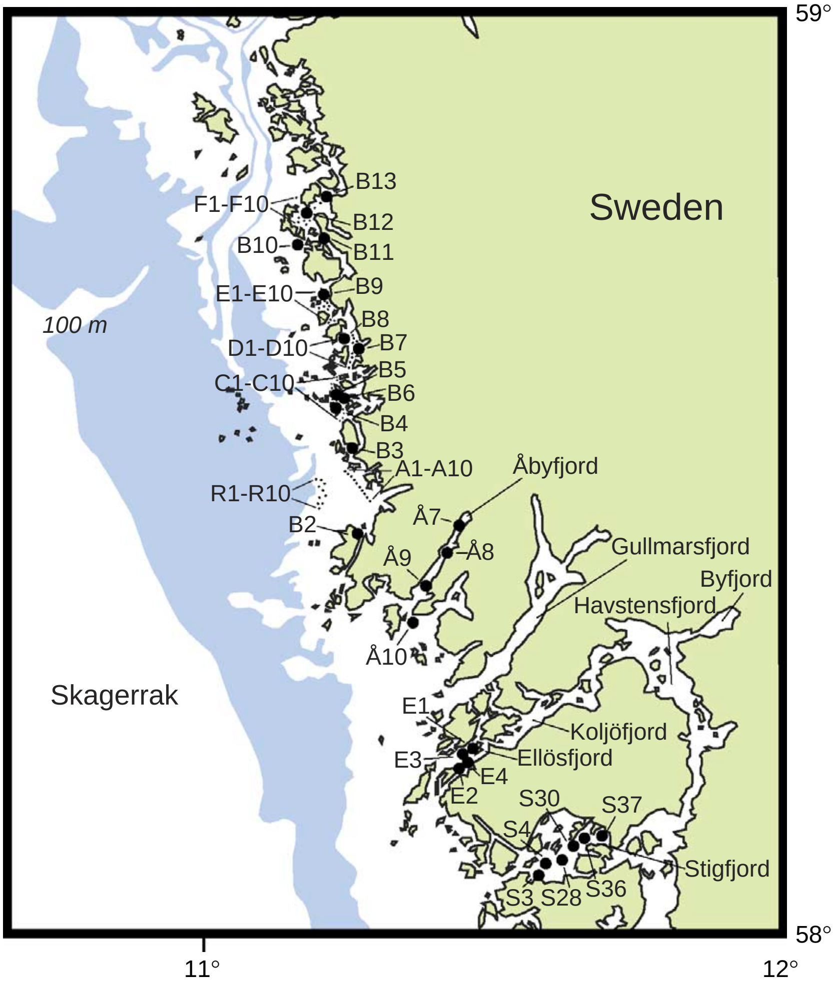

Fig. 1. Map of the investigated area with stations (B, Å, E, S) for benthic fauna (large circles) and stations (A, C, D, E, F, R) where sediment profile images were taken (small circles). The depth of the shaded area is between 50 and 100 m.

and biomass (Nilsson and Rosenberg, 2000; Rosenberg et al., 2002).

2. Material and methods

The elongated Åbyfjord is exposed in the outer part and gets gradually more sheltered and shallow (Fig. 1). The Ellösfjord is in most areas shallower than 16 m and has a narrow entrance with an 11 m deep sill in the west and minor canal-like connections towards the east. The Stigfjord has a similar geomorphology to that of the Ellösfjord and a narrow connection with the outer archipelago. The proportions of fine sediment (<50 μm) in the three fjords were between 24 and 70% with greatest proportions of fines in the Ellösfjord (Josefson and Rosenberg, 1988). The stations in the coastal study are situated in the middle part of the Swedish Skagerrak archipelago and distributed over a distance of about 22 nautical miles (Fig. 1). The stations are protected from strong winds from the west, but the distance to the open sea is generally only ~1 nautical mile.

In the fjord study, three 0.1 m^2 grab samples were taken in October 1976 and in July 1986 with a 0.1 m^2 Petersen grab, and in December 1997 and March 2001 with a 0.1 m^2 Smith-McIntyre grab at depths between 7 and 18 m, except station Å10 which was 27 m deep.

The Smith-McIntyre grab is more efficient than the Petersen grab in sampling fauna and sediment (Rosenberg and Möller, 1979). Thus, the decline in numbers and biomass in the later period that is shown below cannot be attributed to the change of grab. Results from 1976 and 1986 are from Josefson and Rosenberg (1988).

