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Zoobenthos of the outer archipelago waters (N. Baltic Sea) — the importance of local conditions for spatial distribution patterns

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The variability in species number and abundance of the soft-sediment benthic animal communities of the Archipelago Sea and western Gulf of Finland (SW Finland) is described in relation to environmental variables using multivariate analysis. The results show assemblages along the outer archipelago zone, facing the open sea, illustrating the importance of local conditions for the functioning of the zoobenthos. Based on clustering and multidimensional scaling of species abundance, the sampling sites formed distinct groups (benthic assemblages) linked to different geographical subareas. The main group, dominated by the amphipod *Monoporeia affinis,* was mainly found between the outer islands and skerries of the Archipelago Sea. Five additional groups were identified, which were geographically scattered and dominated either by the bivalve *Macoma balthica,* by *M. affinis*, or by oligochaetes. Based on rank correlation between the (dis)similarity matrices of species composition and environmental characteristics, the combination of dissolved oxygen saturation, temperature and sediment organic matter content best explained the species distribution and community structure of benthic fauna. The groups could also be positioned along an environmental gradient with increasing distance from the mainland, increasing depth and salinity, decreasing organic content (i.e. food availability), and declining temperature. The results are discussed in relation to environmental properties, highlighting the need for a baseline survey for future coastal monitoring, and in relation to the EC Water Framework Directive (2000/60/EC), stressing the relationship between environmental typology and biological (ecological) indicators of environmental health.

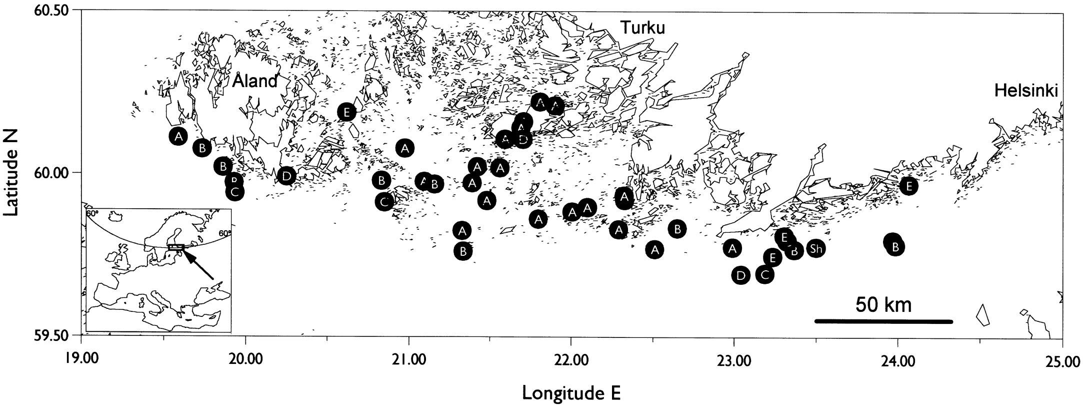

Fig. 1. Map of the investigated area (SW Finland), and the geographic location of all sampling sites. The sampling sites are marked by their corresponding MDS grouping (groups A–E, and station Sh) in Fig. 2. The basic map was derived from the GEBCO Digital Atlas, published by the British Oceanographic Data Centre, 1997.

