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Changes in zoobenthic community structure after pollution abatement from fish farms in the Archipelago Sea (N. Baltic Sea)

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Abstract

Long-term changes in sediment macrofauna communities at two sites affected by fish farming in the Archipelago Sea, south-west Finland have been investigated. Sampling stations in the Särkänsalmi Strait and Kaukolanlahti Bay, previously investigated 1982–1991, were revisited in 1994, 1995 and 1998 to detect signs of recovery following a decrease in organic load since 1990 and 1991, respectively. The results indicate a partial recovery in Särkänsalmi during post-pollution years, whereas no improvement has taken place in Kaukolanlahti. The improvement in Särkänsalmi is shown by a significant increase in the number of species and total abundance, and by the community structures becoming more similar over time. On the other hand, a significantly decreased number of species, abundance and biomass values over time as well as the occurrence of defaunated anoxic sediments, are clear signs of continued deterioration in Kaukolanlahti. Differences in the recovery potential of the two water areas are interpreted as consequences of topography and water exchange patterns causing differences in oxygen saturation. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Aquaculture; Eutrophication; Long-term changes; Organic enrichment; Recovery; Sediment macrofauna; Baltic Sea

1. Introduction

During the 1980s, fish farming increased rapidly in the Finnish Archipelago Sea (Enell & Ackefors, 1991; Mattila, 1993), which recently has drawn attention to the

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ecological consequences of aquaculture (Bonsdorff, Blomqvist, Mattila & Norkko, 1997a, b; Jumppanen & Mattila, 1994). Several monitoring programs focusing on environmental problems in connection with fish farming have been initiated. However, many of these programs have suffered from a lack of background data or lack of comparable control sites. In addition, all programs hitherto have been terminated after pollution cessation or abatement.

Structural changes in benthic macrofauna due to fish farming have been reported world-wide (e.g. Camargo, 1992; Johannessen, Botnen & Tvedten, 1994; Ritz, Lewis & Shen, 1989; Tsutsumi, Kikuchi, Tanaka, Higashi, Imasaka & Miyazaki, 1991), although only a few authors have focused specifically on the community recovery following organic pollution abatement (Karakassis, Hatziyanni, Tsapakis & Plaiti, 1999; Lu & Wu, 1998; Oug, Lein, Kufner & Falk-Petersen, 1991). The recovery potential of an area after organic enrichment depends on the abiotic and biotic factors that determine the benthic community and on the tolerance among the species of hypoxia and anoxia (Diaz & Rosenberg, 1995). The recovery after periods of hypoxia is relatively quick in open coastal areas regulated by abiotic factors (Bonsdorff, 1983; Bonsdorff, Leppäkoski & Österman, 1986), whereas the recovery in sheltered communities, driven by biotic interactions, often may be delayed due to occurrence of permanent changes (Duineveld, Künitzer, Niermann, De Wilde & Gray, 1991). The vulnerability of a receiving water area and the scale of an impact also vary depending on the size of the farm, the amount of pollutants discharged and the carrying capacity of the surrounding sea area (Wallin & Håkansson, 1992). More specifically, basic characteristics of the water area such as topography, hydrodynamic conditions, water turbidity, presence or absence of a sharp temperature stratification and water exchange patterns will be crucial both for the community responses and for the ability of the affected ecosystems to recover after pollution abatement.

Despite a large amount of background literature describing macrozoobenthic communities in Finnish coastal waters, long-term investigations of anthropogenically induced effects are still scarce (Bonsdorff, Aarnio & Sandberg, 1991; Bonsdorff et al., 1997a, b; Häkkilä, Puhakka, Rajasilta & Bach, 1993; Mattila, 1993). Long-term studies are essential in order to provide information about the natural variability in undisturbed areas as well as for interpretation of chronic impact on whole ecosystems. Similarly, many pollution studies have solely used univariate statistical techniques, they have had difficulties in separating anthropogenic disturbance from natural variability (Kraufvelin, 1998; Morrisey, Howitt, Underwood & Stark, 1992) and they have often lacked appropriate methods to identify the structuring abiotic factors in a complex system of biotic interactions (Aschan, 1990; Dauer, Luckenbach & Rodi, 1993). We feel that a combination of univariate methods with non-parametric multivariate statistics cover both sophisticated techniques and straight-forward methods easily conceived by environmental managers and legislators.

The objectives of this paper are to detect structural changes in time and space in two different areas over a period of organic pollution (1982–1991) and after pollution abatement (1991–1998), and to search for possible signs of community recovery and plausible explanations for observed changes. Stations and years are compared by univariate and multivariate statistical techniques and the results are interpreted in light of information on environmental variables and previous findings about colonisation, ecological succession and general responses to stress in brackish water and marine environments. The two areas are first analysed independently to emphasise the changes over time and later as a whole to reveal past and present differences and to give a hint of the major modulating factors.

2. Materials and methods

2.1. Study areas

The sediment infauna were investigated in Särkänsalmi (60°28′N, 21°55′E) and Kaukolanlahti (60°27′N, 21°50′E) off Turku in the inner parts of the Archipelago Sea, south-west Finland (Fig. 1). The two study areas differ markedly with regard to topography, water exchange rate and hydrodynamic conditions. The sediment community structure and physical characteristics of Särkänsalmi and Kaukolanlahti are well documented in local monitoring reports since 1982 (Water Protection Association of south-west Finland, unpublished data). Part of this extensive background data set has been incorporated into this study.

2.1.1. Särkänsalmi

Särkänsalmi is a 9-km-long strait, which is divided into two basins by a sill at 12 m depth. The water masses in the two basins are exchanged independently (deep water of the northern basin moves northwards and deep water of the southern basin moves southwards). The total area of the strait is 4 km^2, mean water depth is 11.3 m and maximum depth is 38 m. Fish have been cultured since 1979 at a varying annual intensity. The mean annual production has been 78 tons of rainbow trout, reported as annual weight increase. In addition to organic load from the fish farms, the area is affected by nutrient input from agriculture and by municipal effluents. The total nutrient load has decreased considerably thanks to the construction of a municipal effluent treatment plant (1987) and markedly decreased production of fish from 1991 onwards, from a mean daily production of 540 kg in the 1980s to 180 kg in the 1990s. Between 1983 and 1987, the total annual input of phosphorus and nitrogen was 2500 and 19,000 kg, respectively. Since 1991, the pollution load into the area has decreased continuously and during recent years it has been estimated at 400 kg phosphorus and 3300 kg nitrogen per year.

