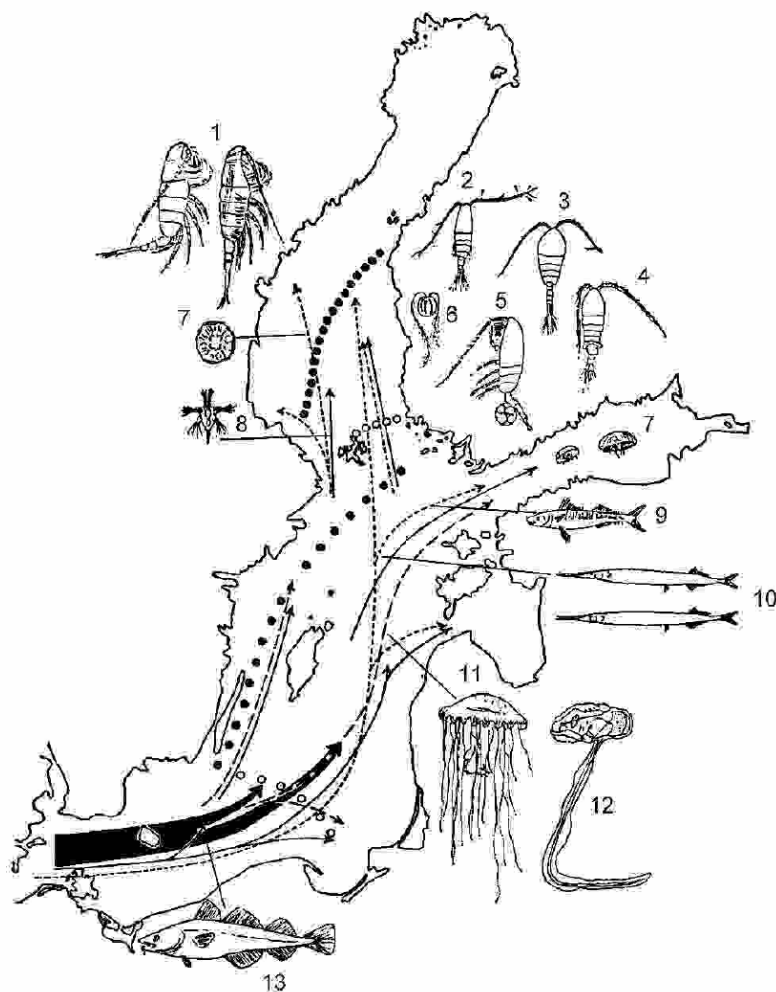


# *Environmental Factors Shaping the Littoral Biodiversity in the Finnish Archipelago, northern Baltic, and the Value of Low Biodiversity*

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Cover illustration:

Map of the Baltic Sea, with examples of the most important marine animals which extended/narrowed their range as a consequence of the salinity rise during the first half of the century (modified from Segerstråle 1969). The arrows indicate direction of spread. Continuous lines: widening of range with reproduction. Broken lines with long strokes: widening of range without reproduction. Broken lines with short strokes: occasional invasion, 'guests'.

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## *Abstract*

Aquatic littoral habitats form an invaluable element for human recreation and economy. During the recent decades they have lost part of their biological diversity, due to human impact. More remote areas, for instance the outer archipelagos, are considered as most valuable in terms of natural and pristine biodiversity. Thus protective measures e.g. founding of nature protection areas and reserves have been directed predominantly there.

Our aim was to describe how changing archipelago environmental characteristics in the rocky shores (the most common habitat type), influence the biodiversity of littoral communities in the northern Baltic Sea. Geographic classification of northern Baltic sea- and landscape is formed in a natural way due to the existence of inner, middle, and finally the outer archipelago areas, or zones (in it's most simple form measured by the relation between land and water in the landscape). We found that, littoral environmental characteristics were more uniform within an archipelago zone than between the zones, corroborating the existence of geographic zonation also in the littoral environment. The most important environmental factors shaping littoral communities were arranged in a bipolar way,

nutrient levels decrease from the mainland towards the outer archipelago, while marine environmental characteristics increase (salinity, Secchi depth and relative wave exposure). Our results point out an ecotone effect together with a series of gradients, both of which increase the biodiversity in the middle and inner parts of the studied area rather than in the most remote and least human-affected areas.

Our conclusion is that if, in a management point of view, high biodiversity is taken as a value in itself, then the inner and middle parts of the archipelago should be preferred in the protection. We argue that measures to protect biodiversity should be aimed there rather than to the outer zones that are traditionally taken as the target for environmental protection work, and where most of nature protection and biosphere areas have been founded. Then, finally, if the natural or pristine biodiversity is valued high, then we should protect the outer archipelago, but that would actually mean protecting areas of lower biodiversity.

*Keywords: Protection of the Biodiversity; Littoral Habitat; Northern Baltic archipelago*

## Introduction

Aquatic habitats form a most invaluable element of human recreation and economy. During the recent decades loss of biological diversity has proven to be a complicated environmental problem in the coastal areas. Impoverishment of the aquatic environment is partly due to changes in land-use management and practices, but more importantly due to eutrophication. Therefore it has been a common “silent” understanding that nature protection measures, e.g. foundation of nature protection areas and biosphere reserves should be done predominantly in areas least affected by humans. There is, however, only limited information available on actual environmental factors and processes that shape the natural biodiversity in the coastal littoral areas.

The littoral zone is the most important reproduction, nursery, feeding and hiding area for coastal marine biota, while the pelagial and benthos are known to support “few species and many individuals”. Studies carried out in the littoral zone are few when compared to research done in pelagic and benthic habitats. In the Baltic Sea area Sven Segerstråle collected first facts about species diversity in the littoral zone in the 1920s (Segerstråle 1927) in his study of the “*Fucus*-fauna”, which, indeed, could not show any reference to previous work. During the 1960s and 1970s there was a growing interest and a lot of publications came out, many of them summarised by Bengt-Owe Jansson in his “Ecosystem Approach to the Baltic Problem” (Jansson 1972).

Since the studies of Ravanko (1972), the macro phytobenthos on rocky shores is the most intensively studied group of littoral organisms in the northern Baltic. The studies have illustrated the drastic deterioration of the bladder wrack since the 1950s (Rönnerberg *et al.* 1985), change in the composition (Mäkinen *et al.* 1984), and increase of the filamentous algae (Vahteri *et al.* 2000). The result of this change has been a demonstrated impoverishment of littoral biodiversity, for instance the dramatic decline in individual abundance of littoral non-commercial fish species (Rajasilta *et al.* 1999).

