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Macrozoobenthic zonation in relation to major environmental factors across the Archipelago Sea, northern Baltic Sea

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Benthic macrofaunal assemblages from a series of samples taken between 1994 and 2000 across the Archipelago Sea are described, and community structure in relation to major environmental factors analysed. Results provided a clear division of the Archipelago Sea into three zones based on benthic species composition. Environmental factors which best explained the observed species distribution, i.e. temperature, salinity, dissolved oxygen, and sediment organic carbon were seen to operate along a cline of increasing depth. An east–west comparison of adjacent zones was also investigated. These closely resembled one another showing few significant differences. Local environmental factors were considered responsible where differences were observed. Evidence of a marked temporal difference in species composition in the middle parts of the archipelago was shown. The results, in line with ordination analysis, indicated a seawards shift of the more polluted/impacted zones. The predictive capabilities of the canonical ordination method of redundancy analysis (RDA) were discussed.

Introduction

Since the 1960s, eutrophication has been the major environmental change affecting the water quality of the Baltic Sea both basin-wide and locally (Bonsdorff *et al*. 1991, Wulff *et al*. 1994). Several types of effects were previously attributed to increasing eutrophication in the benthic communities in the Baltic Sea, both in the main basin and in shallow areas. Cederwall and Elmgren (1980) showed that macrofaunal abundance and biomass have increased significantly in the central Baltic proper since the 1920s. Leppäkoski (1975), Pearson and Rosenberg (1978), and more recently Bonsdorff *et al*. (1991) have found that, depending on the degree of eutrophication, the alteration in benthic macrofauna in shallow waters could be expressed as a functional, i.e. reduced complexity in terms of diversity and evenness, or a structural response (increased abundance and biomass of species). They showed that, at low levels of eutrophication, the principal mechanism for changes initially involved increased primary production, leading to higher organic content in sediments (beneficial effect), but continued enrichment above a certain threshold, resulted in temporal oxygen deficiency in near bottom waters (deleterious effect).

Geographical and biological zonation in the Archipelago Sea ranges from the sheltered inner archipelago, to the intermediate zone and, finally to the more open outer archipelago (Häyrén 1900, Jaatinen 1960, Granö *et al.* 1999). In addition to horizontal gradients, the area is characterised by vertical gradients of nutrients, salinity, temperature and oxygen (Helminen *et al.* 1998, Hänninen *et al.* 1999, Vahteri *et al.* 2000). Despite the general decrease of nutrient concentrations with increasing distance from the mainland, there may be local deviations such that, in the middle archipelago, high concentrations may occur locally, e.g. in the area of intensive fish farming (Hänninen and Vuorinen 2001, Vahteri *et al.* 2000). In the outer archipelago, the macrobenthic assemblages comprise two groups, i.e. those typical to shallow waters, and those with species more often encountered in the deeper areas (Hänninen and Vuorinen 2001, Bonsdorff *et al.* 2003). The macrobenthic communities in the northern Baltic Proper are typically composed of few species, i.e. ≤ 20 on soft-sediment bottoms (Elmgren *et al.* 1984, Rumohr *et al.* 1996), with 1–3 species as numeric and/or gravimetric dominants (Bonsdorff *et al.* 1991). A special problem in this environment is that the depth forms a cline along which several other environmental variables change, thus rendering difficult the interpretation of purely pollution-oriented benthic studies (a review by Vuorinen *et al.* 1998).

This analysis is based on species abundance and the variability of community structure in relation to environmental variables. The aim of the present work is to investigate whether zonation is found in the benthic communities of the Archipelago Sea and, if it occurs, what are the underlying causes for the observed delineation.

Study area

The study area (Fig. 1) is an extensive archipelago situated on the SW coast of Finland, northern Baltic Sea (59°45´–60°45´N and 21°00´–23°00´E). The geo- and biological zonation in the Archipelago Sea ranges from the sheltered inner archipelago (land/sea ratio > 1) to the intermediate zone (land/sea ratio = 1) and, finally to the more open outer archipelago (land/sea ratio < 1). This zonation is due to a slow postglacial land uplifting (ca. 0.5 cm a^{-1}) connected with a tilting coastal plain. The area is characterised by a strong seasonality, with average annual salinities ranging between 3.5S and 7S (Vuorinen and Ranta 1987, Viitasalo *et al.* 1990). Temperatures range between below zero to +20 °C. During the winter months, the sea is covered with ice and permanent ice cover may exceed 100 days (Seinä and Peltola 1991).