2.1.2. Kaukolanlahti

Kaukolanlahti is a sheltered bay connected to the sea through two narrow and shallow straits, which give the area a semi-isolated character with the bottom water separated from the outer sea during summer stagnation. The water depth in both straits is less than 4 m, while the mean depth of the bay is 5 m. The area of the bay is 2 km^2 and the catchment area is 11 km^2. Farming of rainbow trout took place in the central basin between 1975 and 1991. In the 1980s, the diffuse background load of phosphorus and nitrogen to the bay was estimated at about 440 and 6600 kg per

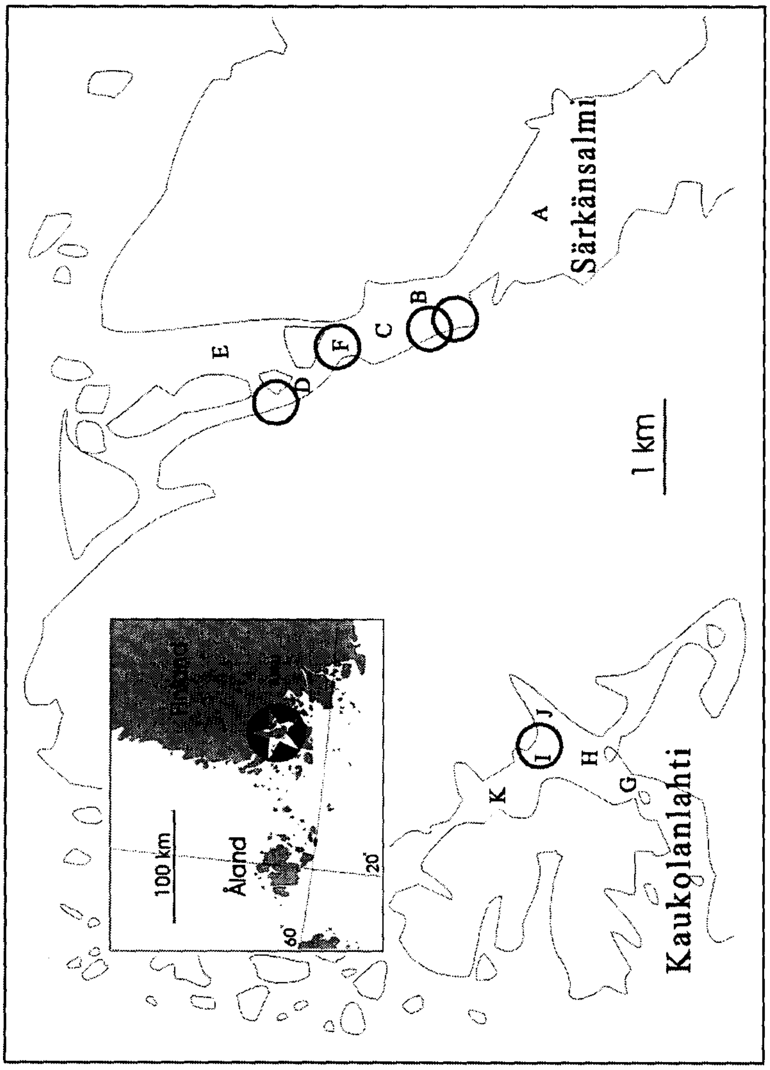

Fig. 1. Map of the investigated areas: Särkänsalmi stations A–F, Kaukolanlahti stations G–K. Circles indicate where fish farms have been located or are still operating. The star on the inset figure shows the location of the investigated areas.

year, respectively. The additional pollution load from the fish farm was of a similar extent: 400–600 kg phosphorus and 2000–5000 kg nitrogen per year. The fish production varied between 25 and 35 tons annual growth, which meant a mean annual food addition of 50 tons. The sedimentation in the area was 3 cm per year before the farming of fish started, while during the years of fish farming the yearly increase in sediment under the nets was about 6 cm. The pollution load from the fish farm in combination with the diffuse load has led to eutrophication of the bay with intermittent oxygen deficiency in the central basin.

2.2. Methods

Ten former field sampling stations for soft bottom macrofauna (Water Protection Association of south-west Finland, unpublished), five in Särkänsalmi (Stations A–E in Fig. 1) and five in Kaukolanlahti (Stations G–K in Fig. 1), were revisited in late summer 1994, 1995 (only Särkänsalmi) and 1998. All stations were relocated on the basis of photographed landmarks and depth measurements. In addition, samples were taken from a sixth station (F) below one of the former fish cages in Särkänsalmi. Five replicate samples were taken by an Ekman–Birge sampler (400 cm^2). All samples were sieved at sea through a mesh size of 500 μm. The samples were preserved in 4% hexamine-buffered formaldehyde solution. Additional sediment samples for analysis of organic content (loss on ignition) and water samples for temperature measurements and analysis of the oxygen concentration (Winkler analysis) were also taken at all stations. In the laboratory the animals were determined to lowest possible taxon. Determination of species was judged as unnecessary for oligochaetes and chironomids, since these groups had not always been separated into species at previous investigations (1982–1991). All animals were counted and weighed (precision 0.1 mg blotted wet wt.) and all five replicates were analysed separately. Because pooling was carried out during the previous investigations (1982–1991), the samples for each station and each year also had to be pooled to enable comparative statistical analyses.