Introduction

In order to accurately assess the potential impact of environmental stress on biota, it is vital to have baseline descriptions of diversity. In the present study we describe and analyze the benthic infauna of the archipelago waters of SW Finland. The archipelago area studied, encompassing the Åland Islands in the west, the Archipelago Sea and the westernmost archipelago region of the Gulf of Finland (59°45´–60°45´N and 21°00´–24°00´E) (Fig.1), is located at the junction between the Gulf of Finland, the Gulf of Bothnia and the Baltic Proper. It is characterized by an enormous topographic complexity, a mosaic of islands separated by basins and sounds. The Archipelago Sea, for instance, including about 35 000 islands, covers some 15 000 km^2, but the water volume is not more than about 300 km^3, as the average water depth is only 23 m (the deepest trenches reach about 150 m; Granö *et al.* 1999). The southwestern archipelago area is characterized by a strong seasonality, the average annual salinity range is between 5.5‰ and 7.5‰, and the surface temperature between slightly subzero and 22 °C (Haapala and Alenius 1994). During winter months the sea is covered with ice for up to three months (Seinä and Peltola 1991). The sea is non-tidal, but irregular water level fluctuations of up to one meter occur as a result of variations in air pressure and prevailing winds. The ecological state of the marine biota in the Archipelago Sea was described in Bonsdorff *et al.* (1997a, 1997b), and the overall state was recently reviewed by Suomela (2001). The current state of the coastal waters is assessed in Kauppila and Bäck (2001). Both these reviews report on gradual changes occurring in the coastal ecosystem, underlining the need for baseline surveys.

The geological and biological zonation in the Archipelago Sea ranges from sheltered inner bays (the ratio of land/sea > 1. Macrophyte vegetation belts, such as dense stands of *Phragmites australis* and in shallow bays Charophytes, are common as a buffer between land and water) to the intermediate zone (the ratio of land/sea is roughly equal) and the open outer archipelago (the ratio land/sea < 1; rocky shores and green/brown algal belts dominating). This zonation is caused by slow postglacial land uplift (about 0.5 cm a^{-1}) in combination with a tilting coastal plain, and to the water balance, with fresh water runoff from land, and upwelling of brackish water in the outer regions. The outer archipelago area forms an ecological transitory zone between the more sheltered inner coastal archipelago and the open sea, characterized by highly variable bottom topography and quality. Previous studies on zoobenthos in the outer archipelago include the classic pioneering work by Segerstråle (1933a, 1933b, 1960) for the Finnish south coast, and a survey by Sjöblom (1955) from the Archipelago Sea. The first descriptions of the benthic infauna specifically of the outer archipelago in the Åland Islands, was done by Norkko and Bonsdorff (1994). A corresponding but geographically less extensive zonation has been described and studied in the Tvärminne archipelago area, western Gulf of Finland (Häyren 1900, Niemi 1973). While macrofauna studies in the outermost archipelago have been scarce, the long-term succession of macrozoobenthos in one representative archipelago basin is well documented (Segerstråle 1933a, 1933b, Karjala and Lassig 1985, Kangas *et al*. 2001).

This study aims at describing the zoobenthic infaunal assemblages of the outer archipelago previously not comprehensively studied in SW Finland, northern Baltic Sea. The information serves as a first description of this coastal zone under the environmental typology requested by the EC Water Framework Directive (WFD 2000/60/EC). The importance of background information covering spatial heterogeneity for baseline studies is emphasised in e.g. Eberhardt and Thomas (1991) and in Osenberg and Schmitt (1996). The analysis is based on species richness and faunal abundance (biomass excluded in accordance with the WFD), and the variability of community structure in relation to environmental variables (cf. Elliott *et al*. 1999). The hypothesis for this effort is that although only small variations in species composition are expected to be found, the differences in dominance patterns will reflect the differences in environmental quality, and that this is best illustrated using multivariate methods.

Material and methods

In June 1995, the outer archipelago area (Fig. 1) extending from the western Gulf of Finland to the Åland Islands was sampled for soft bottom infauna above and below the depth of the thermo- and haloclines. In addition to macrofauna, sediment was sampled for organic content (measured as loss on ignition, hereafter referred to as LoI) in the 2 cm surface layer. Estimates of total carbon (C_{tot}; μmol g^{-1} dwt) and total nitrogen (N_{tot}; μmol g^{-1} dwt) of the sediment were made using equations linking LoI with N_{tot} and C_{tot} ($N_{tot} = 33.52 + 35.16 \times \text{LoI}$; $C_{tot} = 34.08 + 288.68 \times \text{LoI}$; Å. Danielsson, unpubl. data). Salinity, temperature and dissolved oxygen (saturation and concentration) were recorded for the near-bottom water layer about 50 cm above the sediment surface, using a CTD probe.