In the costal study, three 0.1 m^2 Smith-McIntyre grab samples were taken at 12 stations in September 1987, October 1990 and January 1998 at depths between 14 and 34 m. Results from the studies in 1987 and 1990 are from reports by Tunberg (1988) and Hammar Martinsson (1995), respectively. Stations were relocated by latitudal and longitudal data and depth. The animals retrieved on 1 mm meshes were analysed under 6 x magnification and preserved in 70% ethanol and later weighed for biomass including shells (wet weight). All stations were predominantly muddy (silt-clay) and the grabs penetrated ~15 cm into the sediment. The top (1-2 cm) sediment was sub-sampled (n=2) in the grab and analysed for ignition loss (IL) after drying in 80 °C and then combusted at 500 °C for 5 h (same methods were used for all samples).

In January 1998, 10 SPIs were taken in each of six different areas along the coast in the vicinity of the coastal stations for benthic faunal studies (Fig. 1). In the same month, SPIs were also taken at the benthic faunal sites in the Ellösfjord and the Stigfjord and at some other randomly selected sites within these fjords, in total 12 and 9 stations, respectively. Images were taken through a prism (30 cm long, 22 cm wide (Rosenberg and Diaz, 1993). The contrast of the colours was digitally enhanced in Adobe Photoshop 6.0; depth of mean aRPD was analysed in NIH image 1.6. The aRPD was shown to correlate with RPD measured by electrodes (Rosenberg et al., 2001). From each image, the BHQ index was calculated. This index parameterises sediment surface structures, sub-surface structures, and the apparent depth of the aRPD. The BHQ index ranges from 0 (severely disturbed with no macrofauna) to 15 ('undisturbed' with mature benthic community) and is related to the successional stages (SS) of the benthic fauna according to the Pearson and Rosenberg (1978) model, 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 (Nilsson and Rosenberg, 2000).

In August 2003, the sediment surface was sampled for mats of vegetation (drift algae). A 20 × 50 cm Agassiz trawl was dredged 1–2 times on all stations at ~2 knots for ~3 min.

Temporal differences were analysed by one-factor ANOVA and a Student Neuman Keul (SNK) posterior test on log-transformed data. Correlations were calculated as linear regressions. Significance was set at $p<0.05$. Multi dimensional scaling (MDS) was performed on species-abundance, square root transformed, data using PRIMER (Clark and Warwick, 1994).

3. Results

3.1. Sediment ignition loss (IL)

IL was analysed of the top sediment at all fjord stations in 1986 and 2001 (Table 1), but no overall significant difference was found between years. In 1986, the highest ILs were found in the Ellösfjord followed by the Stigfjord and lowest ILs were found in the Åbyfjord. In 2001, no general trend was found. Comparisons between the years showed that IL declined significantly in the Ellösfjord, but increased at all other stations, except at station Å9 where it was similar between years. IL at the coastal stations varied between 2 and 11% of the DW for the years 1987 and 1990, but without any significant differences between years (Table 1).

Table 1
Ignition loss in percent of dry weight of the top sediment at the fjord stations in 1986 and 2001 (left) and the coastal stations in 1987 and 1990 (right) Data 1986 from Josefson and Rosenberg (1988); 1987 and 1990 from Hammar Martinsson (1995)

Station/Year	1986	2001	Station/Year	1987	1990
E1	17.3	14.3	B2	3.4	9.2
E2	20.3	16.9	B3	9	6.4
E3	22.2	10.3	B4	6.8	5.8
E4	17.4	6.1	B5	9	11.1
S3	9.6	16.2	B6	3.6	4
S4	7.2	9.2	B7	5.3	5.5
S28	10.8	13.9	B8	10	10.2
S30	11.8	13.8	B9	5.2	4.2
S36	10.6	11.6	B10	8	2
S37	9.4	10.2	B11	5.4	5.2
Å7	6.7	11.7	B12	5.5	5.7
Å8	5.3	10.4	B13	6.1	3
Å9	7.5	7.2			
Å10	6.4	13.7			

3.2. Benthic fauna and SPI at the fjord stations

Temporal changes in mean number of species, abundance and biomass are shown for the 14 fjord stations in Fig. 2. Number of species and abundance showed a significant temporal decline, and the posterior (SNK) test showed the following significances for species in different years: 1976 = 1986 > 2001 > 1997, and for abundance: 1976 > 1986 = 2001 > 1997. Biomass showed no significant trend (P = 0.087). The fauna was particularly impoverished in 1997; in the Stigfjord no animals were found at station S30 and only one individual in each of three samples at stations S28 and S36. In the Ellösfjord only between 6 and 8 species were recorded in total at each station.