2.3. Statistical analyses

Both univariate and multivariate statistical techniques were used. The development with time for number of species, abundance and biomass values in the investigated areas was presented graphically and a two-way factorial analysis of variance (ANOVA) without replication (using pooled data for stations) was used for the testing of differences among stations and years (same variables as above plus Shannon–Wiener diversity, calculated as base 2). The ANOVA was performed after checking for normality with Kolmogorov Smirnov's test and homogeneity of variances with Levene's test. When necessary, values were $\log_{10}(x+1)$ transformed. The multivariate techniques used were non-parametric ones as recommended for biological data by Clarke (1993). To obtain a reasonable balance between dominant and rare species, all data were square root transformed prior to analysis. Spatial and temporal differences among groups were tested by use of a two-way crossed analysis of similarity with no replication (ANOSIM2), after which non-metric multidimensional scaling (NMDS) was used for graphical presentation of between group and within group similarities. Finally, stress levels were examined tentatively both by use of a meta-analysis approach and by analysis of multivariate dispersion (MVDISP), once again using square root transformed data. The meta-analysis was expected to visualise the relative difference in community composition between Särkänsalmi and Kaukolanlahti in a combined NMDS-ordination of abundance data, whereas the analysis of multivariate dispersion intended to examine possible changes in relative variability between the stations over time. On several occasions the multivariate biotic community structure has been reported to show an increased variability at disturbed conditions compared to undisturbed ones (Warwick & Clarke, 1993). All univariate analyses were carried out on SPSS 7.5 for Windows, whereas multivariate analyses were carried out using the PRIMER software (Carr, 1996; Clarke & Warwick, 1994).

3. Results

3.1. Environmental data

In addition to the environmental variables recorded during the renewed sampling in 1994–1998, water monitoring data were available from two stations in Särkänsalmi and one in Kaukolanlahti. Oxygen levels were generally higher in Särkänsalmi than in Kaukolanlahti. The lowest value in Särkänsalmi (2.9 mg O_2 l^{-1} 1994) was registered at the shallowest and most sheltered station, D (Fig. 1), while all other stations presented values above 4 mg O_2 l^{-1}. In Kaukolanlahti, very low oxygen levels were found at the deeper inner stations in 1994 and 1998. Station H was anoxic both in 1994 and 1998. Station I was hypoxic (0.6 mg O_2 l^{-1}) in 1994, whereas the oxygen concentration was 2.7 mg O_2 l^{-1} in 1998. At station J, the concentration was 2.5 mg O_2 l^{-1} in 1994, whereas hypoxia (0.25 mg O_2 l^{-1}) could be registered 4 years later. Background values from Kaukolanlahti in 1982–1990 were generally higher, within the range 2.2–8.8 mg l^{-1}, which indicate a worsened oxygen situation during more recent years. Organic content of the sediment was lower in Särkänsalmi (mean value 8.3%) than in Kaukolanlahti (mean value 12%), where a large amount of organic material seems to be deposited in the middle of the bay.

3.2. Background data on biological variables

In the 1980s, Särkänsalmi was characterised by chironomids, oligochaetes and the clam *Macoma balthica* (L.) (Water Protection Association of south-west Finland, unpublished), all of which may benefit from moderate organic pollution (Leppäkoski, 1975). At that time, an area of 4 km^2 was described as semi-polluted, while the surroundings of station D (Fig. 1) were described as polluted with occurrence of hydrogen sulphide in the sediment and a fauna characterised by chironomids and the oligochaete *Potamothrix hammoniensis* (Mich.). By 1991, the sediment quality in the polluted area had started to improve and a thin oxygen-rich layer could be noted on top of the sediment. With regard to sediment fauna, the results from 1991 were similar to those in previous years.

In the 1980s, the total area of Kaukolanlahti was classified as eutrophic with bottoms closest to the fish farm (at 8 m) characterised as very polluted (Water Protection Association of south-west Finland, unpublished). At best, these communities were dominated by chironomids, including *Chironomus* cf. *plumosus*, which is able to tolerate almost oxygen-free conditions (Bonsdorff et al., 1996), but defaunated areas also occurred. Further away from the farm (< 6 m depth), the bottom was classified as semi-polluted with a relatively diverse community dominated by *Macoma balthica* and *Nereis diversicolor* O. F. Müller. The total abundance and biomass were lower in the deeper central areas than in the more shallow areas. The bottom fauna of Kaukolanlahti was probably impoverished before the initiation of fish farming, due to poor water exchange with the sea and relatively large pollution load from diffuse sources.

3.3. Post-pollution community analyses

Between 1983 and 1998, the macrofauna community in Särkänsalmi was represented by 18 species/taxa (Table 1). Station A differed from the other stations due to a numerical dominance (mostly > 80%) of *Monoporeia affinis* (Lindström). At B–E the communities were numerically dominated by either oligochaetes or chironomids. Biomass values were dominated by *Macoma balthica* (> 85%) at C and E, whereas chironomids dominated at D and crustaceans at A and B. The lowest mean number of species was found at station D (4.7), otherwise the values varied between 6 (B) and 7 (F). Mean total biomass showed the highest values for station C (135.2 g m^{-2}) mainly due to the presence of large individuals of *Macoma balthica* and *Saduria entomon* (L.), whereas the values were rather low for B (15.6 g m^{-2}) and D (29.5 g m^{-2}). Considering temporal changes in Särkänsalmi, an increase in the number of species has taken place, which is partly due to the colonisation of *Marenzelleria viridis* (Verrill), *Mytilus edulis* L., *Hydrobia* spp., *Corophium volutator* (Pallas) and *Gammarus* spp. Also, total abundance seems to have increased with time.

In Kaukolanlahti, the macrofauna community was represented by 12 species/taxa (Table 1). Seven years after pollution abatement, totally defaunated sediments still occurred. An area with a mean radius of about 300 m from the spot where the fish farm had been situated was devoid of animals or had only one or two species present. Chironomids were the most dominant group at all stations, except at station K, which was numerically dominated by both chironomids and oligochaetes and where the biomass mainly was made up of *Macoma balthica*. During the study period a decrease in biomass could be noticed over time. Some species such as *Harmothoe sarsi* (Kinberg), *Halicryptus spinulosus* (von Siebold) and *Prostoma obscurum* Schulze have disappeared from station K, whereas *Monoporeia affinis* has disappeared from station G. Instead, *Potamopyrgus antipodarum* (Gray) has colonised both stations G and K and *Marenzelleria viridis* has colonised station K.