Macrofauna was analyzed from 43 sites (positioned using GPS and digitized on-board charts; between 15 and 88 m deep) (Fig. 1). The sites were selected to represent the scarcely studied outer archipelago zone, between the deeper open waters of the northern Baltic Proper and the Gulf of Finland, and the shallow and sheltered Archipelago Sea. The sites were selected to represent all soft-sediment types in the region (clay, sand, gravel, mud, and detritus-covered sediments, i.e. areas with high deposition of fresh organic matter), but potentially hypoxic or anoxic deep trenches were avoided. Three replicate samples per site were taken with a modified Olaussen-box corer (20 × 20 cm), sieved on a 0.5 mm screen, and stored in 4% buffered formaldehyde solution for later analysis in the laboratory. All animals (except oligochaetes and chironomids) were identified to species level and counted under a dissecting microscope. The entire material has been treated as one data set, following standard procedures for coastal monitoring (however using a 0.5 mm sieve rather than the commonly used 1.0 mm mesh, in order to be able to include also small and juvenile individuals of bivalves, amphipods and worms, not contributing much to biomass, but correctly reflecting the species dominance relationships; Bonsdorff (1988)).

The data (species richness and abundance data; biomass was not used in accordance with the guidelines for the EC WFD for linking environmental typology and zoobenthos) were analyzed using clustering techniques based on Bray-Curtis similarities, and non-parametric multidimensional scaling (MDS; non-transformed abundance values to maintain the faunal dominance patterns). Environmental variables (non-transformed) were related to abundance data (square root transformed; higher *r*-value than non-transformed) using rank correlation between the (dis)similarity matrices (BIOENV). All analyses were performed using the PRIMER software (Clarke and Ainsworth 1993, Clarke and Warwick 1994).