Material and methods

Field sampling

A number of selected stations in the Nauvo area were first sampled during the summer cruise of the research vessel *Aranda*, on two separate visits to the Archipelago in 1954 (Sjöblom 1955). Material was collected with a van Veen grab (0.1 m^{-2}) and washed through metal sieves of 1 mm mesh before being preserved in formalin. Almost identical sites were investigated as part of the 1995 sampling-regime (*see* below).

In 1994, the Airisto inlet, south-west of the city of Turku was sampled using an Ekman-Birge corer (sample area 231 cm^2) at thirty localities divided into ten sub-areas (Hänninen and Vuorinen 2001). Five replicate grab samples were taken per site, sieved on a 1.0 mm mesh screen, and stored in buffered seawater formalin (4%) solution. Temperature (°C), salinity (PSU), and oxygen saturation (mg l^{-1}) were analysed from approximately 0.5 m above the sediment surface. Sediment was described qualitatively and organic content measured as loss on ignition (3 h at 500 °C) after drying for 24 h at 60 °C (Dybern *et al.* 1976).

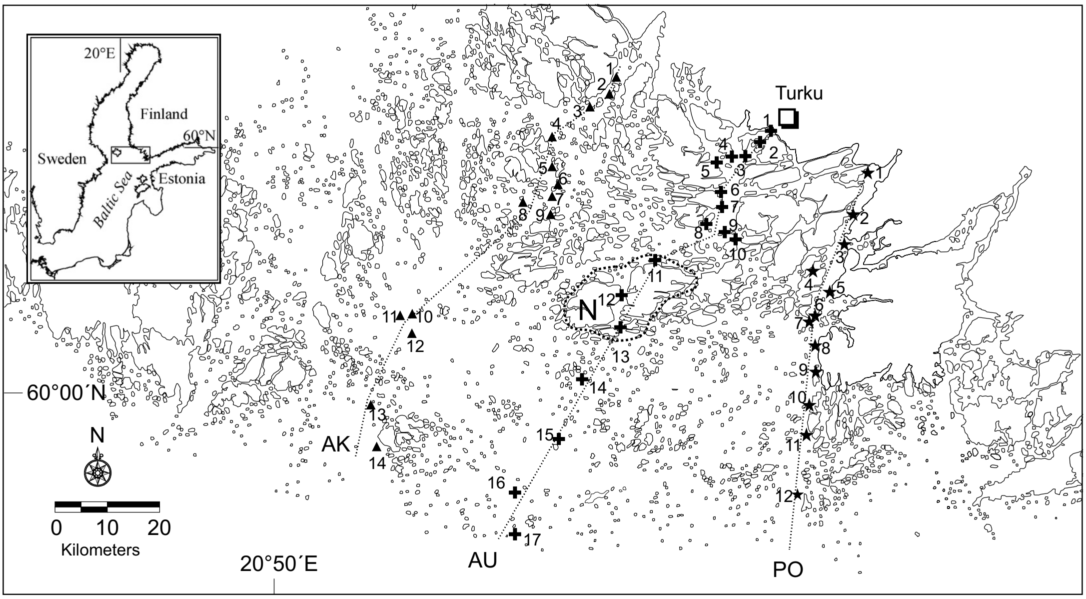

Fig. 1. The study area in the Archipelago Sea, northern Baltic Sea, with three sampling transects and their numbered stations, i.e. AK (western transect), AU (central transect) and PO (eastern transect). The sampling location of Sjöblom (1955) in the Nauvo area of the archipelago is marked by a dashed line and labelled 'N'.

In 1995, a series of 43 stations extending along the outer archipelago zone from Åland Island in the east to the Gulf of Finland were sampled also using an Ekman-Birge corer (400 cm^2) (Bonsdorff *et al.* 2003). This sampling line also extended from the outer archipelago rim in a north-westerly direction to the southern end of the Airisto inlet. Surficial sediments were also sampled for organic content, and off-bottom salinity, temperature and dissolved oxygen were recorded.

In 1996, a ten station transect was sampled in Paimionlahti from the inner archipelago zone extending southwards through the middle and outer archipelago, using an Ekman-Birge box corer (sample area 231 cm^2). No environmental parameters except station depth were recorded for this transect.

In summer 2000, 12 sites extending from the Askainen area, approximately 30–75 km southwest of the city of Turku were sampled for macrofauna. Three replicate samples per site were taken with a van Veen grab (33.5 cm × 31.5 cm) and sieved on a 0.5 mm mesh screen. Samples were stored in buffered 4% seawater formalin solution before further analyses in the laboratory. Sediment quality was described, and organic content of the surficial layer measured as loss on ignition. Water conductivity for temperature, salinity and dissolved oxygen were recorded both for the near-bottom and surface water layers.