The main faunal attributes were analysed with respect to temporal changes and differences among stations in the two areas. Data from all stations and at all points in time were used. For Särkänsalmi, six stations (A–F) and six years (1983, 1987,

Table 1
Abundance (number of individuals/m^2) in Särkänsalmi (stations A–F) and Kaukolanlahti (stations G–K) 1982–1998

Species/group	Särkänsalmi						Kaukolanlahti				
	1983	1987	1991	1994	1995	1998	1982	1986	1990	1994	1998
Bivalvia											
Macoma balthica	138	87	364	145	94	275	206	50	91	17	16
Mytilus edulis	–	–	–	1	3	–	–	–	–	–	–
Gastropoda											
Potamopyrgus antipodarum	–	–	11	4	11	6	–	–	236	35	21
Hydrobia sp.	–	–	–	1	–	3	365	–	–	–	6
Crustacea											
Saduria entomon	6	2	–	8	6	4	–	–	–	–	–
Corophium volutator	–	–	–	–	1	2	–	–	–	–	–
Monoporeia affinis	74	495	331	307	933	648	2	–	–	1	–
Pontoporeia femorata	–	–	11	2	9	–	–	–	–	–	–
Gammarus sp.	–	–	–	2	–	–	–	–	–	–	–
Neomysis sp.	–	–	–	–	2	–	–	–	–	–	–
Polychaeta											
Harmothoe sarsi	14	25	–	–	61	8	2	–	–	–	–
Nereis diversicolor	5	–	–	–	–	1	16	13	–	2	2
Manayunkia aestuarina	–	–	7	–	–	–	–	–	–	–	–
Marenzelleria viridis	–	–	–	78	86	20	–	–	–	2	1
Polydora redeki	–	–	–	–	–	–	–	–	2	–	–
Oligochaeta	365	225	208	959	878	748	18	36	187	194	518
Insecta											
Chironomidae	343	341	435	747	213	498	1142	820	1126	284	201
Nemertinea											
Prostoma obscurum	–	–	4	–	–	–	4	–	20	–	–
Priapulida											
Halicryptus spinulosus	2	2	11	8	7	5	2	–	–	–	–
Total abundance	947	1176	1382	2261	2302	2218	1757	919	1662	535	765
Number of taxa	8	7	9	12	13	12	9	4	6	7	7

1991, 1994, 1995, 1998) were compared to each other, whereas five stations (G–K) and five different years (1982, 1986, 1990, 1994, 1998) were analysed for Kaukolanlahti (Fig. 2). Means and 95% confidence intervals are given for years with stations used as replicates. A two-way factorial ANOVA without replication was used on number of species, total abundance, total biomass as well as Shannon–Wiener diversity and showed that there were significant differences among stations for most

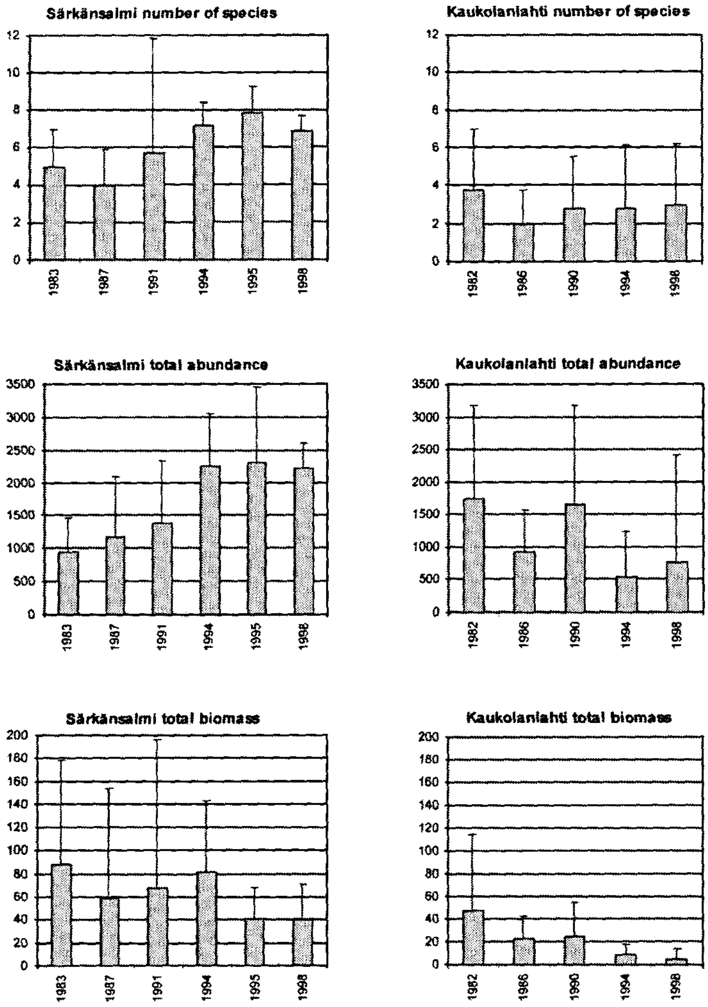

Fig. 2. Temporal differences in mean values (±95% confidence intervals) for number of species, total abundance and total biomass in Särkänsalmi (pooled samples from stations A–F) and Kaukolanlahti (pooled samples from stations G–K) 1982–1998.

variables (Table 2). Regarding recovery, however, it is more interesting that significant differences over time have also occurred, i.e. an increase in the number of species and total abundance in Särkänsalmi, as well as a decrease in the number of species, total abundance and total biomass in Kaukolanlahti. The increase in the number of species in Särkänsalmi and the decrease in biomass in Kaukolanlahti are still significant after correcting for the 16 comparisons performed by Holm's sequential Bonferroni (Legendre & Legendre, 1998). A multivariate two-way crossed ANOSIM with no replication (ANOSIM2) further establishes the significant differences among stations at both sites and for both abundance and biomass data (Table 3). Regarding

Table 2
Two-way factorial analysis of variance (ANOVA) without replication on differences in number of species, abundance values, biomass values and Shannon–Wiener diversity among stations and years in Särkänsalmi (df = 5) and Kaukolanlahti (df = 4)[a]