The aims of the present work are to study how changing environmental characteristics of the predominant habitat type, rocky shores, influence littoral biodiversity in different parts of the Archipelago Sea, and to describe the composition of contemporary littoral communities. We selected study areas to constitute a more or less straight environmental gradient through the Archipelago Sea. One special characteristic of the Archipelago Sea is its topographical zonation according to the relative proportions of land/water in the land- or seascape. The zonation ranges from the sheltered inner archipelago to the intermediate zone and, finally to the more open outer archipelago. Our working hypothesis was that due to this zonation the littoral communities are shaped differently in various parts of the archipelago. The existence of these zones is due to a slow postglacial land uplifting about 0.5 cm a<sup>-1</sup> of tilting coastal plain. Häyrén (1900) divided the archipelago into these three zones on a biogeographical basis, and Jaatinen (1960), von Numers & van der Maarel (1998), Granö *et al.* (1999) and Korvenpää *et al.* (2004) using geo- and bio-geographical criteria later confirmed this. Hänninen *et al.* (2000) showed that the zonation was evident also in water quality. They illustrated that archipelago zones could be traced by nutrient concentrations of seawater, thus revealing a hydrographical zonation comparable to those found in geo- and biogeographical studies. Kirkkala (1998) and Erkkilä & Kirkkala (2000) have shown that corresponding gradients could also be traced from visibility, Secchi depth and chl-a content of the seawater. The highest visibility was generally found in the outermost areas and the lowest in the inner parts, whereas chl-a concentrations were similar to the pattern found for nutrients. Mattila & Räisänen (1998) have studied experimentally periphyton growth as an indicator of eutrophication. They found that it varied significantly among different parts of the archipelago. The strongest growth was observed in the inner archipelago and in areas with relatively slow water exchange. Periphyton biomass was positively correlated with

concentrations of total nitrogen, total phosphorus and chl-a in the productive layer of seawater. A significant inverse correlation was also shown between periphyton biomass and Secchi depth. Moreover, based on the rate of periphyton growth they were able to identify archipelago areas with different levels of eutrophication, which were in correspondence with the previous division of archipelago zones.

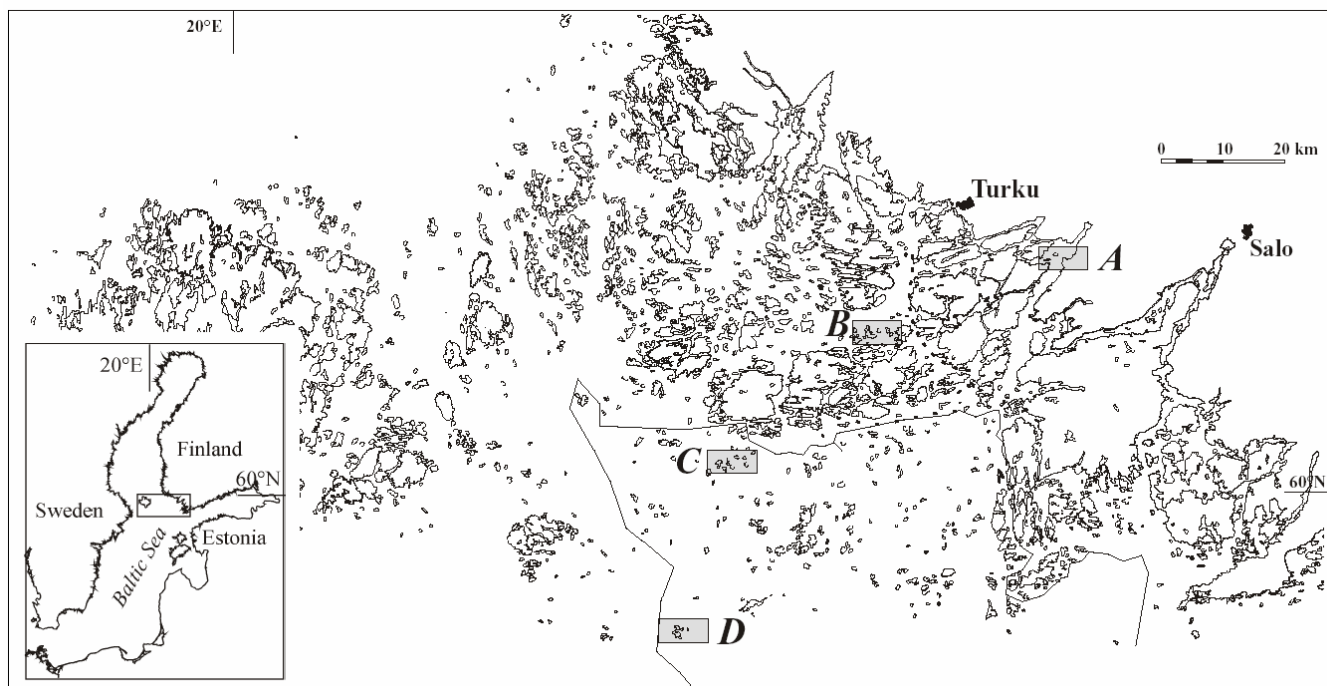
### Materials and methods

The study area is an extensive archipelago on the SW coast of Finland, northern Baltic Sea 59°45'– 60°45'N and 21°00'– 23°00'E . It is characterised by an enormous topographic complexity, including about 25 000 islands. The average water depth is only 23 m, and the deepest trench reaches 146 m. The total area of the Archipelago Sea is 9.436 km<sup>2</sup> and the water volume is 213 km<sup>3</sup>. The total drainage area is about 8.900 km<sup>2</sup> of which lakes cover fewer than 2 % and arable lands 28 %. The non-tidal sea is characterised by a strong seasonality. The summer temperature of the seawater reaches +20°C, and there is an annual ice cover during winter (HELCOM 1993, 1996).

Sampling was done in several littoral sites of three archipelago zones, or areas (Fig.1). Here

we define a littoral site as a shore profile ranging from shoreline to the outer edge of the belt of red algae, in depths of 10-15 metres. We studied only the rocky shores, which constitute the bulk of possible habitat types at all of the locations studied. Area *A* represented sheltered inner archipelago in the Bay of Paimionlahti, area *B* was located in more open middle archipelago (off the Island of Seili), area *C* stood for middle/outer archipelago (close to the Island of Brunskär), and the area *D* was situated in the outer archipelago in the vicinity of the open sea.

Several samples or measurements were done at each sampling site. The modified effective fetch was used as a measure of relative wave exposure for each sampling site (Harper *et al.* 1991). Sampling also included hydrographic parameters of water and seabed, as well as phytoplankton, zooplankton, periphyton, macrophytobenthos, and benthic fauna and fishes. Sampling was conducted during August-September 1997, consistently at the same hour inside a site. It was performed as stratified random sampling (three replicate sites in each of the four areas) according to standard methods. In some locations one reference station was sampled in the pelagic area, too.



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Figure 1. Studied locations in the Archipelago Sea. *A* = Paimionlahti, *B* = Seili, *C* = Brunskär, and *D* = Utö. Dotted line shows the outer limit of inner (between *A* and *B*) and middle (between *B* and *C*) archipelago zones. Continuous line = borders of the Archipelago national park.

In three replicate littoral sites per area we measured Secchi depth (m), temperature (°C), salinity (PSU) and oxygen content (mg/l) near the surface (0-1 m). Beyond the outer edge of *Fucus* belt we also collected three replicate water samples from the depth of 1-2 m using a tube sampler (*Limnos*-sampler of 3.6 l capacity). Reference sampling was done in the open water area close to the proper littoral sites. Samples were analysed for chl-a (µg/l), N<sub>tot</sub> (µg/l), NH<sub>4</sub>-N (µg/l), NO<sub>3</sub>-N (µg/l), P<sub>tot</sub> (µg/l), PO<sub>4</sub>-P (µg/l), TOC (mg/l), pH, turbidity (FTU), and colour (Pt mg/l) in an accredited laboratory at the Southwest Finland Regional Environment Centre (SFREC), Turku, Finland.