In the Stigfjord, *Corbula gibba* was dominant at many stations in all years of sampling. A mean of 815 *Abra alba* per 0.1 m^2 was recorded at station S30 in 1976. *Thyasira flexuosa* and *Phoronis mülleri* were frequently found at some stations in 1976 and 1986, and *Scalibregma inflatum* was abundant in 1986. In 1976, *Corbula gibba* was abundant at station E1 in the Ellösfjord, and *Heteromastus filiformis, Chaetozone setosa* and *S. inflatum* at station E4. In other years only few individuals were recorded at all E-stations. *Abra alba, Abra nitida, Nucula nitidosa, Mysella bidentata* and *Amphiura filformis* were dominants in the Åbyfjord, the latter species at the deep station Å10. Some large, calcareous species found only occasionally were excluded from the biomass recordings (see legend of Fig. 2).

A separate MDS ordination analysis (not shown) for each of the three fjords and each of the four years showed within-year similarity to be highest. Thus, the fauna had a more similar composition within a certain year at the various stations than within a particular station between years. The combined MDS plot for all stations and years is shown

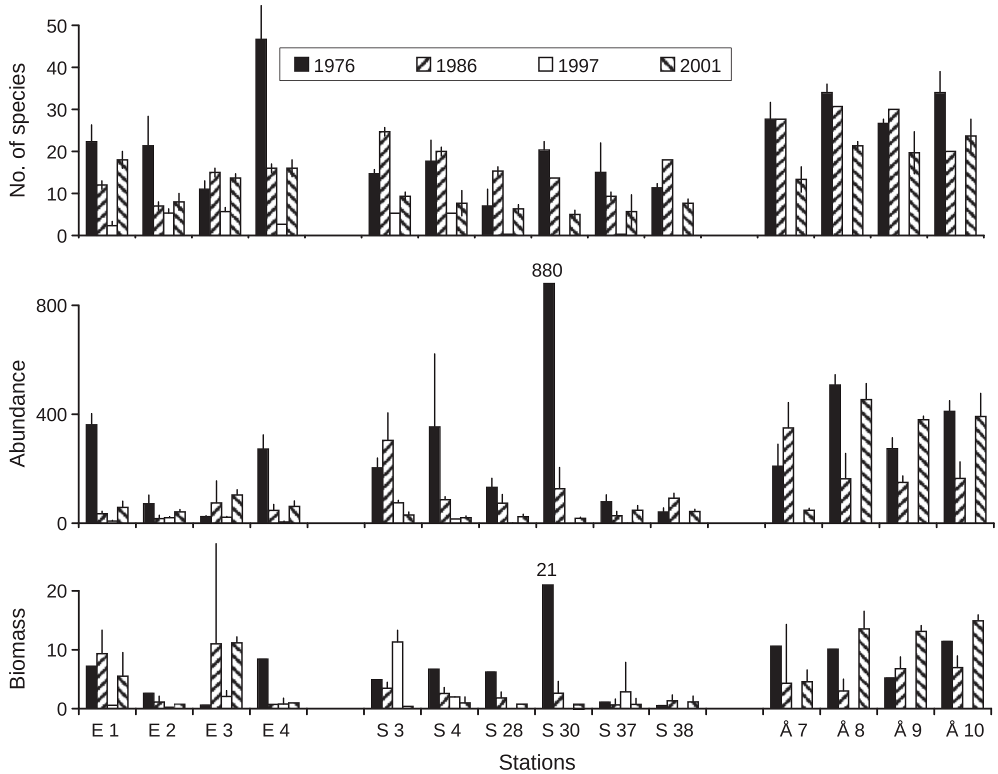

Fig. 2. Mean (with SD, n = 3) number of species, abundance and biomass (wet weight) per 0.1 m^2 of the benthic infauna in the Ellösfjord (E stations), Stigfjord (S stations) and the Åbyfjord (Å stations) in 1976, 1986 (from (Josefson and Rosenberg, 1988), 1997 and 2001. *Arctica islandica, Brissopsis lyrifera, Echinocardium cordatum* and *Aporrhais pespelicani* were excluded from the biomass data presentation.