Variable	F-value	Uncorrected significance value	Corrected significance value
Särkänsalmi stations			
Number of species	2.454	0.069 ns[c]	0.345 ns
Total abundance	0.565	0.726 ns	1.000 ns
Total biomass[b]	11.219	< 0.001***	< 0.001***
Shannon diversity	4.055	0.011*	0.090 ns
Särkänsalmi years			
Number of species	6.873	0.001***	0.008**
Total abundance	3.544	0.019*	0.133 ns
Total biomass	2.224	0.090 ns	0.360 ns
Shannon diversity	0.560	0.729 ns	1.000 ns
Kaukolanlahti stations			
Number of species	58.299	< 0.001***	< 0.001***
Total abundance[b]	10.773	< 0.001***	0.002**
Total biomass[b]	24.163	< 0.001***	< 0.001***
Shannon diversity	25.320	< 0.001***	< 0.001***
Kaukolanlahti years			
Number of species	4.736	0.010*	0.090 ns
Total abundance	3.999	0.020*	0.133 ns
Total biomass[b]	8.000	0.001***	0.010**
Shannon diversity	1.200	0.349 ns	1.000 ns

[a] Both uncorrected significance levels and values corrected by a sequential Bonferroni are given.
[b] $\log_{10}(x+1)$ transformation due to heterogeneous variances.
[c] ns, non-significant.
*$0.01 < P \leqslant 0.05$.
**$0.001 < P \leqslant 0.01$.
***$P \leqslant 0.001$.

temporal differences (with stations used as replicates at each time), this technique demonstrates that a significant change in macrofauna abundance has taken place in Kaukolanlahti, whereas all other differences are non-significant. Fig. 2 reveals that the temporal change in abundance in Kaukolanlahti constitutes a change for the worse.

NMDS-ordinations on Särkänsalmi (Fig. 3a) and Kaukolanlahti (Fig. 3b) abundance data visualise the development of community structure over time at the different stations. The sample from station H (1998) in Kaukolanlahti has been omitted for clarity, since it was 100% dissimilar (Bray–Curtis similarity) to all other samples. From the ordination it is evident that the station most distant to the farms and presumably the least disturbed is Särkänsalmi's station A, which is clearly different from all other stations throughout the investigation. It may also be noted that all stations appear to become more similar to station A over time. In particular stations B and D go through rapid changes after pollution abatement. In Kaukolanlahti,

Table 3
Two-way crossed analysis of similarity (ANOSIM) with no replication applied on differences between stations and years in Särkänsalmi and Kaukolanlahti on square-root transformed macrofauna data for global tests among stations and years[a]

Variable	Global Rho	Uncorrected significance value	Corrected significance value
Särkänsalmi abundance			
Differences among stations	0.675	< 0.001***	< 0.001***
Differences among years	0.114	0.175 ns[b]	0.525 ns
Särkänsalmi biomass			
Differences among stations	0.559	< 0.001***	< 0.001***
Differences among years	0.021	0.411 ns	0.525 ns
Kaukolanlahti abundance			
Differences among stations	0.426	0.001***	0.006**
Differences among years	0.370	0.003**	0.015*
Kaukolanlahti biomass			
Differences among stations	0.316	0.008**	0.032*
Differences among years	0.070	0.241 ns	0.525 ns

[a] Both uncorrected significance levels and values corrected by a sequential Bonferroni are given.
[b] ns, non-significant.
*$0.01 < P \leqslant 0.05$.
**$0.001 < P \leqslant 0.01$.
***$P \leqslant 0.001$.

the stations most distant from the former fish farm, G and K, cluster out separately, whereas the inner stations (H–J) seem to form a group of their own. It is noteworthy that all stations in Kaukolanlahti seem to go through a series of similar changes with time. All start at the bottom of the ordination scheme and head towards the top with time. At the same time the differences between stations seem to increase.

In the meta-analysis combination of Särkänsalmi and Kaukolanlahti abundance data into the same NMDS-ordination, Särkänsalmi stations generally cluster out to the left, whereas Kaukolanlahti stations may be found more or less in the middle or to the right (Fig. 4). Additionally, it may be noted that the two deepest stations in Särkänsalmi, A and B, appear to cluster out at one side of the ordination scheme, whereas the deepest stations in Kaukolanlahti, H–J, cluster out at the opposite side. The outer presumably less polluted stations, G and K, in Kaukolanlahti seem to have a community structure which resembles the poorer Särkänsalmi stations (C–F).

If the relative multivariate variability among all stations during all the years is calculated by MVDISP and plotted out for abundance and biomass data separately for Särkänsalmi and Kaukolanlahti, changes in 'stress' level in the two areas over time may be revealed (Fig. 5). A decrease in the relative multivariate dispersion (lower variability among stations A–F), suggesting a change towards less disturbed conditions, seems to take place in Särkänsalmi after 1991 for both abundance and biomass data. At the same time, the development of the relative multivariate dispersion goes in the opposite direction in Kaukolanlahti, i.e. the abundance and biomass lines rise during post-pollution years, which suggests continued deterioration rather than recovery.

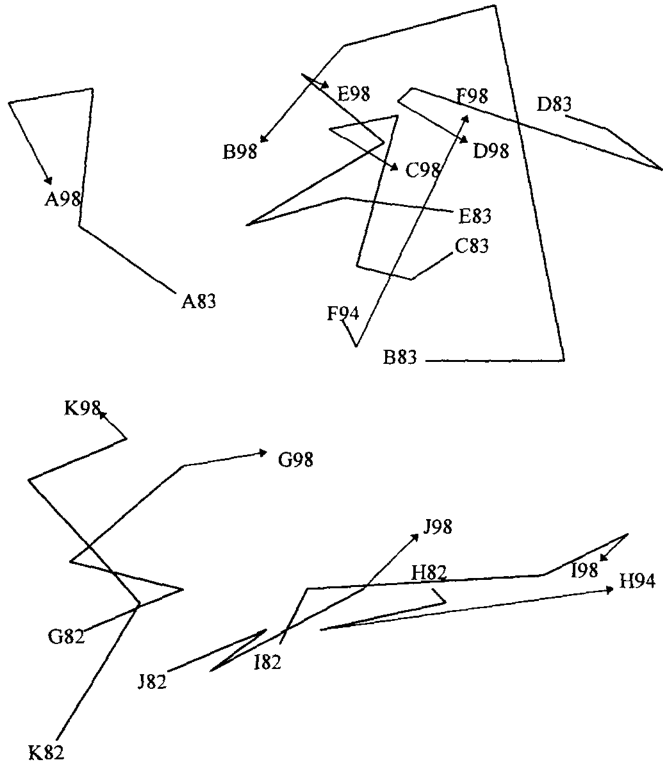

Fig. 3. Non-metric multidimensional scaling (NMDS)-ordination of square-root transformed abundance data in (a) Särkänsalmi (1983–1998; stations A–F), stress = 0.15; and (b) Kaukolanlahti (1982–1998; stations G–K), stress = 0.06. Station H (1998) in Kaukolanlahti has been omitted from the ordination.