Statistical analyses

In order to compare the different transects, each sampling line, i.e. east, centre and west, was extended in to the outer archipelago proper by including certain stations taken during the outer archipelago survey of 1995. This was to allow a better appreciation and comparison of each archipelago zone between the sampling lines, and to enable an east-west as well as an inner-outer comparison. Comparisons between datasets derived from different benthic sampling methods were made by converting species abundances to individuals per metre squared. Each species was assigned a six-letter label, by an abbreviation of its generic and specific name. For example, the bivalve *Macoma baltica* and the amphipod *Monoporeia affinis* were designated "Macbal" and "Monaff" respectively. Prior to statistical analysis, all data were log-transformed to attain homogeneity of the variances and normality options. To elucidate patterns in community structure along each transect, the ordination programme CANOCO (Ter Braak and Smilauer 1988) was used. Here, a constrained form of linear ordination, i.e. Redundancy Analysis (Rao 1964) or RDA was deemed appropriate to compare within transect patterns of species assemblages. Centering and normalising options were employed producing scores centred and standardised to unit variance. The significance of the eigenvalues and species-environment correlations of the first three axes were determined by Monte Carlo tests (199 permutations). Axes were scaled to allow representation of samples, species and environmental variables, and the site scores for samples represent the weighted sum of the species scores. Single comparisons of biodiversity parameters, i.e. number of species, species abundance, species biomass, species evenness and species richness, Shannon-Wiener Index of species diversity (Krebs 1989), as well as the various measured environmental parameters between sub-areas were tested using a Bonferroni adjusted Mann-Whitney *U*-test (SPSS 1999). Statistical significance for all tests was inferred when $p < 0.05$. Finally, a separate temporal comparison was made between biological and environmental parameters of stations of the Nauvo area of the archipelago sampled in 1954 and again in 1995 using a Bonferroni adjusted Mann-Whitney *U*-test (SPSS 1999).

Results

Redundancy analyses

Western transect (AK)

The eigenvalues of the first three axes were recorded at 0.377, 0.116 and 0.051 respectively, indicating a relatively strong gradient along the first axis (Table 1). The first two axes alone explain 49.3% of the total variation in the entire dataset. The cumulative percentage of species-environment relation expresses the amount of variation explained by the RDA axes as a fraction of the total explainable variance of species abundance. The first two axes together explain ca. 82% of the variation that could be explained by the variables chosen. When spatial differences between zones were tested, temperatures were significantly higher in the middle zone than in the outer zone (Mann-Whitney $U = 0.0$, $p = 0.021$), with significantly higher salinity ($U = 0.0$, $p = 0.018$) and depths ($U = 4.0$, $p = 0.015$) in the outer than in the middle zone.

Table 1. Results of benthic macrofauna data analyses of the AK (western) transect. RDA eigenvalues, species-environment correlations, cumulative variances and significance tests for the first three axes, and all canonical axes (ACA). RDA intra-set correlations between axes 1–3 and environmental variables.

	Axis 1	Axis 2	Axis 3	ACA
Eigenvalues	0.377	0.116	0.051	0.598
Species-environment correlations	0.964	0.835	0.767	
Cumulative percentage variance of species data	37.7	49.3	54.4	
Cumulative percentage variance of species environment relation	63.0	82.4	91.0	
Monte Carlo test				
F-ratio	4.837	1.828	0.897	2.378
p-value	0.005	0.3	0.905	0.005
Sum of all unconstrained eigenvalues = 1.00				
Intra-set correlations				
Depth	0.98	0.08	–0.08	
Temperature	–0.75	–0.17	0.33	
Dissolved oxygen (mg l^{-1})	–0.54	–0.16	–0.44	
Sediment organic carbon (%)	–0.39	–0.04	0.35	
Sediment type	0.12	–0.89	–0.01	

Central transect (AU)

Eigenvalues for the first three axes were recorded at 0.313, 0.127 and 0.028, respectively (Table 2). The first axis and second axis explain a total of 44% of the variation in species abundance. Of the cumulative percentage of species-environment relation, the first two axes explain almost 90% of the variation of species abundance together. The Mann-Whitney *U*-test revealed depth and temperature to be marginally significantly different (for each, $U = 0.0$, $p = 0.051$) between inner and outer zones, the latter being deeper with cooler off-bottom temperatures. Dissolved oxygen ($U = 0.00$, $p = 0.006$), percentage oxygen saturation and salinity (both $U = 3.00$, $p = 0.030$) were also significantly higher in the outer zone than in the middle zone.