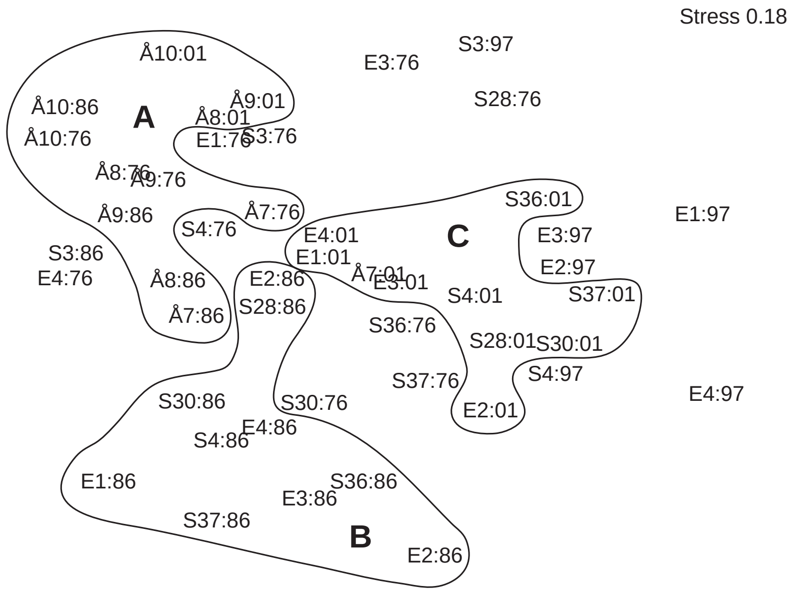

Fig. 3. Multi dimensional scaling (MDS) plot for the faunal composition at the stations in the Ellösfjord (E), the Stigfjord (S) and the Åbyfjord (Å) for 1976 (76), 1986 (86), 1997 (97) and 2001 (01). The encircled areas are discussed in the text.

in Fig. 3. All stations from the Åbyfjord, except station Å7 in 2001, grouped rather well together (Group A) indicating that the faunal composition was different from the other two fjords. Ten stations in the Ellösfjord and the Stigfjord tended to group together in 1986 (Group B), and so did 9 stations from these two fjords in 2001 (Group C). In 1976 and 1997, the faunal composition was more heterogeneous in these two fjords.

In the SPI study of January 1998, the mean (and SD) depth distribution of aRPD at the stations in the Ellösfjord was 1.2 cm (0.44) and at the stations in the Stigfjord it was 2.0 cm (0.41). Corresponding values of the BHQ indices were 2.6 (0.73) and 3.7 (0.89), respectively. These BHQ indices correspond to the faunal successional stage 1 of the Pearson-Rosenberg model indicative of significant disturbance.

3.3. Benthic fauna and SPI at the coastal stations

Temporal changes in mean number of species, abundance and biomass at the 12 coastal stations are shown in Fig. 4. Highest numbers of species over the three years combined were found at stations B6, B7 and B12. The three most abundant species at any station and sampling year are listed in Table 2. The number of species was significantly lower in 1998 compared to in 1987 at stations B2, B3, B8, B9 and B13, but significantly higher at stations B5 and B11 (SNK test). In 1998, only 2–4 species 0.1 m^{-2} were recorded at stations B2, B3, B8, B11 and B13. Station B11, located in a 30 m deep depression, was the most enclosed station in this study and with a poor fauna. *Corbula gibba, Glycera alba, Nephtys hombergi, Mysella bidentata* and *Nassarius* spp. were among species recorded several times as the three highest ranked species. Number of species, including all stations and years, increased significantly with depth ($r^2 = 0.28$).

In 1998, the abundances were <15 ind 0.1 m^{-2} at stations B2, B3, B4, B8, B10, B11 and B13, and at five of these stations the abundances were significantly lower than in 1987. Dominance ranks varied greatly between stations as well as between years. *Corbula gibba, Mysella bidentata* and *Nephtys hombergi* showed the greatest constancy. Abundance, including all stations and years, increased significantly with depth ($r^2 = 0.26$).