4. Discussion

Qualitative and quantitative aspects of spatial and temporal changes in macrofauna community structure and their possible relations to organic enrichment have been analysed at two field localities during a time span of almost two decades covering both a pollution (9 years) and a post-pollution period (7–8 years). Unfortunately, no data are available from the period prior to the start of fish farming activities, but there are still signs that Särkänsalmi has gone through a recovery phase after pollution abatement in 1990, whereas no improvement has taken place in Kaukolanlahti during the same period. Differences in the recovery potential of the two water areas can mainly be interpreted as consequences of differences in topography, water exchange patterns and sediment conditions rather than the extent and duration of the pollution load.

Since the communities of the low-saline Baltic Sea are naturally stressed, it has been argued that they would be more resilient to perturbations than communities in full-saline and more benign environments (e.g. Gray, 1981; Jernelöv & Rosenberg,

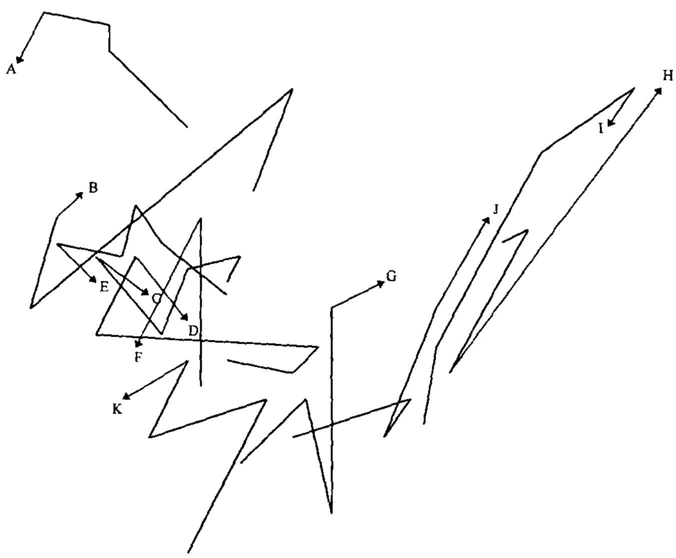

Fig. 4. Non-metric multidimensional scaling (NMDS)-ordination of square-root transformed abundance data in Särkänsalmi (1983–1998; stations A–F) and Kaukolanlahti (1982–1998; stations G–K), stress = 0.14. Lines demonstrate the development with time of the community structure at each station, whereas letters and arrowheads indicate the situation at each station 1998 (1994 at station H).

1976). However, many communities in the Baltic Sea contain just one species per functional group (Bonsdorff & Pearson, 1999), which probably means that the Baltic is more vulnerable to perturbations, at least those causing species reductions, than fully marine areas. Furthermore, due to the low number of species present, the early recovery is mainly driven by season and developmental stage within the normally dominating animal groups (Bonsdorff & Blomqvist, 1993). This means that the low species richness in itself may be considered as a factor delaying the recovery, at least compared to communities with a very high diversity. Nevertheless, the recovery potential for coastal benthic biota in the northern Baltic Sea has proven to be high (Bonsdorff, 1985).

The impact of, and subsequent recovery from, organic pollution are strongly affected by the local characteristics of the affected water area, such as hydrography and topography. In this study the recovery in Särkänsalmi is reflected by the successive increase in total abundance and species richness during the study years (sharpest increase during the early years of recovery, i.e. between 1991 and 1994). At the same time, the spatial differences between stations have become smaller, which is noted as a decreased relative multivariate dispersion. For Kaukolanlahti no similar trends can be noted. On the contrary, the communities of this area seem to have become poorer after cessation of fish farming, which can be observed as a decrease in the number of species, abundance and biomass values and an increase in relative multivariate dispersion, i.e. increased differences among stations. Throughout the investigation, Kaukolanlahti also had a poorer sediment fauna than Särkänsalmi