Eastern transect (PO)

The eigenvalues of the first three axes were recorded at 0.209, 0.359 and 0.131 respectively (Table 3). The first axis (depth) explains approximately 21% of the total variation of species

Table 2. Results of benthic macrofauna data analyses of the AU (central) transect. RDA eigenvalues, species-environment correlations, cumulative variances and significance tests for the first three axes, and all canonical axes (ACA). RDA intra-set correlations between axes 1–3 and environmental variables.

	Axis 1	Axis 2	Axis 3	ACA
Eigenvalues	0.313	0.127	0.028	0.494
Species-environment correlations	0.945	0.803	0.751	
Cumulative percentage variance of species data	31.3	44.0	46.8	
Cumulative percentage variance of species environment relation	63.4	89.1	94.7	
Monte Carlo test				
F-ratio	5.011	2.491	0.575	2.147
p-value	0.005	0.235	1.00	0.005
Sum of all unconstrained eigenvalues = 1.00				
Intra-set correlations				
Depth	–0.96	0.09	0.22	
Temperature	0.70	–0.68	0.04	
Dissolved oxygen (mg l^{-1})	0.02	0.90	–0.19	
Salinity	0.03	0.54	0.00	
Sediment organic carbon (%)	0.07	–0.73	–0.60	

Table 3. Results of benthic macrofauna data analyses of the PO (eastern) transect. RDA eigenvalues, species-environment correlations, cumulative variances and significance tests for the first three axes, and all canonical axes (ACA). RDA intra-set correlations between axes 1–3 and environmental variables.

	Axis 1	Axis 2	Axis 3	ACA
Eigenvalues	0.209	0.359	0.131	0.209
Species-environment correlations	0.817	0.000	0.000	
Cumulative percentage variance of species data	20.9	56.8	69.9	
Cumulative percentage variance of species environment relation	100	0.000	0.000	
Monte Carlo test				
F-ratio	2.468			
p-value	0.045			
Sum of all unconstrained eigenvalues = 1.00				
Intra-set correlation				
Depth	–1.00	0.00	0.00	