Biomass values were significantly lower in 1987 than in 1998 at stations B2, B5 and B13, while biomass was higher at station B7 in 1998 than in previous years. The increase at station B7 was caused by high numbers (402 ind 0.1 m^{-2}) and biomass (61.1

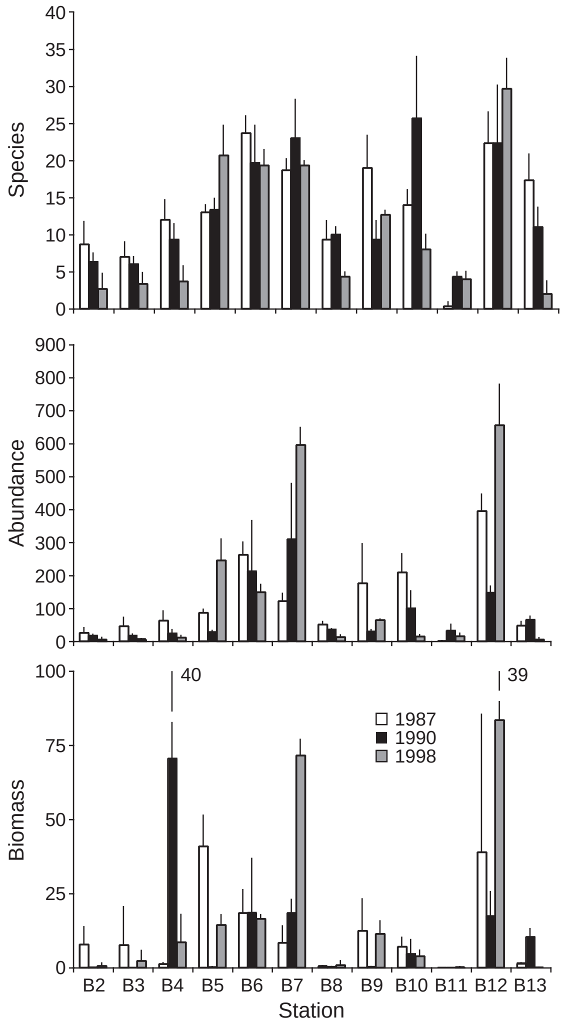

Fig. 4. Mean (with SD, n=3) number of species, abundance and biomass (wet weight) per 0.1 m^2 of the benthic infauna at the coastal stations in 1987 (from Tunberg, 1988), 1990 (from Hammar Martinsson, 1995) and 1998.

g 0.1 m^{-2}) of *Corbula gibba*. At stations with few species, biomass values were also low: <9 g 0.1 m^{-2}. Large individuals of Arctica islandica with high biomass were recorded at station B12 in 1987 (1 ind 85 g) and 1998 (2 ind 224 g) and at station B4 in 1990 (4 ind 211 g).

The MDS ordination separated the sampling results into two groups (Fig. 5): those sampled in 1987 (Group A) and those from 1990 (Group B). The faunal composition was more heterogeneous in 1998, but the deeper (mean depth 24 m) stations C5, C6, C7 and C12, with dominants such as *Abra* spp. and *Mysella bidentata,* were closer together than the other more scattered and shallow (mean depth 15 m) C stations.

Mean BHQ indices analysed from the SPIs at the six transects were similar over the whole area: between 3.5 and 5.1 with 4.4 as a mean of all 60 stations. These BHQ indices correspond to successional stage 1 or a low stage 2 in the Pearson-Rosenberg model, i.e. they are indicative of disturbed benthic habitats.

3.4. Detached vegetation on or in the sediment

Macroalgae or *Zostera marina* were found at 20 of all 26 stations sampled with the Agassiz trawl. In most