Phytoplankton samples were collected with a *Limnos*-sampler from surface water (0-1 m) at the same place as the water samples. One sample per site was considered adequate for subsequent analyses due to only insignificant variation between the replicates. Samples were concentrated with a 25 µm mesh, fixed with Lugol's solution and stored with buffered formaline. In the laboratory of the SFREC the phytoplankton taxa were identified and their biomass estimated (wet weight mg/l) according to Utermöhl (1958).

Periphyton communities were studied placing experimental growth plates (Whatham GF/C class fibre filters) in the immediate vicinity of the littoral sites. Three anchored plate constructions (including four replicate plates each) per basin were incubated for 3 weeks (see e.g., Mattila & Räsänen 1988), after which they were stored frozen. Chl-a contents (mg chl-a/m<sup>2</sup>) of the plates were analysed according to the SFS 5772 standard in the SFREC laboratory.

The underwater vegetation was studied by SCUBA diving according to e.g. Mäkinen *et al.* (1984). At each littoral site we marked three replicate transects with a rope at a right angle to shoreline extending to the distance of 50 m and a depth of 10-15 m (or to the outer edge of the red algae belt). With one-meter intervals we recorded the vegetation cover (percentage of each species) using a 1 m<sup>2</sup> metal frame subdivided in 0.1 m<sup>2</sup>s. We also measured upper and lower limits of vegetation belts (blue-green, green, *Fucus* and other brown algae, and red algae). The same interval was used for records of the seabed depth, amount of sediment (in a

scale of 1-5) and bottom type (rocks, stones, gravel, sand, silt, mud).

Zooplankton samples were collected from the surface with a *Limnos*-sampler (in triplicate for each location with a pelagic control site) beyond the outer edge of the *Fucus* belt. Samples were concentrated with a 50 µm mesh, stored in buffered seawater-formaline solution (4 %) and analysed according to HELCOM (1988), with the exception of cladocerans and copepods that were analysed only for adult stages. The counts were converted to wet weights using the average individual volumes for each taxa (Hernroth 1985).

The macro zoobenthos was sampled both in the sediment and inside *Fucus* vegetation. SCUBA-sampling was done along the same transects that were used for macro phyto-benthos sampling. The bottom living animals were sampled with a tube-sampler (3-5 replicates of 220 cm<sup>3</sup>) from three depths (the belts of green, brown and red algae). Samples were sieved through a 500-µm mesh and stored in buffered seawater-formaline solution. In the laboratory the macro zoobenthos species were identified, counted and weighted. Animals living within vegetation were collected from the stands of *Fucus vesiculosus* by divers. Three stands per transect were individually enveloped in a bag underwater, cut out and stored in buffered seawater-formaline solution. In the laboratory the animals were sorted, identified, counted, weighted and, finally represented per wet weight of the *Fucus* stand.

The fish were sampled both in the nearby open water area and in the littoral zone. We applied *NORDIC* series of multi-mesh gill nets of 10, 12, 15, 20, 30, 35, 45, and 55 mm mesh. Fishing was done under one overnight fishing period with three nets located in three settings (littoral, pelagial, profundal). The number and biomass of fish species in each mesh-size was recorded separately. Furthermore, we sampled in the littoral zone small-sized shore fish by a beach seine (mouth area 8.0 m<sup>2</sup>). At three sites per basin 5 replicate hauls were taken and stored separately in 70 % ethanol. In the laboratory the fish were identified to species, counted and weighted.

## Statistical analyses

We performed principal component analysis (PCA) to environmental variables (ter Braak & Smilauer 1998). For this analysis three or more samples or measurements representing each littoral site were pooled as counts. Scores were centered and standardised to unit variance. In order to illustrate within-area patterns in species assemblages, we treated data by canonical correspondence analysis (CCA) (ter Braak 1986, ter Braak & Verdonschot 1995, ter Braak & Smilauer 1998). We pooled the species data sets to larger taxonomic levels if numbers within species were insufficient for reliable tests. Species abundance and biomass data sets, and when necessary also the environmental variables were  $\log_{10}(X+1)$  transformed. We analysed within-location patterns separately for each area, as they were to serve as a basis for later comparisons among the archipelago zones. The significance of the eigenvalues and the species-environment correlations of the first three axes were determined by Monte Carlo tests (999 permutations). Axes were scaled to compromise representation of samples and taxa, and the scores for samples represented weighted mean scores for species. The most applicable CCA-model, i.e. the best combination of exploratory environmental variables describing

assemblages of species, was determined by backward selection on the basis of the total inertia and the significance level of the model. Statistical significance for tests was inferred when  $p < 0.05$ .

We performed a non-parametric Kruskal-Wallis ANOVA (SPSS 1999) in order to test for differences of biodiversity parameters between the areas (number of species, species abundance, species biomass and the Shannon-Wiener Index of species diversity (e.g. Krebs 1989)(sporadically, and for phytoplankton, we used higher taxonomic units than species). When needed, a Bonferroni adjusted Mann-Whitney U-test was used in single comparisons of differences between sub-areas (SPSS 1999).

The periphyton data (chl-a biomass  $\text{mg}/\text{m}^2$ , log-transformed as  $\log_{10}(x+1)$ ) were treated with parametric One-way ANOVA. Multiple comparisons between the areas were made with a Tukey's honestly significant difference (HSD) method. Again, statistical significance for all tests was inferred when  $p < 0.05$ .

## Results

PCA revealed that littoral sites within all four areas clustered together, indicating that environmental characteristics were more similar within than between the areas, thus corroborating the idea of different environmental characteristics controlling littoral biota. According to the eigenvalues the areas were mainly arranged along the first two axes (Fig.2). The first axis was largely a trophic gradient, as nutrient levels and Secchi depth described mostly clustering of sampling sites in areas A and C. The second ordination axis was strongly associated with total organic carbon (TOC), oxygen content and salinity. Those factors described especially the clustering of sampling sites of areas B and D. Area D sites were also well associated with the relative exposure. Pelagic reference sites inside each location did not differ from littoral sites.

For phytoplankton the most suitable CCA-model included salinity, inorganic nutrients,

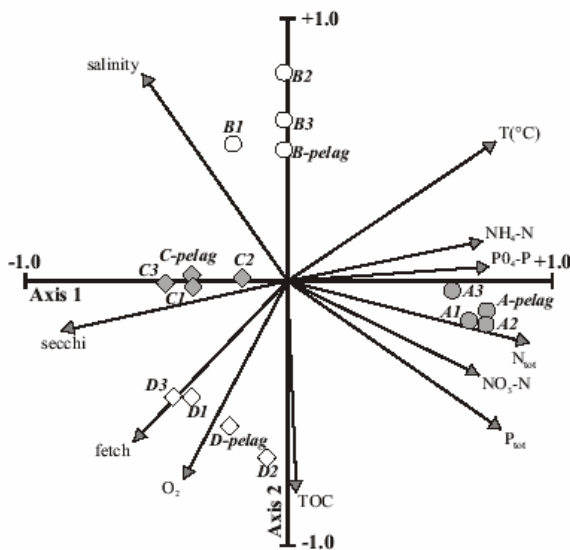


Figure 2. PCA-ordination plot of the sample locations (A, B, C and D) and environmental variables. The term 'pelag' after sites refers to pelagic reference station

Secchi depth and modified effective fetch (Table 1). These variables arranged along the first axis, which could thus be regarded as a trophic gradient (Fig.3). Littoral sites in areas *A* and *D* clustered separately, but areas *B* and *C* showed a more overlapping pattern. Kruskal-Wallis ANOVA revealed that there were statistically significant differences in species diversities and in the number of taxa among the locations, whereas species biomass diverged only negligibly (Table 1). The species composition in *A* distinguished itself clearly from the other areas in that the share of *Diatomophyceae* was relatively higher (Fig.3). The highest diversities were found in area *C* and the lowest in *D* (Fig.3).