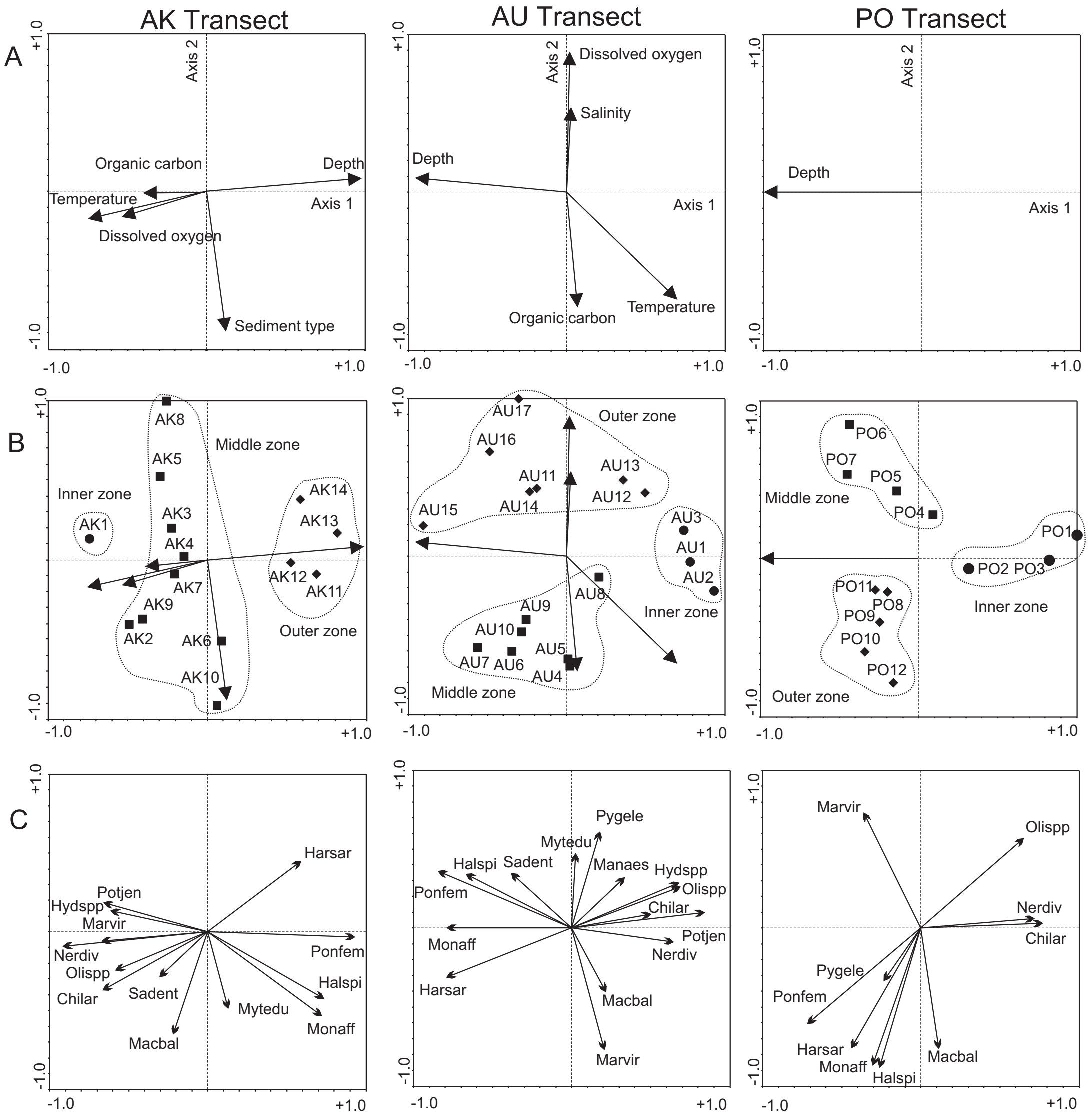

Fig. 2. Redundancy Analysis (RDA) of the AK (western), AU (central) and PO (eastern) transects respectively. — **A**: environmental variables. — **B**: sampling sites and environmental variables. — **C**: species.

abundance in the entire dataset. Of the parameters tested, only density was found to be significantly higher in the outer zone than in the middle zone (Mann-Whitney $U = 0.0$, $p = 0.42$).

In all transects, Monte Carlo permutation tests show that only the first axis was significant. Nevertheless, for each individual transect all canonical axes combined were significant. Intraset correlations, i.e. the correlation coefficients between the environmental variables and the ordination axes, show that on the first canonical axis, depth (with salinity and water visibility as covariables) and temperature were most important, followed by dissolved oxygen and then sediment organic carbon in the western transect (Table 1). A similar pattern was observed for the central study line (Table 2). Sampling locations along all of the transects studied divide into three archipelagial zones, which were designated inner, middle and outer (Fig. 2B). The inner zones were characterised by being shallow and low in salinity. Off-bottom temperatures and dissolved oxygen were higher relative to the other zones. Characterising species (Fig. 2C), included

Nereis diversicolor, chironomid larvae, oligochaetes, and particularly, hydrobiid gastropods. For the most part, deeper sites with enriched sediments typified the middle zone. *Macoma baltica* and *Marenzelleria viridis* characterised these zones, although inner zone species, i.e. chironomid larvae, oligochaetes and gastropods were also important in the western transect's middle zone. The outer archipelago zones were generally characterised by the deepest stations with lowest off-bottom temperatures and sediments that were not organically enriched. All outer zones were characterised by amphipod species, *Monoporeia affinis* and *Pontoporeia femorata*, the priapulid *Halicryptus spinulosus*, the blue mussel, *Mytilus edulis*, and the polychaete *Harmothoe sarsi*. In the eastern transect, the outer zone was also characterised by *M. baltica*, while in the central study line, inner zones species such as chironomid larvae and oligochaetes were relatively abundant at the shallowest outer stations.

Comparisons between adjacent transect zones

The Mann-Whitney U-test revealed significantly higher density and depth in the middle zone of the central transect than in the adjacent zone of the western transect ($U = 0.00$, $p = 0.009$ and $U = 1.00$, $p = 0.015$ respectively) and *vice versa* for temperature ($U = 0.00$, $p = 0.009$). Depth was also significantly greater in the middle zone of the eastern transect than in the adjacent zone of the western transect ($U = 1.00$, $p = 0.33$). A higher significant difference in diversity and species evenness were recorded in the eastern transect middle-zone than in the central middle zone, and *vice versa* for density ($U = 0.00$, $p = 0.042$ for all parameters).

Temporal comparisons

Species density increased markedly between sampling times (570 ± 471.2 in 1954 to 7213 ± 2956.6 in 1995), while the number of species had approximately doubled from 5 to 10. Both parameters were shown to be significantly higher during the 1995-sampling regime (Mann-Whitney $U = 0.0$, $p = 0.008$ and Mann-Whitney $U = 2.50$, $p = 0.026$ respectively).