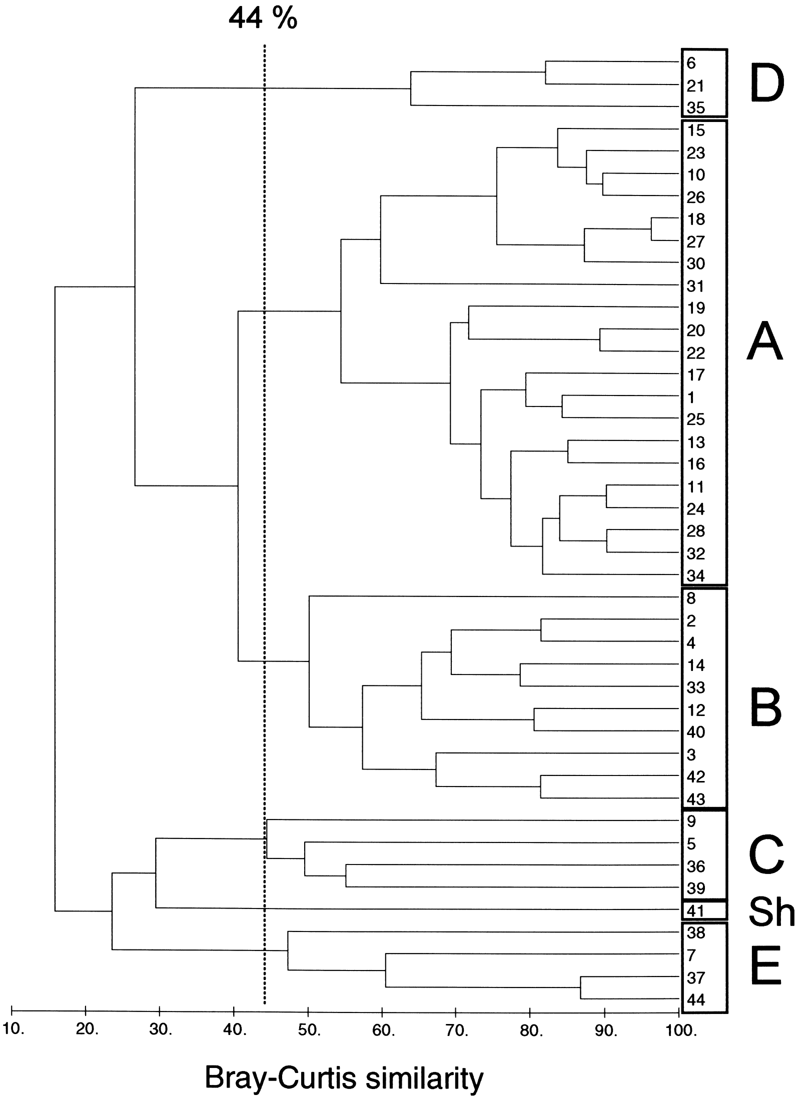

Fig. 2. Dendrogram for hierarchical clustering of the 43 sites sampled (group-average linking of Bray-Curtis similarities, non-transformed abundance data). The clustering of the sites corresponds to the major division line fixed at 44% similarity level.

Results

Based on clustering (Fig. 2) and MDS ordination (Fig. 3) of species abundance, the benthic fauna at the sampling sites form five distinct assemblages (A–E), with one sampling site (Sh) differing clearly from all others (Fig. 4 and Table 1). These assemblages are found in different environmental regimes, with differing characteristics (Fig. 1 and Table 1).

The largest group (A) is mainly comprised of sites inside the outer islands and skerries in the Archipelago Sea, characterized by abundant *Monoporeia affinis–Macoma balthica* dominated communities (Fig. 4). This group could be categorized as the "basic benthic archipelago community", with the highest number of species (21) present. In all, 21 of the 43 sites belong to this category (Table 1). The groups B and C are located outwards towards the open sea of group A. These groups are characterized by lower diversity (11 and 7 species, respectively), total abundance and role of the amphipod *M. affinis*. The groups D and E are more spatially scattered and dominated by either the bivalve *M. balthica* or oligochaetes and some chironomids.

The relationship between grouping of sites and their community structure and environmental variables (depth, organic content of the sediment, momentary bottom water temperature, salinity and oxygen saturation, as currently done in most Baltic Sea monitoring programs) is illustrated in Fig. 4. Based on correlation between the (dis)similarity matrices of species composition and environment, the combination of dissolved oxygen saturation, temperature and sediment organic matter content best explained the species distribution and community structure ($r = 0.44$, weighted Spearman rank correlation).

Groups A, B and C form an environmental cline with increasing depth (from 46 to 65 m; Table 1) and salinity (6.7 to 7.0 psu), and declining temperature (5.9 to 3.6 °C), and with high but declining oxygen saturation (86% to 71%). This environmental gradient coincides with reduced abundance and dominance of *M. affinis*. Group D represents shallow (22–39 m) sites characterized by good oxygen conditions, higher temperatures, but low organic content (4.8% LoI, i.e. about 1400 μmol C g^{-1} dwt sediment) supporting a *Macoma balthica* and chironomid-dominated assemblage, able to utilize the food sources available. Group E is characterized by high organic content (12.4% LoI, i.e. about 3600 μmol C g^{-1} dwt sediment) and low oxygen saturation (about 50%), which favors oligochaetes and partly *M. balthica*. Site Sundharun (Sh) differed from all other sites being coldest (3.3 °C) and with low diversity and total abundance.

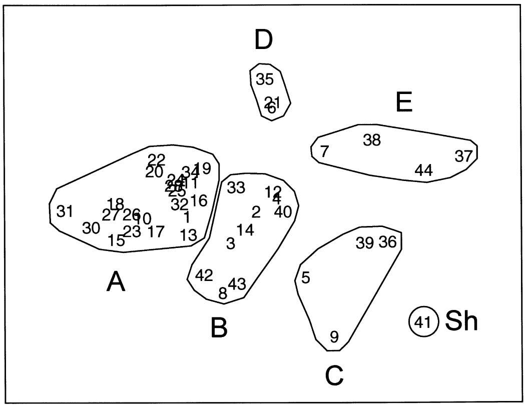

Fig. 3. A two-dimensional MDS ordination (stress = 0.12) of the sampling sites, based on similarities and groups, as presented in Fig. 2.