One-way ANOVA showed that there was a statistically significant difference in periphyton chl-a biomass between the areas (Table 2). The highest periphyton biomass was found in *A*, and

the lowest in *B* and *C* (Fig.4). The biomass comparison indicated significant differences between extremes and middle areas but not between middle locations (Table 2).

We found that inorganic nutrients, Secchi depth, modified effective fetch and amount of

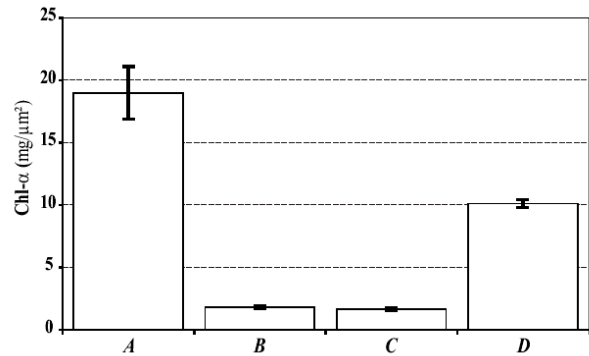


Figure 4. Average biomass of chl-a (mg/m<sup>2</sup>) in the periphyton growth plates in each study area. The bars indicate the standard errors.

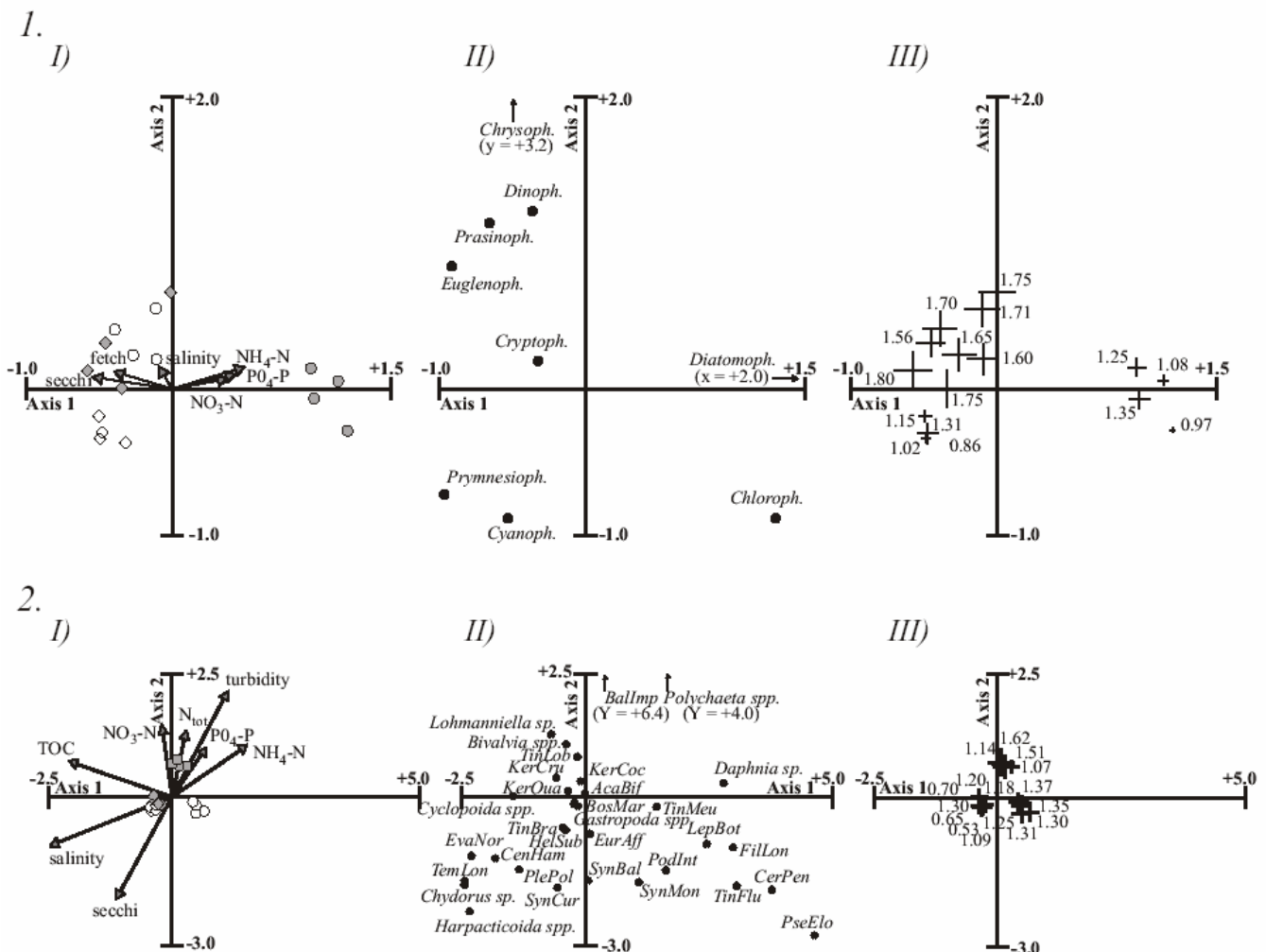


Figure 3. CCA-ordination of the 1) phytoplankton and 2) zooplankton samples; (I) sample scores (● = area *A*, ○ = area *B*, ◆ = area *C* and ◇ = area *D*) and environmental variables, (II) species scores, (III) Shannon-Wiener diversity indices of sampling sites.



Table 1. Results of the plankton data analyses. I) CCA eigenvalues, species-environment correlations, cumulative variances and significance tests for axes 1-3 and all canonical axes (ACA). II) CCA inter-set correlations between axes 1-3 and environmental variables. III) Kruskal-Wallis ANOVA for comparing Shannon-Wiener index, species abundance, species biomass and species number among the areas. (TI = total inertia).

	Phytoplankton (TI=0.642)				Zooplankton (TI=0.420)				
	Axes	1	2	3	ACA	1	2	3	ACA
I)									
Eigenvalue	0.390	0.102	0.051	0.581	0.141	0.108	0.043	0.371	
Species-environment correlation	0.998	0.916	0.929		1.000	0.982	0.961		
Cumulative percentage variance of species data	60.8	76.7	84.6		33.5	59.1	69.3		
Cumulative percentage variance of species-environment relation	67.2	84.8	93.5		38.0	67.0	78.6		
Monte Carlo test, F-ratio	7.747	3.421	2.560	7.925	1.518	1.880	0.997	2.810	
p-value	0.040	0.333	0.151	0.040	0.037	0.238	0.043	0.037	
II)									
Salinity (PSU)	-0.13	0.43	0.76		-0.90	-0.41	-0.07		
Turbidity (FTU)	-	-	-		0.41	0.88	-0.01		
N <sub>tot</sub> (µg/l)	-	-	-		0.10	0.55	0.72		
NO <sub>3</sub> -N (µg/l)	0.59	0.22	-0.25		-0.08	0.59	0.44		
NH <sub>4</sub> -N (µg/l)	0.78	0.44	0.05		0.55	0.42	0.34		
PO <sub>4</sub> -P (µg/l)	0.68	0.29	-0.22		0.25	0.40	0.29		
Secchi depth (m)	-0.86	0.23	-0.32		-0.41	-0.85	0.11		
TOC (mg/l)	-	-	-		-0.77	0.29	-0.03		
Fetch	-0.62	0.34	-0.32		-	-	-		
III)									
<b>Kruskal-Wallis</b>									
<b>ANOVA</b>									
	$\chi^2$	<i>df</i>	<i>P</i>		$\chi^2$	<i>df</i>	<i>p</i>		
Shannon-Wiener	8.33	3	0.040		5.62	3	0.132		
Abundance (Ind./m <sup>3</sup> )	-	-	-		9.36	3	0.025		
Biomass (mg/l)	7.05	3	0.070		-	-	-		
Biomass (wwt µg)	-	-	-		9.46	3	0.024		
Number of Taxa	10.39	3	0.016		9.47	3	0.024		