Discussion

Geographic *versus* benthic zonation

The pooled species data for each transect forms three relatively distinct benthic archipelagial zones. If lines joining the respective inner, middle and outer areas are drawn on a map (Fig. 3), it is evident that macrobenthic zonation of the present sudy is quite similar to that of Jaatinen (1960) which was based on land/sea ratio. The eastern and central transects most closely resembled Jaatinen's divisions, although the middle zone of the western study line, was designated by Jaatinen (*loc. cit*) as "outer" archipelago. Further, some outer stations of this work were identified in Jaatinen's (1960) middle zone in the central study line. Land-sea ratio at a location does not necessarily reflect its depth, which may explain the differences observed in the present study. The relatively shallow middle zone of the western study line, despite its low land-sea ratio, reflects this. Conversely, the presence of relatively deep water outer archipelago species, in Jaatinen's (1960) middle zone of the central study line, in spite of a higher land-sea ratio than in the western transect, further suggests that zoobenthic communities are not delineated by surface boundaries, but by the depth and factors related to it. This was corroborated also when adjacent zones were compared. A significant difference in density, diversity, and species evenness between the middle zones of the three transects were evident. Specifically, species density was found to be significantly higher in the middle zone of the central transect than in either of the other lines studied. This may be explained by the fact that the relatively deeper, organically enriched middle Airisto area was capable of supporting greater densities of amphipod species, and allowing the extension of distribution of other already dominant species like *Macoma baltica*. Such a model was also proposed by Hänninen and Vuorinen (2001) for increased abundances observed in the Airisto

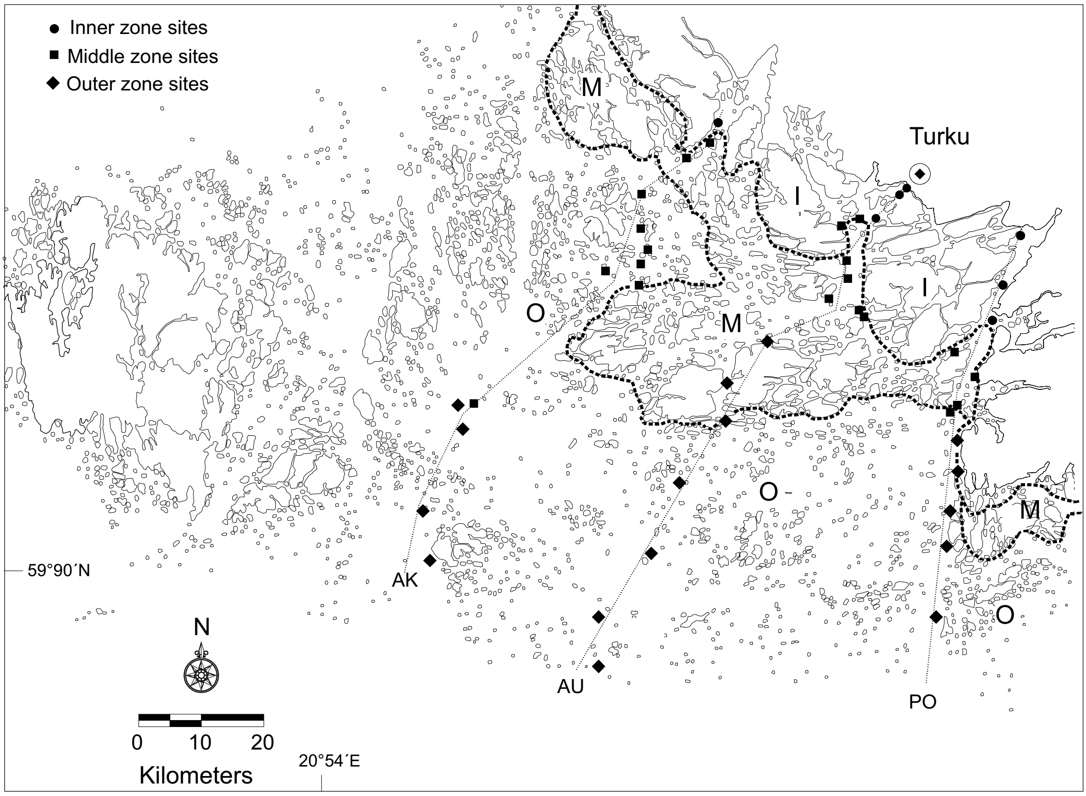

Fig. 3. Comparison of geographical and macrofaunal archipelago zonation: Archipelago zones according to land-sea ratio (Jaatinen 1960), marked by dashed line. I = inner archipelago; M = middle archipelago; O = outer archipelago. Sampling sites delineated by RDA analysis (*see* legend). AK = western transect, AU = central transect, PO = eastern transect.