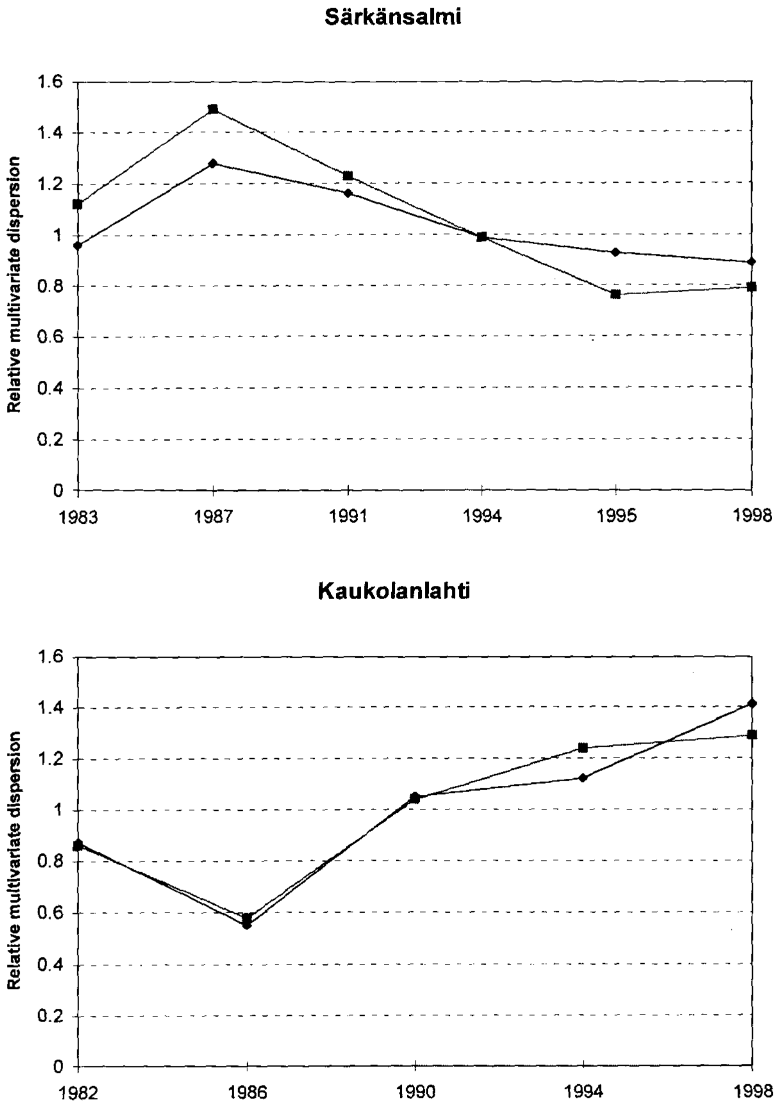

Fig. 5. Relative multivariate dispersion calculated for abundance and biomass data in Särkänsalmi (1983–1998) and Kaukolanlahti (1982–1998) (diamonds = abundance data and squares = biomass data).

despite the much higher organic load in the latter area, both at present and in the past. The marked differences in the physical environment between the two areas must therefore be responsible for the differences in recovery potential. The most important factors seem to be the poor water exchange in Kaukolanlahti (due to the narrow and shallow straits) combined with a strong summer stratification of the water, which has caused regular oxygen depletion in the central basin.

Occurrence of hypoxia is often the most harmful change in connection with organic enrichment and a major factor structuring benthic communities (Diaz & Rosenberg, 1995; Rosenberg & Loo, 1988; Schaffner, Jonsson, Diaz, Rosenberg & Gapcynski, 1992). In areas with regularly occurring hypoxic conditions, the benthic community often remains in a poor, pioneer, stage (Weigelt, 1991). In Särkänsalmi low oxygen values were found at the most sheltered inner stations, while oxygen concentrations were higher at the deeper stations further south in the strait where water circulation was good. The total defaunation in Kaukolanlahti during summer stratification appeared to depend on oxygen deficiency in the bottom water and accumulation of hydrogen sulphide in the sediment. Anoxic conditions were registered both in 1994 and 1998. A poor sediment fauna, solely consisting of *Chironomus* cf. *plumosus*, was also present in Kaukolanlahti in areas with oxygen concentrations as high as 3.6 mg l^{-1}. According to Diaz and Rosenberg (1995), a radical change in oxygen concentrations occurs just above the sediment surface. Therefore, it might be suspected that the oxygen concentrations reported in the present study did not correctly describe the actual situation in the water–sediment interface, i.e. they may sometimes have been over-estimated, since water sampling may not always have been carried out right above the sediment surface.

A comprehension of successional patterns in connection with the recovery of estuarine ecosystems requires thorough insight into the system considered, knowledge of the factors affecting community development and the ability to separate successional patterns from natural long-term variations in the ecosystem (Bonsdorff, 1985; Rumohr, Bonsdorff & Pearson, 1996). Since the benthic communities had not been investigated prior to the start of fish farming in 1975 in Kaukolanlahti and in 1979 in Särkänsalmi, it is difficult to specify exactly the degree of recovery after pollution abatement. Furthermore, the investigation suffers from a lack of an extensive environmental data set and its poorly designed sampling in space and time, which complicates interpretations of causal relationships (Bignert, Göthberg, Jensen, Litzén, Odsjö, Olsson & Reutergårdh, 1993; Eberhardt & Thomas, 1991; Hurlbert, 1984). This study would also need a longer time perspective in order to be more decisive with regard to whether the recovery in Särkänsalmi can be considered as permanent and how long the recovery in Kaukolanlahti will be delayed.

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References

Aschan, M. (1990). Changes in softbottom macrofauna communities along environmental gradients. *Annales Zoologici Fennici, 27*, 329–336.

Bignert, A., Göthberg, A., Jensen, S., Litzén, K., Odsjö, T., Olsson, M., & Reutergårdh, L. (1993). The need for adequate biological sampling in ecotoxicological investigations: a retrospective study of twenty years pollution monitoring. *Science of the Total Environment, 128*, 121–139.

Bonsdorff, E. (1983). Recovery potential of macrobenthos from dredging in shallow brackish water. In L. Cabioch, M. Glémarec, & J.-F. Samain, *Oceanologica Acta*, Proceedings 17th European Marine Biology Symposium, pp. 27–32.

Bonsdorff, E. (1985). *Recovery potential of the fauna of brackish-water softbottoms and marine intertidal rockpools*. PhD thesis, Department of Biology, Åbo Akademi University, pp. 1–37.

Bonsdorff, E., & Blomqvist, E. M. (1993). Biotic couplings on shallow water soft bottoms — examples from the Northern Baltic Sea. *Oceanography and Marine Biology: an Annual Review, 31*, 153–176.

Bonsdorff, E., & Pearson, T. H. (1999). Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: a functional group approach. *Australian Journal of Ecology, 24*, 312–326.

Bonsdorff, E., Leppäkoski, E., & Österman, C.-S. (1986). Patterns in post-impact successions of zoobenthos following physical and chemical disturbance in the northern Baltic Sea. Publication of the Water Research Institute, National Board of Waters, Helsinki *68*, 117–121.

Bonsdorff, E., Aarnio, K., & Sandberg, E. (1991). Temporal and spatial variability of zoobenthic communities in archipelago waters of the northern Baltic Sea — consequences of eutrophication? *Internationional Revue der gesamten Hydrobiologie, 76*, 433–449.

Bonsdorff, E., Diaz, R. J., Rosenberg, R., Norkko, A., & Cutter, G. R. (1996). Characterization of softbottom benthic habitats of the Åland Islands, northern Baltic Sea. *Marine Ecology Progress Series, 142*, 235–245.

Bonsdorff, E., Blomqvist, E., Mattila, J., & Norkko, A. (1997a). Coastal eutrophication: causes, consequences and perspectives in the archipelago areas of the northern Baltic Sea. *Estuarine, Coastal and Shelf Science, 44*, 63–72.