Discussion

The archipelago area from a Baltic perspective

Benthic community analysis of coastal and archipelago waters of the northern Baltic Sea have been performed in many areas, most often in connection with regular monitoring programs and/or point-source pollution control (e.g. Tulkki 1960, 1964, Leppäkoski 1975, Andersin *et al.* 1977, among the pioneers in Finland). Along the Estonian coast, southern Gulf of Finland, Seire (1992) and Kotta *et al.* (1999, 2000) have applied similar sampling designs in order to study point source and diffuse pollution, and in Sweden (northern Baltic Proper) Cederwall and Elmgren (1980) demonstrated the linkage between eutrophication and coastal benthic biomass. This was followed up by Modig and Olafsson (1998), who tested the specific sensitivity of the benthic infauna to hypoxic events. Similar efforts to the present one have been conducted in other local regions (for the southern Baltic Sea, e.g. Warzocha 1995, and Kube *et al.* 1996). In a wider, Baltic Sea, perspective, Rumohr *et al.* (1996) classified the benthic communities along the entire Baltic Sea gradient (from the Belt Sea to the inner reaches of the Gulf of Bothnia and Gulf of Finland) into successional stages in relation to oxygen conditions and sediment characteristics (basically organic content), and they identified a "basic Baltic community" resembling that described for the Archipelago Sea here (groups A and B). Laine (2003) analysed the Baltic Sea zoobenthos in relation to environmantal variability, also finding distinct assemblages, depending on local (regional) conditions in the sediment and water. It is evident, that the sediment-animal interactions are of great importance for gas- and nutrient exchange between the sediment and the water column, and the role of bioturbation is crucial in this process (Snelgrove and Butman 1994, Pearson 2001). In exposed regions, such as the present study area, the interactions between physical disturbance of the sediment surface and organic enrichment (*see* Karlson *et al.* 2002 for a review) may be crucial (Hall 1994, Widdicombe and Austen 2001), as is the seasonal input