Inlet, and may explain the similarity observed in the outer zone of the eastern study line.

Environmental parameters and zonation

In the present study, the environmental variables were seen to change in a coherent way and were evidently strongly affected by depth, a view also taken by Olenin (1997) in his analysis on benthic zonation at eastern Gotland Basin, central Baltic Sea. The greatest part of species variation in the western and central transects was explained best by the environmental variables depth and temperature. In the western line, salinity and turbidity were strongly correlated with depth, while dissolved oxygen and sediment organic carbon were of lesser importance on the first axis. In the central transect, RDA analysis also showed good intra-set correlations for salinity, dissolved oxygen and sediment organic carbon. However, their direction and position on the second axis suggests that they are little correlated with the other variables on the first axis, and show a more marginal than conditional effect. Nevertheless, Monte Carlo testing showed a high significance in all canonical axes for both western and central transects, indicating a meaningful relationship between variation in species abundance and environmental variables chosen for both study lines. Only one environmental variable, i.e. depth, was recorded for the PO (eastern) transect, and alone accounted for approximately 20% of the variation in species abundance. A higher second eigenvalue suggests that there was a larger part of the variation of species abundance, accounted for by some other variable. Nevertheless, the spatial pattern of environmental variables was broadly similar for each zone between each transect.

Although a general increase in salinity with increasing depth was noted for both the western and central transects, a significant difference was only found between the middle and outer zones for both study lines. This was taken to reflect the influence of river- and general runoff in the inner and middle areas, while higher salinity in the deeper outer sites is more influenced by the open sea with its occasional saline upwellings. For example, Laine *et al*. (1997) studied natural factors analysis of long-term data on macrobenthos in the Gulf of Finland and the deeper Gotland Basin in relation to the hydrographical regime. They found that fluctuations in salinity affected the structure of the community. Increased salinity favoured more marine species, while freshwater species showed an inverse trend.

Dissolved oxygen levels in the middle zones of the central transect were significantly lower than in the outer zone. This may be explained by sediments of the middle zone were nutrient and organically-enriched (sediment organic carbon = 44% at site AU6) which, combined with relatively warm off-bottom temperatures, may have contributed through eutrophication to hypoxic conditions. The source of organic enrichment in the central transect derives primarily from runoff from the Aurajoki river as well as the dumping of dredge spoil from the economically important Turku Harbour. Between 1989 and 1995 runoff from Turku Harbour exceeded 1.3 × 105 m^3 a^{-1} (Kauppila and Wright 1997) causing further changes in the composition of the sea bed due to increased siltation and turbidity. By comparison, less intense eutrophication due to deeper, more saline and organically poor (e.g. sediment organic carbon = 1.4% at AU17), outer zone sites of the central study line may have been responsible for the higher level of dissolved oxygen recorded here. Further, oxygenation due to increased wind-induced disturbance or "fetch" in the outer zones should not be discounted. The inner and middle zones of the western transect are not subject to as much freshwater runoff or impact from harbour activities. Thus, one might expect that dissolved oxygen levels would be higher because sediment organic enrichment was lower, e.g. the highest recorded in the middle zone 11.2% at site AK9. However, the middle zone does experience hypoxic conditions. Dissolved oxygen levels at stations AK3 and AK8 were recorded as low as 3.1 and 5.6 mg l^{-1} respectively, with further evidence of hydrogen sulphide production at the sites AK4 and AK5. Sites in the middle zone of the western transect were significantly shallower than those in the central study line, as a result bottom temperatures were significantly higher.

Qualitative descriptions of bottom sediments from the western and central lines revealed a mosaic of deposits in the Archipelago Sea (Hänninen and Vuorinen 2001). In the inner zones, fines were in evidence underlining the sedimentation impact of river and general runoff. Dredging and dumping of spoil further enhance siltation and turbidity. In general, the presence of sand, clay and mud in all of the bottom sediments suggests that along both western and central study lines some sediment deposition is taking place. Some gravel and coarse deposits were found in the outer-middle and outer zones of the western transect, which may reflect occasional scouring effects by currents or storms, but even at such sites mud and clay deposits were in evidence suggesting overall a more depositional than erosional regime. In the western transect, sediment type was generally a poor descriptor in explaining the observed species distributions, the most notable exception was the high correlation between coarse sediment and the bivalve *Mytilus edulis*. More important was sediment organic carbon which was shown to be highly correlated with *Macoma baltica* and *Marenzelleria viridis*. In support, Olenin (1997), studying the benthic zonation of the eastern Gotland Basin, noted that the organic content of sediments in general also correlated well with particle size.