suspended solids described most appropriately the assemblages of macro phytobenthos in the study area (Table 2). However, the model was only marginally significant. Again, the sites were mainly arranged along a trophic gradient as the first axis (Fig.5). All littoral sites within the areas clustered together, although areas *B*, *C* and *D* showed a slightly overlapping pattern. Species abundance showed a statistically significant difference, but species diversity diverged only marginally significantly while the number of taxa showed no difference at all between the areas (Table 2). The species composition in area *A* distinguished itself from others, as there the abundance of vascular plants *Potamogeton pectinatus* and *Ranunculus* sp.

was evidently higher than in the other areas (Fig.5). The highest species diversity was found in area *B* and the lowest in *C* (Fig.5).

Of the environmental variables salinity, turbidity, nutrients, total organic carbon and Secchi depth described best the composition of zooplankton (Table 1). Littoral sites within areas *A* and *B* clustered as separate groups, but outer areas *C* and *D* showed an overlapping pattern and were associated more with salinity and visibility of the seawater (Fig.3). There were statistically significant differences in species abundance, biomass and number of taxa, but species diversity showed no difference between the areas (Table 1). Ciliates (e.g. *Lohmanniella* sp., *Tintinnopsis meuneri*) and

Table 2. Results of the peri-/macrophyton data analyses. I) Kruskal-Wallis ANOVA for comparing periphyton chl-a biomass (mg/m<sup>2</sup>). Factor in the analysis is area (areas *A*, *B*, *C* and *D*). Subsequently, Bonferroni adjusted Mann-Whitney U-tests for single comparisons of differences between areas. II) Macrophytes CCA eigenvalues, species-environment correlations, cumulative variances and significance tests for axes 1-3 and all canonical axes (ACA). III) CCA inter-set correlations between axes 1-3 and environmental variables. IV) Kruskal-Wallis ANOVA for comparing Shannon-Wiener index, species abundance and species number among areas. (TI = total inertia).

I)

Source	<i>n</i>	$\bar{x}$	SD	$\chi^2$	<i>d.f</i>	<i>p-value</i>
Between areas	32	8.16	9.96	23.73	3	<0.001

**Mann-Whitney U-test (Bonferroni adjusted)**

Comparison	<i>n</i>	U	<i>p-value</i>
<i>Basin A vs. Basin B</i>	18	0.0	<0.001
<i>Basin A vs. Basin C</i>	17	0.0	0.006
<i>Basin A vs. Basin D</i>	15	15.0	0.936
<i>Basin B vs. Basin C</i>	17	31.5	1.000
<i>Basin B vs. Basin D</i>	15	0.0	0.006
<i>Basin C vs. Basin D</i>	14	0.0	0.012

**Macrophytes (TI=1.040)**

Axes	1	2	3	ACA
II) Eigenvalue	0.416	0.167	0.081	0.747
Species-environment correlation	0.940	0.936	0.906	
Cumulative percentage variance of species data	40.0	56.0	63.8	
Cumulative percentage variance of species-environment relation	55.7	78.0	88.8	
Monte Carlo test, F-ratio	2.125	1.828	1.072	0.747
p-value	0.045	0.204	0.680	0.091
III) NO <sub>3</sub> -N (µg/l)	0.46	0.56	0.23	
NH <sub>4</sub> -N (µg/l)	0.63	0.39	-0.32	
PO <sub>4</sub> -P (µg/l)	0.53	0.21	0.60	
Secchi depth (m)	-0.80	0.33	0.13	
Fetch	-0.42	0.78	-0.10	
Suspended solids	0.43	-0.60	0.16	

IV)

**Kruskal-Wallis ANOVA**

	$\chi^2$	<i>df</i>	<i>p</i>
Shannon-Wiener	6.51	3	0.089
Abundance (Ind./m <sup>2</sup> )	8.77	3	0.032
Number of Taxa	4.48	3	0.214

rotifers (*Keratella* spp., *Synchaeta* spp.) were more abundant in areas *A* and *B* than were marine cladocerans *Evadne nordmanni*,

*Pleopsis polyphemoides* while neritic copepods *Centropages hamatus*, *Temora longicornis* were mostly found in *C* and *D* (Fig.3).

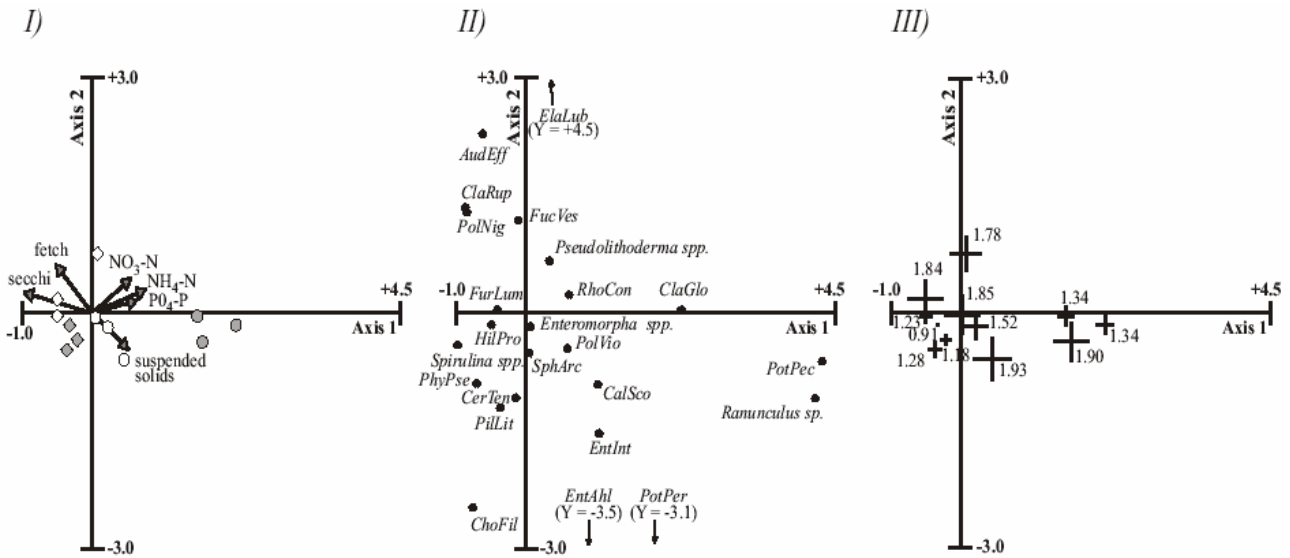


Figure 5. CCA-ordination of the macrophytobenthos samples; (I) sample scores (● = area A, ○ = area B, ◆ = area C and ◇ = area D) and environmental variables, (II) species scores, (III) Shannon-Wiener diversity indices of sampling sites.