Table 2
List of species being among the three dominans

Species/Years	1987	1990	1998
Abra spp.	6 (5)	9 (2)	10 (4)
Ampelisca brevicornis	4 (1)	0 (0)	3 (0)
Amphiura filiformis	1 (0)	3 (0)	4 (3)
Asteroidea	0 (0)	9 (2)	0 (0)
Asteropecten irregularis	0 (0)	9 (2)	0 (0)
Capitella capitata	1 (1)	1 (1)	1 (0)
Corbula gibba	9 (1)	12 (6)	11 (5)
Echinocardium cordatum	3 (0)	4 (3)	7 (2)
Echiurus echiurus	5 (1)	0 (0)	0 (0)
Echinoidea	5 (4)	1 (0)	0 (0)
Gattyana cirrosa	4 (1)	0 (0)	0 (0)
Glycera alba	2 (0)	4 (0)	7 (3)
Heteromastus filliformis	9 (2)	2 (0)	7 (1)
Hydrobidae	0 (0)	0 (0)	4 (1)
Luidia spp.	0 (0)	2 (1)	0 (0)
Malacoceros fuliginosus	1 (0)	0 (0)	1 (1)
Mysella bidentata	11 (3)	9 (5)	7 (4)
Nassarius spp.	0 (0)	10 (1)	6 (3)
Nephtys hombergi	11 (2)	9 (1)	5 (3)
Nephtys spp.	0 (0)	1 (0)	6 (1)
Nucula nitidosa	9 (4)	7 (2)	5 (3)
Onoba vitrea	2 (0)	3 (1)	0 (0)
Pectinaria koreni	10 (5)	1 (0)	0 (0)
Philine spp.	5 (0)	9 (3)	3 (0)
Pholoe spp.	6 (0)	6 (2)	6 (1)
Phoronis muelleri	8 (1)	5 (0)	4 (0)
Scoloplos arminger	9 (1)	0 (0)	0 (0)
Spisula subtruncata	5 (1)	0 (0)	2 (0)
Thyasira spp.	8 (0)	9 (4)	6 (0)
Venus spp.	0 (0)	8 (2)	3 (0)

Numbers indicate the number of stations the species was present (n=12) (and being among the top three species).

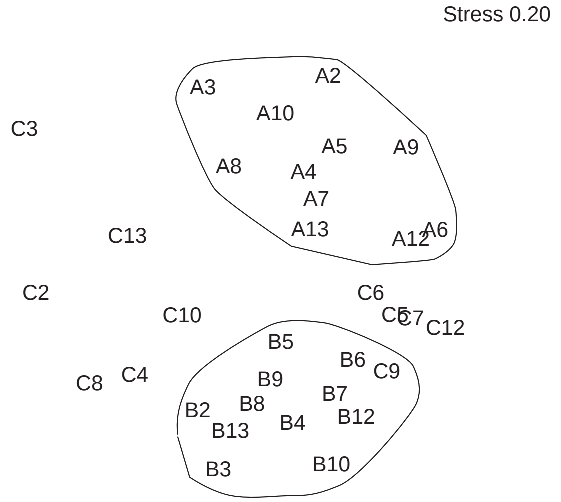

Fig. 5. Multi-dimensional scaling (MDS) plot for the faunal composition at the 11 coastal stations in 1987 (A stations), 1990 (B stations) and 1998 (C stations).

cases the amount was a few pieces of algae or a few blades of *Z. marina*. At five stations, however, the trawl was more than half-filled with macroalgae. These stations were: S36 (*Spermatochnus paradoxus, Polysiphonia fucoides, Gracelaria verrucosa*), E3 (same as for S36 plus *Laminaria* sp., *Fucus vesiculosus* and *Z. marina*), B9 (*Cystoclonium purpureum*, *Ceramium nodulosum, Plumaria plumosa, Ulva* sp., *Chondrus crispus*), B10 (*Polysiphonia fibrillosa, Lomentaria clavellosa*) and B13 (*S. paradoxus, F. vesiculosus,* Cyanobacteria).

4. Discussion

4.1. Organic matter in the sediment

The high organic contents, measured as ignition loss, observed in the present study indicate that most fjord stations were enriched compared to general conditions in the Skagerrak and Kattegat (Cato, 1992) both in 1986 and in 2001. Coastal stations seemed to have been enriched at B2 in 1990, and at B3, B5, B8 and B10 in 1987. These elevated ILs were associated with low number of species, abundance and biomass at stations B2, B3 and B8, which may have been due to reduced and unfavourable sedimentary conditions.

4.2. Possible impact of enrichment and hypoxia

The present study demonstrated that the fauna was significantly reduced in number of species and abundance in the Ellösfjord and the Stigfjord in 2001 compared to in 1976, and particularly so in 1997 when no animals were found at some stations. The benthic fauna in the Åbyfjord had comparatively more species, individuals and biomass. This was probably because the Åbyfjord is open towards the SW, the main wind direction, whereas the Ellösfjord and the Stigfjord are much more protected and have sills at the entrances. There was, however, a clear increase of organic matter between 1986 and 2001 at three of the four Å-stations, indicating increasing organic enrichment of these sediments.