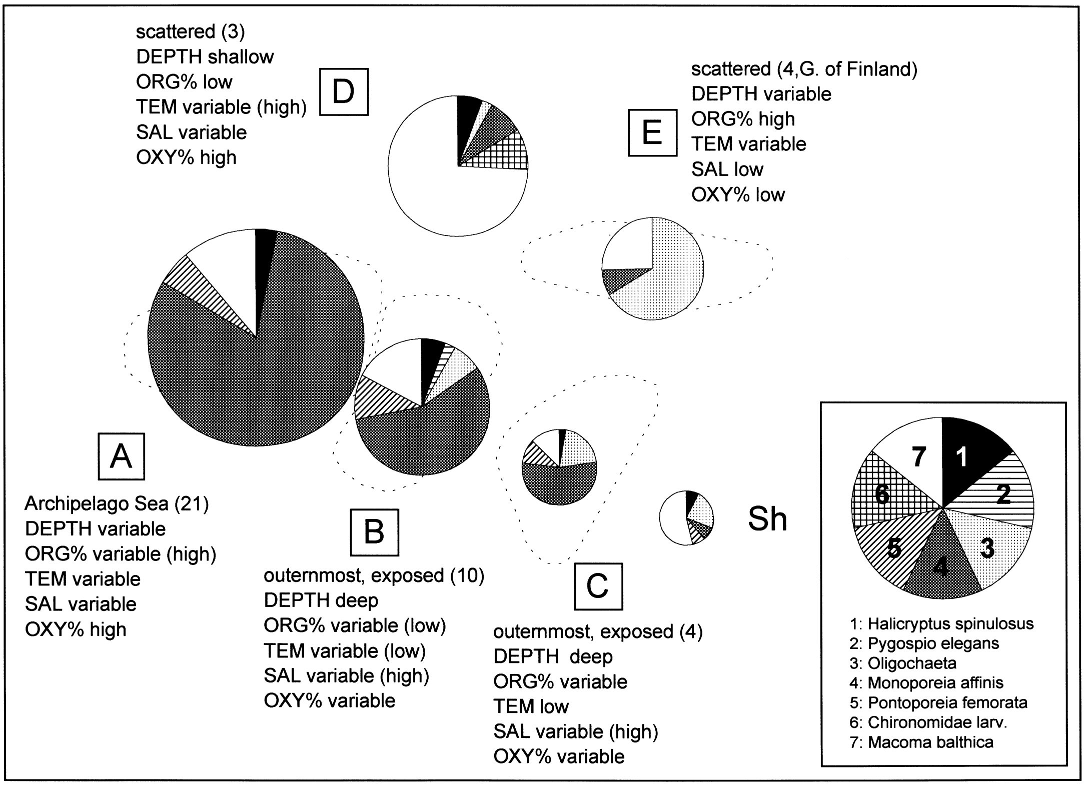

Fig. 4. Benthic community structure within MDS groups in relation to environmental parameters. The pie graphs illustrate the average species composition of the groups, pie diameter being relative to the total abundance (only species forming 95% of total abundance included, data from Table 1). The environmental conditions of the area (no. of stations per grouping indicated) characterized based on averages and variability within the groups (Table 1).

of fresh organic matter from the pelagic zone (Bianchi *et al.* 2002).

Benthic infauna in monitoring

The interpretation of spatial patterns of zoobenthic communities along the Finnish coast and outer archipelago regions is complicated by the topographic complexity of the environment. This aspect has been studied along both environmental gradients (inner–outer archipelago; Aschan 1990), and along the coast in the deeper waters of the Gulf of Finland (e.g. Andersin and Sandler 1991). Bonsdorff (1988) described the gradual shifts from near-shore shallow (< 5 m) sandy bottoms, down to the deep (> 200 m) waters off SW Åland, and found a clear depth-dependency for most species recorded. In such upwelling zones, the importance of episodic events must also be stressed (Haapala 1994). For the inner, sheltered archipelago regions, extensive surveys have been performed on both spatial and temporal patterns of distribution and change of benthic infauna (Bonsdorff and Blomqvist 1992, Häkkilä *et al.* 1993, Hänninen and Vuorinen 2001, Kraufvelin *et al.* 2001). The changes recorded have generally been attributed to eutrophication (Bonsdorff *et al.* 1991, 1997a, 1997b, Jumppanen and Mattila 1994, Mattila 1994, Hänninen *et al.* 1999), but truly long-term data exist only for the innermost regions, already affected by anthropogenic stress when the first surveys were conducted (Sjöblom 1955, Tulkki 1960, 1964, Leppäkoski 1975). Thus we face the problem of “shifting baselines” when assessing the state of the environment for archipelago waters (*sensu* Dayton *et al.* 1998). As the current area of study is hydrographically and dynamically characterized by horizontal and vertical gradients of exposure, salinity, temperature, oxygen, nutrients, and productivity (Hänninen *et al*. 1999, Perus *et al*. 2001), it further stresses the importance of covering and identifying the habitat variability and spatial scales affecting the zoobenthic assemblages (Hewitt *et al*. 1998, 2001). The general spatial habitat pattern has been verified by both geographers and biologists

Table 1. Average number of species and abundance (ind. m^{-2} ± SD for total abundance; SD for individual species misleading, as the data in each group is based on information from 3 to 21 single stations), and environmental variables (mean and min/max values for all stations within the cluster) for the identified MDS groups (A–E and Sh). Species contributing 95% of total abundance in each group included.