Turbidity, inorganic nutrients, Secchi depth, modified effective fetch, suspended solids and periphyton biomass described best the assemblages of zoobenthos (Table 3). Littoral sites within area A clustered together and were associated with the trophic level of the seawater. Also the remaining areas showed distinct clustering but with much shorter distance among them (Fig.6). There was only a marginally significant difference in species diversity, whereas species abundance, biomass and number of taxa showed no statistical divergence between the areas (Table 3). The highest species diversity was found in area A, where the shares of some polychaetes (e.g. *Polydora redeki*, *Manayunkia aesturina*), bivalves (e.g. *Macoma baltica*, *Mya arenaria*) and amphipods (e.g. *Leptocheirus pilosus*) were higher than in other areas (Fig.6).

The largest variety of taxa was found in the fauna associated with *Fucus*. Turbidity, nitrogen concentrations, Secchi depth, relative exposure, periphyton biomass and density of *Fucus* stands described best the composition of the fauna (Fig.6). However, we were not able to detect any statistical significance, therefore littoral sites within areas indicated a more or less overlapping pattern (Fig.6). The number of taxa between the areas showed a statistically significant difference, but species abundance and biomass diverged only marginally

significantly, species diversity did not differ (Table 3).

Fish could be sampled only in areas A, B and C due to autumnal storms. Oxygen concentration, inorganic nutrients, Secchi depth and relative exposure described best the assemblages of fish caught with multi-mesh net (Table 4). However, the model showed no statistical significance (Fig.7). There were only marginally significant differences in species diversity and abundance, but species biomass and number of taxa showed no statistical divergence between the areas (Table 4). The highest species number was to be found in area A, where the share of cyprinidae (e.g. *Abramis brama*, *Blicca bjoerkna*) and fish favouring turbid water (e.g. *Stizostedion lucioperca*, *Gymnocephalus cernuus*) was higher than elsewhere (Fig.7). Total nutrient concentrations, total organic carbon and relative exposure described best the composition of fish caught by beach seine (Table 4). Again, however, we were not able to detect any statistical significance for the model, and littoral sites within the areas showed no distinct clustering (Fig.7). The number of taxa, species abundance, biomass and diversity showed no statistically significant difference among the areas (Table 4).

Table 3. Results of the benthic data analyses. I) CCA eigenvalues, species-environment correlations, cumulative variances and significance tests for axes 1-3 and all canonical axes (ACA). II) CCA inter-set correlations between axes 1-3 and environmental variables. III) Kruskal-Wallis ANOVA for comparing Shannon-Wiener index, species abundance, species biomass and species number among areas. (TI = total inertia).

Axes	Zoobenthos (TI=0.674)				Fucus associated (TI=0.572)			
	1	2	3	ACA	1	2	3	ACA
I)								
Eigenvalue	0.247	0.990	0.750	0.567	0.174	0.122	0.061	0.485
Species-environment correlation	0.996	0.963	0.953		0.996	0.977	0.993	
Cumulative percentage variance of species data	36.6	51.3	62.4		30.4	51.6	62.3	
Cumulative percentage variance of species-environment relation	43.5	61.0	74.2		35.8	60.9	73.4	
Monte Carlo test, F-ratio	1.734	0.907	0.887	1.994	1.308	1.318	0.846	2.093
p-value	0.047	0.272	0.390	0.047	0.169	0.310	0.787	0.277
II)								
Turbidity (FTU)	-0.85	-0.44	0.11		0.93	-0.08	-0.07	
N <sub>tot</sub> (µg/l)	-	-	-		0.75	0.03	0.45	
NO <sub>3</sub> -N (µg/l)	-0.56	-0.29	0.29		0.87	0.03	0.37	
NH <sub>4</sub> -N (µg/l)	-0.52	-0.54	0.37		0.67	0.52	-0.16	
PO <sub>4</sub> -P (µg/l)	-0.66	-0.25	0.12		-	-	-	
Secchi depth (m)	0.88	0.30	-0.11		-0.79	0.09	0.12	
Fetch	0.78	0.08	0.24		-0.42	0.37	0.34	
Suspended solids	-0.81	-0.11	-0.32		-	-	-	
Periphyton biomass (chl- <i>a</i> )	-0.19	-0.66	0.33		-0.68	0.44	0.13	
<i>Fucus</i> density	-	-	-		-0.42	0.30	0.35	
III)								
<b>Kruskal-Wallis</b>								
<b>ANOVA</b>								
	$\chi^2$	<i>df</i>	<i>p</i>		$\chi^2$	<i>df</i>	<i>p</i>	
Shannon-Wiener	7.23	3	0.065		5.29	3	0.152	
Abundance (Ind./m <sup>2</sup> )	0.55	3	0.909		6.61	3	0.086	
Biomass (wwt g./m <sup>2</sup> )	0.38	3	0.945		6.61	3	0.086	
Number of Taxa	3.38	3	0.337		8.93	3	0.030	

## Discussion

The most important factors changing together with littoral communities were nutrient concentration, Secchi depth and relative wave exposure. The system can be seen as a bipolar one, due to the way these factors interact in the middle archipelago. In the inner archipelago, the predominant variables, which came up almost exceptionally in every CCA-model, were nutrient concentrations in the seawater. In the more open outer areas community compositions

were changing together with higher visibility and increasing wave action. In the middle archipelago, the system was a composite of these extremes, thus communities there were apparently influenced by factors from both directions. Similarly to the environmental factors, also biota arranges bipolarly with the phytal showing more affinity to high nutrient concentrations, and, naturally, the faunal component (with the exception of fish) appearing more related to other environmental factors. In general the highest species diversities