Of all areas sampled in the present study, oxygen was only monitored (about monthly) in the Stigfjord from 1972 to 1989. In that period, at 20 m depth, oxygen concentrations of <2 cm^3 dm^{-3} were recorded ten times and seven times the concentrations were <1.5 cm^3 dm^{-3} (www.bvvf.com). Measurements were made ~1 m above the bottom and oxygen concentration is likely to be lower at the sediment water interface. It is unknown whether short-term hypoxia has occurred in the near-bottom water in the other areas. However, long-term significant declines and rapid seasonal declines (~1 cm^3 dm^{-3} mo^{-1}) in oxygen concentrations have been recorded in adjacent fjords (Rosenberg, 1990; Rosenberg et al., 2001). We therefore suggest that periodic appearance of low oxygen concentrations, perhaps in combination with high organic loading associated with drift algae (see below), is the most likely cause of the impoverished fauna in the Ellösfjord and the Stigfjord, and probably also at some coastal stations.

The sediments smelt of H_2S at some localities and dead leaves of *Zostera marina* were found in the sediment in the Stigfjord. Analysis of SPIs from the Ellösfjord and the Stigfjord showed that the mean aRPD was at 1.2–2.0 cm depth in the sediment, with deep-burrowing animals being rare or absent because the infauna was restricted to the top layer of the sediment. The MDS ordinations showed that the faunal composition changed between years both at the fjord and coastal stations. Thus, the benthic communities seem to be under periodic stress, and therefore development of a more functionally diverse and stable fauna has not occurred over the sampling period. High functional benthic biodiversity is associated with deep burrows of infauna in the sediment.

During hypoxic conditions in the Gullmarsfjord in 1997/98, the mean depth of aRPD in the sediment was ~1 cm but increased to 3–4 cm over the period of re-colonisation. BHQ indices were typically 2–6 at hypoxic stations, but >10 during norm-oxic conditions (Rosenberg et al., 2002). Thus, the low depth of the aRPD measured in the present study may be related to oxygen deficiency in the near-bottom water or too high a loading of organic carbon resulting in reduced conditions in the sediment. In Baltic sediments, an upward migration of the RPD was related to high organic content, increased temperature and low turbulence (Ankar and Jansson, 1973). In the Byfjord (Fig. 1), thinning of the RPD depth distribution in the sediment was associated with declining oxygen concentrations in the near-bottom water (Rosenberg, 1977).

4.3. Impact of the halocline

During 1971–1976, benthic communities were analysed and the faunal composition compared between 11 areas along the Swedish Skagerrak coast (Rosenberg and Möller, 1979). From that study it was concluded that the benthic faunal composition changed sharply relative to the mean vertical position of the halocline at ~15 m depth. Thus, it was suggested that the more stable conditions in salinity and temperature below the halocline supported a richer fauna. The number of species and abundance in the coastal study were positively correlated with depth, which may be a consequence of such stable conditions. Greater variation in salinity and temperature above and around the halocline may, in combination with low oxygen concentrations, induce enhanced disturbance to the infauna at these depths.

4.4. Possible impact of detached vegetation on the benthic fauna

The cover of green filamentous algae (mainly *Cladophora* spp. and *Enteromorpha* spp.) on shallow soft bottoms along the Swedish Skagerrak coast has increased over the last decades. Analysis of aerial photos show that algal mats covered 60 to 90% of the shallow soft bottoms along that coast in the summers 1994 to 1996 (Pihl et al., 1999). The algal mats were particularly abundant in the Stigfjord, just north of the Ellösfjord, and in several coastal areas sampled in the present study. The mats developed rapidly in early summer and typically had a biomass of 50 to 100 g dw m^{-2} and an annual primary production of ~900 g dw m^{-2} (Pihl et al., 1999). Most of the filamentous algae, both on mud flats and attached to hard substrate, are annual species that eventually sink to the bottom, decompose and enter the detritial food web after some time. Oxygen deficiency may develop on the sediment under the algae during the decomposition with significant negative effects on benthic organisms (Bonsdorff, 1992; Norkko and Bonsdorff, 1996; Vahteri et al., 2000). Some weeks after deposition of algal mats on the sediment, organic material from the algae could be incorporated in the superficial sediment (Bonsdorff et al., 1996).

The Fishery Board in Sweden has conducted demersal trawl surveys along the Skagerrak coast in spring and autumn since 2001 with a *Nephrops* trawl (27 m between the boards and 70 mm mesh in the cod-end). In the Stigfjord, four trawlings resulted in notes from 'vegetation present' to 'very, very much vegetation' (predominantly *Zostera marina* and brown algae). Algae were not reported from the Åbyfjord. At the coastal stations, large quantities of algae and *Z. marina* were reported at about half of the trawl stations each season. Most sample sites in the present study were either in enclosed fjord-like areas or within the Swedish Skagerrak archipelago. As the dominant wind is from southwest and west, algae will most probably be trapped and remain within the archipelago, where they will decompose at the bottom.