Bonsdorff, E., Blomqvist, E., Mattila, J., & Norkko, A. (1997b). Long-term changes and coastal eutrophication. Examples from the Åland Islands and the Archipelago Sea, northern Baltic Sea. *Oceanologica Acta, 20*, 319–329.

Camargo, J. A. (1992). Structural and trophic alterations in macrobenthic communities downstream from a fish farm outlet. *Hydrobiologia, 242*, 41–49.

Carr, M. R. (1996). *PRIMER user manual* (pp.1-42), Version 4.0, UK: Plymouth Marine Laboratory.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology, 18*, 117–143.

Clarke, K. R., & Warwick, R. M. (1994). *Changes in marine communities: an approach to statistical analysis and interpretation*. Plymouth Marine Laboratory: Natural Environment Research Council.

Dauer, D. M., Luckenbach, M. W., & Rodi, A. J. (1993). Abundance biomass comparison (ABC method) — effects of an estuarine gradient, anoxic/hypoxic events and contaminated sediments. *Marine Biology, 116*, 507–518.

Diaz, R. J., & Rosenberg, R. (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: an Annual Review, 33*, 245–303.

Duineveld, G. C. A., Künitzer, A., Niermann, U., De Wilde, P. A. W. J., & Gray, J. S. (1991). The macrobenthos of the North Sea. *Netherlands Journal of Sea Research, 28*, 53–65.

Eberhardt, L. L., & Thomas, J. M. (1991). Designing environmental field studies. *Ecological Monographs, 61*, 53–73.

Enell, M., & Ackefors, H. (1991). *Nutrient discharges from aquaculture operations in Nordic countries into adjacent sea areas*. In: International Council for the Exploration of the Sea (ICES). C.M.1991/F:56. Ref. MEQC, pp. 1–17.

Gray, J. S. (1981). *The ecology of marine sediments. An introduction to the structure and function of benthic communities*. Cambridge Stud. Mod. Biol., Vol. 2. Cambridge: Cambridge University Press.

Häkkilä, S., Puhakka, M., Rajasilta, M., & Bach, P. (1993). Spatial and temporal changes of the benthic communities in the SW archipelago of Finland. *Aqua Fennica, 23*, 187–191.

Hurlbert, S. H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monographs, 54*, 187–211.

Jernelöv, A., & Rosenberg, R. (1976). Stress tolerance of ecosystems. *Environmental Conservation, 3*, 43–46.

Johannessen, P. J., Botnen, H. B., & Tvedten, O. F. (1994). Macrobenthos: before, during and after a fish farm. *Aquaculture and Fisheries Management, 25*, 55–66.

Jumppanen, K., & Mattila, J. (1994). The development of the state of the Archipelago Sea and environmental factors affecting it. *Lounais-Suomen Vesiensuojeluyhdistys, Julkaisu, 82*, 1–206.

Karakassis, I., Hatziyanni, E., Tsapakis, M., & Plaiti, W. (1999). Benthic recovery following cessation of fish farming: a series of successes and catastrophes. *Marine Ecology Progress Series, 184*, 205–218.

Kraufvelin, P. (1998). Model ecosystem replicability challenged by the "soft" reality of a hard bottom mesocosm. *Journal of Experimental Marine Biology and Ecology, 222*, 249–269.

Legendre, P., & Legendre, L. (1998). *Numerical ecology* (2nd English ed.). Amsterdam: Elsevier Science B.V.

Leppäkoski, E. (1975). Assessment of degree of pollution on the basis of macrozoobenthos in marine and brackish-water environments. PhD thesis. *Acta Academiae Aboensis, Serie B, 35*, 1–90.

Lu, L., & Wu, R. S. S. (1998). Recolonization and succession of marine macrobenthos in organic-enriched sediment deposited from fish farms. *Environmental Pollution, 101*, 241–251.

Mattila, J. (1993). Long-term changes in the bottom fauna along the Finnish coast of the southern Bothnian Sea. *Aqua Fennica, 23*, 143–152.

Morrisey, D. J., Howitt, L., Underwood, A. J., & Stark, J. S. (1992). Temporal variation in soft-sediment benthos. *Journal of Experimental Marine Biology and Ecology, 164*, 233–246.

Oug, E., Lein, T. E., Kufner, R., & Falk-Petersen, I. B. (1991). Environmental effects of a herring mass mortality in northern Norway. Impact on and recovery of rocky-shore and soft-bottom biotas. *Sarsia, 76*, 195–207.

Ritz, D. A., Lewis, M. E., & Shen, M. (1989). Response to organic enrichment of infaunal macrobenthic communities under salmonid seacages. *Marine Biology, 103*, 211–214.

Rosenberg, R., & Loo, L. O. (1988). Marine eutrophication induced oxygen deficiency: effects on soft bottom fauna, western Sweden. *Ophelia, 29*, 213–225.

Rumohr, H., Bonsdorff, E., & Pearson, T. H. (1996). Zoobenthic succession in Baltic sedimentary habitats. *Archives for Fisheries and Marine Research, 14*, 179–214.

Schaffner, L., Jonsson, P., Diaz, R. J., Rosenberg, R., & Gapcynski, P. (1992). Benthic communities and bioturbation history of estuarine and coastal systems: effects of hypoxia and anoxia. *Science of the Total Environment*, 1001–1016 Supplement.

Tsutsumi, H., Kikuchi, T., Tanaka, M., Higashi, T., Imasaka, K., & Miyazaki, M. (1991). Benthic faunal succession in a cove organically polluted by fish farming. *Marine Pollution Bulletin, 23*, 233–238.

Wallin, M., & Håkansson, L. (1992). Morphometry and sedimentation as regulating factors for nutrient recycling and trophic state in coastal waters. *Hydrobiologia, 235/236*, 33–45.

Warwick, R. M., & Clarke, K. R. (1993). Increased variability as a symptom of stress in marine communities. *Journal of Experimental Marine Biology and Ecology, 172*, 215–226.

Weigelt, M. (1991). Short- and long-term changes in the benthic community of the deeper parts of Kiel Bay (Western Baltic) due to oxygen depletion and eutrophication. *Meeresforschung, 33*, 197–224.