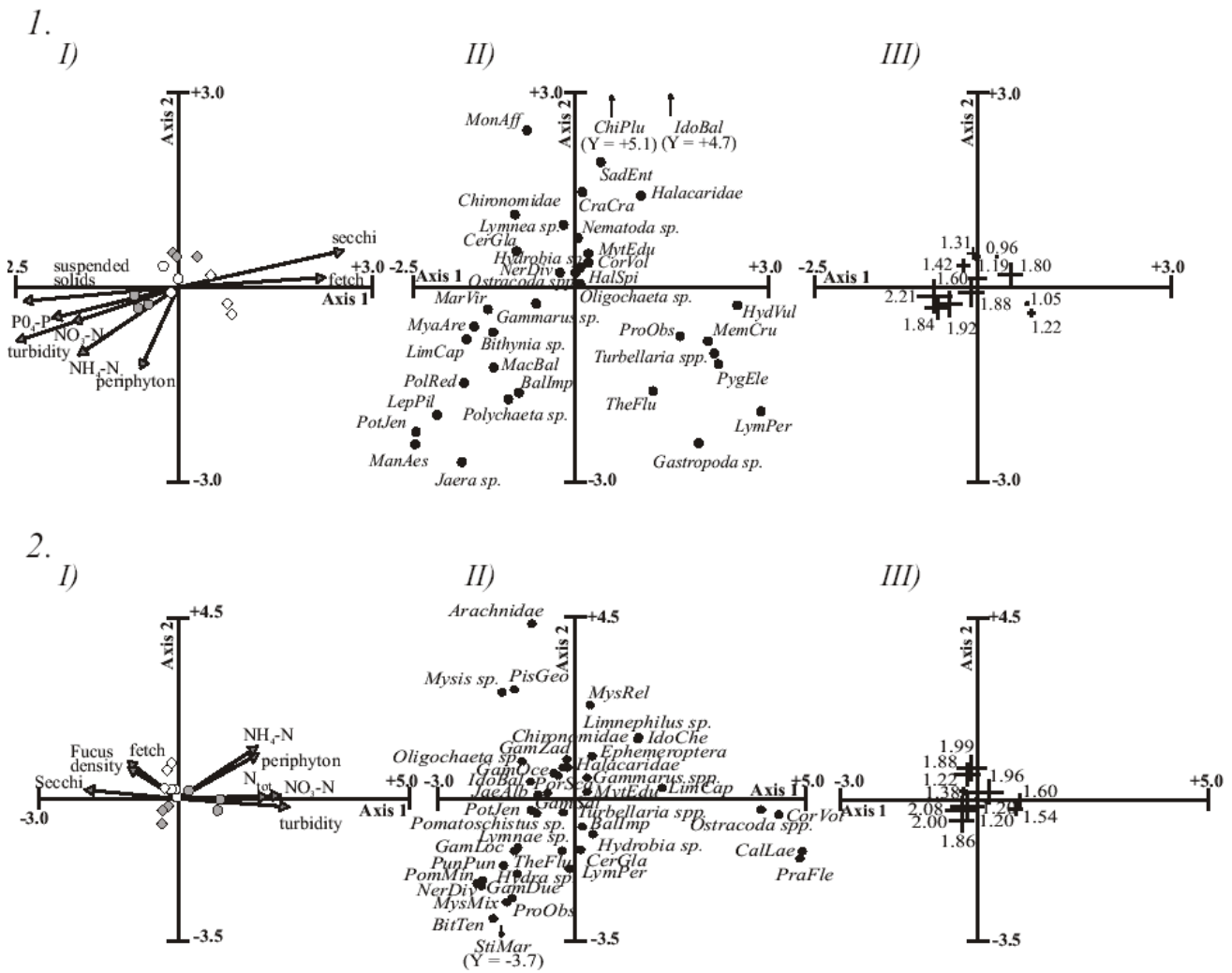


Figure 6. CCA-ordination of the 1) zoobenthos and 2) *Fucus* associated fauna samples; (I) sample scores (● = area A, ○ = area B, ◆ = area C and ◇ = area D) and environmental variables, (II) species scores, (III) Shannon-Wiener diversity indices of sampling sites.

were found in the more sheltered inner and middle archipelago. When considering the influence of habitat type, the largest variety of taxa was found in fauna associated with the *Fucus*-zone. This is in concert with previous studies on the Baltic Sea littoral biodiversity (Segerstråle 1927, Jansson 1972).

Inorganic nutrients and visibility of the seawater proved to be the most important controlling factors for the phytal, i.e. phytoplankton, periphyton and macro phytobenthos. The phytoplankton compositions in the different parts of the Archipelago Sea followed closely the changes in water quality between the archipelago zones. We also found the highest periphyton biomass in the sheltered

inner archipelago associated with high nutrient concentrations and low visibility. Furthermore, our study confirms the importance of trophic conditions in terms of inorganic nutrients as a regulating factor for macro phytobenthic communities. Moreover, physical disturbance (fetch) and its effect on the seabed quality (amount of suspended sediments), are significant influential factors.

On the other hand, zooplankton compositions did not reveal as significant an association with trophic gradient as did phytoplankton or the phytobenthos groups. As for zooplankton, the salinity and factors indicating the transparency of the seawater turbidity and Secchi depth were more important environmental parameters.

Table 4. Results of the fish data analyses. I) CCA eigenvalues, species-environment correlations, cumulative variances and significance tests for axes 1-3 and all canonical axes (ACA). II) CCA inter-set correlations between axes 1-3 and environmental variables. III) Kruskal-Wallis ANOVA for comparing Shannon-Wiener index, species abundance, species biomass and species number among areas. (TI = total inertia).

	<i>Multi mesh net fish</i>				<i>Beach seine fish</i>			
	<i>(TI=0.884)</i>				<i>(TI=2.863)</i>			
<i>Axes</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>ACA</i>	<i>1</i>	<i>2</i>	<i>3</i>	<i>ACA</i>
I)								
Eigenvalue	0.465	0.119	0.072	0.759	0.908	0.823	0.424	2.422
Species-environment correlation	0.968	0.973	0.940		0.998	0.987	0.879	
Cumulative percentage variance of species data	52.7	66.1	74.3		31.7	60.5	75.3	
Cumulative percentage variance of species-environment relation	61.3	77.0	86.5		37.5	71.5	89.0	
Monte Carlo test, F-ratio	2.224	0.795	0.633	2.027	0.465	0.727	0.599	1.374
p-value	0.167	0.323	1.000	0.167	0.329	0.164	1.000	0.180
II)								
O <sub>2</sub> (mg/l)	0.47	-0.26	-0.70		-	-	-	
N <sub>tot</sub> (µg/l)	-	-	-		0.73	-0.65	0.05	
NO <sub>3</sub> -N (µg/l)	-0.49	-0.55	0.22		-	-	-	
NH <sub>4</sub> -N (µg/l)	-0.92	0.13	-0.20					
P <sub>tot</sub> (µg/l)	-	-	-		0.32	-0.87	0.21	
PO <sub>4</sub> -P (µg/l)	-0.65	-0.26	-0.29		-	-	-	
TOC (mg/l)	-	-	-		-0.70	-0.64	-0.10	
Secchi depth (m)	0.77	0.44	0.10		-	-	-	
Fetch	0.61	-0.11	0.58		-0.45	0.85	-0.19	
III)								
<b>Kruskal-Wallis</b>								
<b>ANOVA</b>								
	$\chi^2$	<i>df</i>	<i>p</i>		$\chi^2$	<i>df</i>	<i>p</i>	
Shannon-Wiener	5.42	2	0.066		2.00	2	0.368	
Abundance (Ind./m <sup>2</sup> )	5.60	2	0.061		1.14	2	0.565	
Biomass (wwt g./m <sup>2</sup> )	1.87	2	0.393		2.57	2	0.276	
Number of Taxa	4.48	2	0.107		4.28	2	0.320	

Marine species (neritic copepods and cladocerans) were mainly found in outer areas, whereas freshwater groups, rotifers and freshwater cladocerans were more abundant in the inner archipelago parts near the freshwater outlets. Likewise, also the littoral zoobenthos was controlled by other factors than trophic conditions alone. Their species diversity was more connected with seawater transparency (turbidity and Secchi depth), characteristics of seabed quality (amount of suspended solids) and relative wave action (fetch). None of the CCA-models built for fish caught by either the multi-

mesh or beach seine net showed statistical significance. Nevertheless, the models did reveal the expected situation that fish communities were arranged according to trophic gradients. Species favouring turbid and eutrophic seawater (e.g. pikeperch and cyprinids) were found in the inner areas whereas more pelagic species (e.g. herring, smelt, whitefish) inhabit the outer archipelago.