MDS group	A	B	C	D	E	Sh
No. of sampling sites (*N* = 43)	21	10	4	3	4	1
Species abundance						
Priapulida						
Halicryptus spinulosus	254	153	17	172	28	13
Polychaeta						
Harmothoe sarsi	83	38	12	0	0	0
Marenzelleria viridis	2	2	0	0	0	0
Pygospio elegans	4	68	0	39	47	0
Fabricia sabella	0	0	0	0	3	0
Manayunkia aestuarina	0	0	0	19	0	0
Polychaeta unident.	1	0	0	0	0	0
Oligochaeta	72	187	119	72	915	38
Crustacea						
Saduria entomon	16	12	15	39	0	0
Monoporeia affinis	6406	1483	321	239	110	13
Pontoporeia femorata	420	278	60	8	11	13
Corophium volutator	1	0	0	0	0	0
Insecta						
Chironomidae larv.	94	3	0	275	7	0
Gastroppda						
Hydrobia sp.	9	0	0	28	0	0
Potamopyrgus jenkinsi	3	0	0	6	0	0
Gastropoda unident.	2	0	0	0	0	0
Bivalvia						
Macoma balthica	900	457	77	2192	351	88
Mytilus edulis	9	32	0	11	4	0
Total abundance	8277 ± 4006	2711 ± 667	621 ± 209	3100 ± 809	1477 ± 729	163
Total no. species	21	11	7	12	9	5
Environmental variables						
Depth (m)	46 (15/88)	58 (35/74)	65 (42/80)	31 (22/39)	43 (30/55)	43
Org. matter content % of dwt	9.3 (1.2/14.8)	5.4 (0.7/15.8)	8.6 (3.1/14.1)	4.8 (0.8/9.4)	12.4 (4.1/15.8)	8.0
N_{tot} (μmol g^{-1} sediment dwt)	360.5	223.4	335.9	202.3	469.5	314.8
C_{tot} (μmol g^{-1} sediment dwt)	2718.8	1593.0	2516.6	1419.7	3613.7	2343.5
Temperature (°C)	5.9 (3.0/78.9)	4.2 (2.9/6.3)	3.6 (3.1/4.2)	7.0 (4.5/9.7)	5.1 (3.1/7.2)	3.3
Salinity (psu)	6.7 (6.5/7.5)	6.8 (5.9/7.1)	7.0 (6.4/7.3)	6.5 (5.9/6.8)	6.3 (5.3/7.1)	6.7
Dissolved oxygen (mg l^{-1})	10.7 (9.0/12.6)	10.4 (7.5/13.2)	9.4 (6.2/11.8)	10.4 (10.2/10.5)	6.7 (4.0/10.6)	–
Diss. oxygen saturation (%)	86 (73.2/101.0)	80 (55.6/104.4)	71 (46.2/90.5)	88 (86.1/89.8)	53 (30.3/86.2)	–

(Numers and van der Maarel 1998, Granö *et al.* 1999). However, although defining reference communities for these regions is hard, it can still be done for the outermost regions, as the present data seem to fit the general successional (temporal or spatial) patterns described for outer coastal regions elsewhere in the Baltic (Rumohr *et al.* 1996). Also, the relationships between the fauna and the sediment properties identified in this study resemble those previously described for the Åland archipelago (Bonsdorff *et al.* 1996, 1997b).

It seems as if the coastal zoobenthic assemblages have been relatively stable in the Archipelago Sea since the 1980s, and no clear longterm trends have been recorded (Kangas *et al.* 2001). This further strengthens the potential use of the present information as a reference base for the outermost archipelago region, and the assemblages defined give us a tool for future comparisons. Over a longer time span, however, significant changes in community composition and productivity have been recorded, but generally the studies from the early to mid 20th century do not contain reliable information on environmental conditions (with the exception for salinity and temperature, and sometimes oxygen), and thus evaluation of causal relationships is difficult (Segerstråle 1933a, 1933b, 1960, Kangas *et al.* 2001).