Changes in zonation

While the land/sea (and depth) divisions are relatively static (despite slow land uplift), macrobenthic zonation has the capacity to change at a much faster rate, due to natural changes in population cycles, massive recruitment events, seasonal cycles, etc. More recently too, site-specific as well as large scale anthropogenic influences such as eutrophication, pollution, and fish-farming, have had a direct/indirect (algal mats/depression of *Fucus* and *Fucus*-related fauna) impact on benthic populations (Pearson and Rosenberg 1978, Bonsdorff *et al.* 1991, Jumppanen 2000, 2001) and reflect both local and regional disturbances (Tulkki 1960, 1964, Leppäkoski 1975). Local eutrophication contributed to the shift from suspension feeders to deposit feeders. This was found in the present work in all inner zones with evidence of encroachment into the middle areas by the presence of oligochaetes, chironomid larvae, certain polychaetes, and a decline in suspension feeders. Hänninen *et al.* (1999) found that riverine-derived nutrient inputs remain for the most part within inshore waters. As a result, the impact of eutrophication in inshore sites is locally most severe. Jumppanen (2000, 2001) documented eutrophication-induced changes due to fish-farming in the structure and composition of bottom fauna at the end of the 1990s in the western archipelago area (Kustavi–Taivasalo and the Iniö islands), from mollusc- and amphipod-dominated assemblages to those where chironomid larvae and oligochaetes became temporarily dominant numerically. This ties in with the inner and middle-zone faunal mosaic found in the western transect of the present study, implying that the inner-middle zone boundary of Jaatinen (1960) has been pushed seawards.

Moreover, the presence of chironomid larvae and oligochaetes in the shallowest outer stations of the central transect also reflect local eutrophication (Bonsdorff *et al.* 2003). Similarly, when benthic data taken in the Nauvo area in 1954 (Sjöblom 1955), was compared statistically to similar stations from the 1995 Airisto dataset, the biological parameters density and number of species were found to be significantly higher in the latter samples. When areal means were compared, the number of species had doubled, and species density had increased tenfold due to the dramatic proliferation of the biological dominants, i.e. *Macoma baltica*, and *Monoporeia affinis*. Moreover, at one site chironomid larvae also experienced a tenfold increase in abundance. By contrast, other sites of the 1954 sampling regime returned no chironomids whatsoever. In their review of aquatic biodiversity in the Archipelago Sea, Leppäkoski *et al.* (1999), also noted an approximate doubling in abundance and biomass of soft-bottom fauna in shallow inshore waters of the Åland archipelago between 1976–1994. It is significant that, although the number of species remained unchanged, 40% of the species composition had altered from suspension feeders to deposit feeders (Bonsdorff *et al.* 1997b). A similar pattern of change in community structure was already observed by Hänninen and Vuorinen (2001) in their temporal comparison of Airisto sites first sampled in 1956 and revisited in 1994. In this way, the benthic zone boundaries identified by ordination techniques of species abundances in the present work are far from static and may shift back and forth.

Therefore, although it is difficult to have exclusive zones, the identification of general zonal categories based on species abundance is possible. Such information can also be used in predicting the environmental health of an aquatic zone based on the numbers and types of species recorded therein. For example, RDA analysis shows a high correlation between the polychete species *Marenzelleria viridis* and sediment organic carbon. Although no environmental data was available for the eastern transect, RDA analysis showed *M. viridis* to characterise the middle zone. Thus, some inferences can be made on environmental variables such as sediment quality based on a species presence/absence and abundance. Conversely, it should also be possible to make some inferences on the environmental regime based on information from other transect lines. For example, in the eastern transect, only one environmental variable, i.e. depth, was recorded while in the other transects more variables were measured. That the species distribution within each transect was remarkably similar can lead us to infer that similar environmental conditions also exist in the eastern study line. They may not be identical but the researcher is given a realistic estimate of what is happening. For example, in the eastern transect, *Macoma baltica* was shown by RDA to characterise the outer zone and species density was significantly higher than in the middle or inner areas. This points to a similar seaward shift as found in the benthic communities of the western and central transects. Moreover, the variable depth was found to be highly positively correlated with other variables, i.e. salinity and water visibility, with a significant inverse relationship with temperature. If we can associate species abundance changes with changes in depth, we may also infer a similar or inverse relationship with other variables. Thus, although in the eastern study line only depth was measured, we could infer that species abundance also changed from inner to outer zones with increasing salinity and visibility, and with decreasing temperature. Such inferences are further supported by the similarity in species distributions between all three transects, and highlight the predictive power of canonical ordination techniques when studying the ecology of macrofaunal benthic communities.

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