In a study in the Kungsbackafjord just south of Göteborg in June 1999, using the sediment profile imagery (SPI) technique, it was found that 43% of the 80 sites investigated at 2 to 35 m depth had macroalgae and/or *Z. marina* on or within the sediment, particularly at depths around the halocline (Nilsson and Rosenberg, 1999).

Direct evidence is lacking that detached vegetation has a negative impact on the benthos in the present study because algae were not sampled at the same time as the fauna. However, the observations of mass-occurrence of filamentous algae in shallow areas as well as on trawled bottoms suggest that algal mats on the bottom could contribute to the impoverished conditions for the benthic fauna in the fjords and the archipelago. This needs to be investigated in detail in the future.

4.5. Other possible causes of decline of the fauna

In the long term, climatic factors will probably have an important role in changing faunal composition (Hagberg and Tunberg, 2000), e.g. with enhanced rainfall more nutrients will be transported to the coast and promote primary production, which may increase the benthic faunal abundance and biomass (Josefson et al., 1993). Climatic factors may either enhance or reduce eutrophication-induced hypoxia and are likely to have a significant impact on the magnitude and temporal extension of such events (Justič et al., 1996).

4.6. Nutrient input

Over the last decades, impressive measures have been implemented in Sweden to reduce the input of nitrogen and phosphorus to coastal areas. Sewage treatment has reduced the discharges of these nutrients from urban areas. Despite the implementation of wetlands and several other measures in agricultural areas, no or only minor reductions have been assessed so far. An example is the terrestrial discharges to the Laholm Bay in the SE Kattegat. In this area the local sources have great impact on the primary production, and during the 1960 to 1980 period the transport of nitrogen via rivers more than doubled (Rosenberg et al., 1990). The authors suggested that for the oxygen conditions in this area to improve, the input of nitrogen would need to be reduced by at least half. Instead an increase has been recorded over the 1972 to 2001 period, and this is mainly due to leakage of nitrogen from forest land (Fleischer and Stibe, 1989; Stibe, 2003).

4.7. Tolerant taxa

In autumn 1988, seven abundant species were eliminated in the SE Kattegat during severe seasonal hypoxia, and six of these did not return within the next two years. Among the survivors were *Arctica islandica, Corbula gibba, Phoronis mülleri, Heteromastus filiformis* and *Myriochele* spp. (Rosenberg et al., 1992). These taxa were considered particularly tolerant to declining oxygen concentrations. The first three were also among the dominants together with *Nephtys hombergi, Ophiodromus flexuosus* and *Nassarius reticulata* close to the edge of anoxia in the Byfjord (Rosenberg, 1977). *C. gibba* and *N. hombergi* were also among the most stress-tolerant species towards hypoxia and organic enrichment in the inner part of the Gullmarsfjord (Rosenberg, 1973). Most of these species were also among the dominants along the Swedish Skagerrak coast (Table 2), which shows that these benthic communities were dominated by species tolerant to hypoxia. *C. gibba* has also been recorded in the Adriatic Sea in the Mediterranean as a species tolerant to hypoxia and also as a rapid coloniser after re-oxygenation of the bottom water (Hrs-Brenko et al., 1994). It is also a fast coloniser in Swedish waters and has been recorded in numbers of up to 4458 ind m^{-2} (Rosenberg, 1977). *C. gibba* has been characterised as a species found on the edge of azoic or anoxic zones (Pearson and Rosenberg, 1978). Thus, several of the species repeatedly found in the present study have proved to be tolerant to low oxygen conditions.

5. Conclusions

In the present study, the benthic fauna has been analysed from 14 stations in 3 fjords and 12 stations in the Swedish Skagerrak archipelago. Samples have been taken in 3 to 4 different years over a time span of 11 to 33 years. A generally poor fauna was found in most areas, and conditions had generally worsened relative to the early sampling dates. Oxygen deficiency and possibly associated detached vegetation on the bottom are suggested to be the main causes of this deterioration. In addition, other studies in this part of Scandinavia, e.g. in the Kattegat, the Danish Belt areas, along the Norwegian Skagerrak coast and in the Baltic Sea demonstrate similar impacts, at least since the 1980s.

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