Importance of key species

The combination of sediment organic content (a rough measure of food supply for the infauna; Bonsdorff *et al.* 1991, 1996), temperature and oxygen saturation controls the zoobenthic assemblages of these outer archipelago regions. Hence, high oxygen concentrations and a good supply of food are the best combination for a *Monoporeia affinis*-dominated community, while slightly warmer waters and shallower depths with high organic content favor the *Macoma balthica* community. Segerstråle (1933a, 1933b) reported the depths around 20 meters to be characterized by *M. balthica*, whereas deeper areas were characterized by *M. affinis*. The results from the present study confirm these patterns and in this study the deeper areas (clusters A–C) had the highest abundance of amphipods (*M. affinis* and some *Pontoporeia femorata*). It is noteworthy that the invasive polychaete *Marenzelleria viridis* was commonly found in the predominant communities (clusters A and B, representing 75% of all faunal assemblages). The species has shown a rapid colonization of Finnish archipelago waters since the early 1990s (Norkko *et al.* 1993, Stigzelius *et al.* 1997, Perus *et al.* 2001), and was ranked among the ecologically most important components of the benthic communities in the Åland archipelago by the year 2000 (Perus *et al.* 2001). It is also noteworthy that the basic *Macoma* community seemed to have a very high degree of recruitment of juvenile (< 2 mm) Baltic clams (*M. balthica*), as described for some sites along the Gulf of Finland by Segerstråle (1960). Generally, for coastal waters today, hypoxia and anoxia are considered major threats to the benthic biota (Diaz and Rosenberg 1995), and these phenomena linked to eutrophication have also been reported to increase around the Baltic coasts in recent decades (Karlson *et al.* 2002), and for coastal waters in general (Gray *et al.* 2002). Environmental influence on the biota must be studied both in connection to climate change (Zorita and Laine 2000) and eutrophication (Rönnberg 2001).

The macrozoobenthic assemblages of the outer archipelago include species typical to shallow waters and species more often encountered in deeper areas (Bonsdorff 1988, Bonsdorff *et al.* 1991, 1996, Hänninen and Vuorinen 2001). The macrobenthic communities in the northern Baltic Proper are typically composed of only a few species (maximally some 20 species per region, and up to 50 species in the entire sea area), typically dominated by only 1–3 species (Rumohr *et al.* 1996, Bonsdorff and Pearson 1999). Despite the importance of benthic fauna in the sedimentary environment (*see* Snelgrove and Butman 1994, and Pearson 2001 for general reviews) and their value in local environmental monitoring (e.g. Tulkki 1960, 1964, Leppäkoski 1975, Bonsdorff *et al.* 1991, Bonsdorff and Blomqvist 1992, Norkko and Bonsdorff 1994, Hänninen and Vuorinen 2001, Kangas *et al.* 2001) they have rarely been studied in the transition between archipelago and open waters (Bonsdorff *et al.* 1991, Häkkilä *et al.* 1993, Perus *et al.* 2001).

On the other hand, there is a large body of literature describing the benthos of the open sea area, partly collected primarily for monitoring purposes (Rumohr *et al*. 1996, Laine *et al*. 1997, Bonsdorff and Pearson 1999). A special problem in this habitat is that topography and depth form gradients or clines along which several environmental variables change, thus rendering the interpretation of management-oriented benthic surveys difficult (Jumppanen and Mattila 1994, Hänninen and Vuorinen 1999). The functional aspect of the species-poor Baltic Sea zoobenthos was described and analyzed for both deep (sub-halocline) and shallow coastal (supra-halocline) waters by Bonsdorff and Pearson (1999), who clearly illustrated the relatively greater importance of each individual species in the Baltic Sea compared with fully marine regions (the Kattegat and the North Sea). Hence, the analysis must focus on both the species composition and on the actual abundance dominance patterns of the species. Further, Pearson (2001) evaluated the importance of the benthic infauna for the sediment, illustrating the overall importance of these habitats both from an ecological and monitoring point of view.

The results presented here show a clear division into sub-areas, illustrating the importance of regional conditions (even in complex environments, such as coastal and archipelago waters). This has clear implications for environmental monitoring and protection measures, and stresses the importance in monitoring of having access to prior baseline studies extending over a cline of environmental variables that are not affected by man, or where anthropogenic influences (such as eutrophication) can potentially be filtered out for comparative purposes and for a valid environmental evaluation and classification. This also affects the environmental classification and ecological interpretation of typology, as requested in the EC WFD.

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