Although the CCA-model for fauna associated with *Fucus* showed no statistical significance, it gave some indication of the factors important to species diversity among *Fucus* stands. We

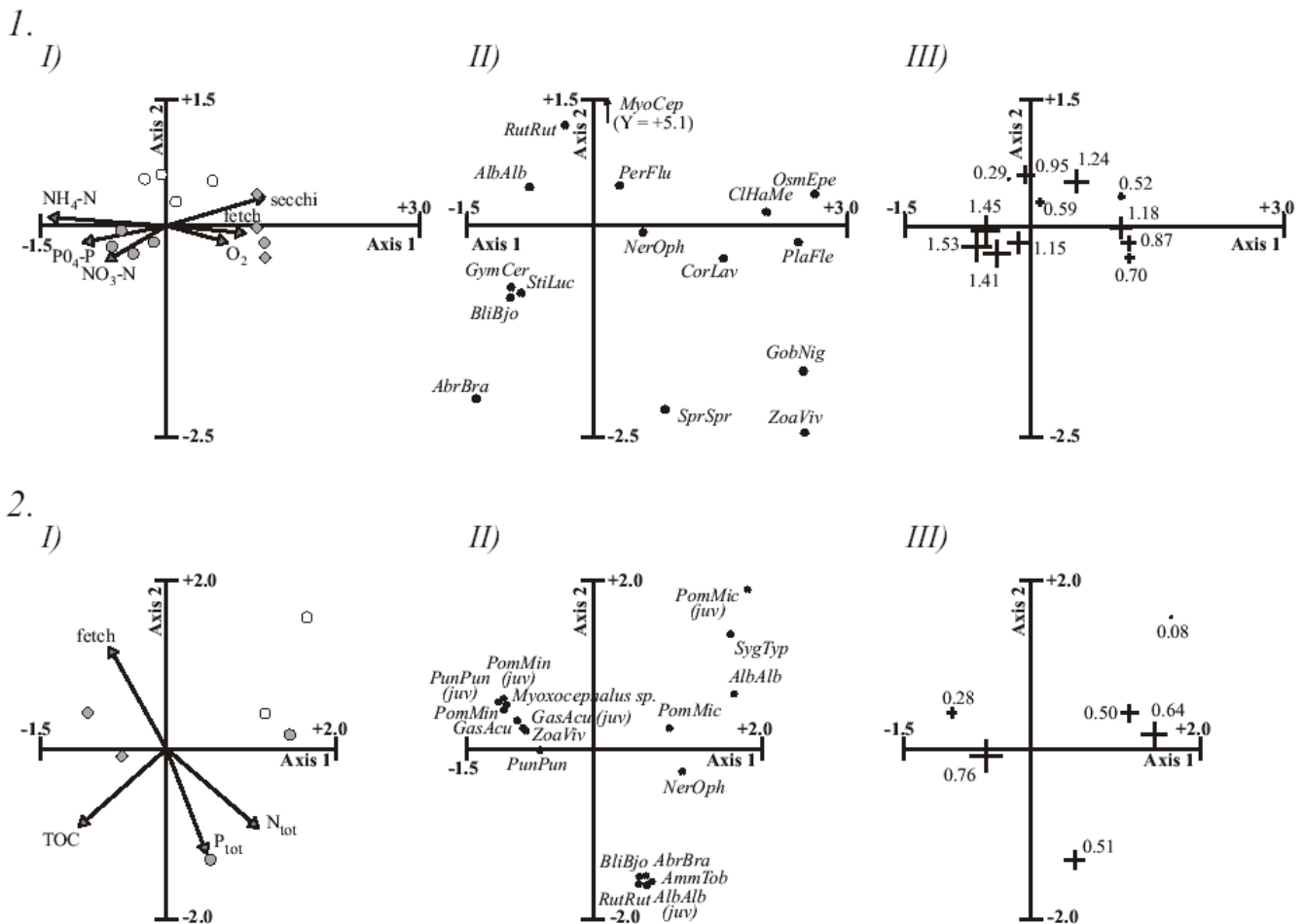


Figure 7. CCA-ordination of the 1) multi-mesh net fish and 2) beach seine net fish samples; (I) sample scores (● = area A, ○ = area B, ◆ = area C and ◇ = area D) and environmental variables, (II) species scores, (III) Shannon-Wiener diversity indices of sampling sites.

suggest that the reason for the unsatisfactory model was that the parameters measured to explain assemblages were not adequate. Most probably some of them should have been linked more closely with the characteristics of the *Fucus* vegetation, for instance distance between stands, occurrence of epiphytes, etc. (for a discussion see e.g. Boström 2001).

Our findings are in accordance with previous work published taking into account the lack of specific studies on littoral phytoplankton, zooplankton and benthos among *Fucus*. These taxa have been studied in the Baltic Sea pelagial and deep areas, however, and some comparisons are therefore warranted. Considering phytoplankton the results generally agree with findings of Kononen & Niemi (1984) from the Gulf of Finland. However, a more precise evaluation of our observation is difficult due to the lack of comparable recent studies, and also due to lacking species identification. For example, Kippo-Edlund &

Niemi (1984) comparing phytoplankton composition and biomass between 1966-1970 and 1979-1982 in the Archipelago Sea suggested that the main factor affecting the phytoplankton species composition is salinity (in the outer areas they found increased abundance of marine species). There was a substantial rise in seawater salinity between these compared periods (e.g. Vuorinen & Ranta 1987), which may have masked other, more delicate relations between phytoplankton and environment. Nutrient levels (Kippo-Edlund & Niemi 1984) influenced mainly phytoplankton biomass (in general no marked changes in species composition in the inner areas). Nevertheless, based on the present work we would not consider it surprising if it later appears that phytoplankton composition show the same divisions into different the archipelago area as did water parameters in our study. Our results with periphyton were highly similar to those of Mattila & Räsänen (1998), who did

not record the relatively high biomass we found in the outer areas. However, their study area was not as extensive as that of ours, and a comparison is therefore not allowed. We suggest, however, that their observation of high variation among different parts of the archipelago could be a plausible explanation also in our study.

Vuorinen & Ranta (1987), Viitasalo *et al.* (1995) and Vuorinen *et al.* (1998) have shown that a major factor controlling the composition of zooplankton community in the Archipelago Sea is the salinity of the seawater. Although their work has considered the coupling of the ecology of pelagic planktonic groups and the large-scale regulating weather patterns of the Baltic Sea, we see the same significance of salinity here, although on a smaller scale. Bonsdorff *et al.* (1991) in the archipelago of Åland Islands, and Hänninen & Vuorinen (2000) in the Archipelago Sea have earlier studied the macro zoobenthos structure in relation to major environmental changes, particularly eutrophication. They have shown that species diversity, biomass and abundance are closely related to trophic status of the seawater. Hänninen & Vuorinen (2000) recorded the highest values in the inner and middle archipelago zones. However, they concentrated mainly on the profundal zone and their study area did not extend as far as ours. Hence, the results are not directly comparable. It also explains why other environmental factors than nutrients were found important in our study and not in theirs. In the Tväminne area using the similar multi-mesh net as in the present work, Lappalainen *et al.* (2001) demonstrated that between 1975 and 1997 the most pronounced change because of excess nutrients has been the increase of cyprinids, particularly roach (*Rutilus rutilus*) stocks. On the other hand Rajasilta *et al.* (1999) showed that during the 1990s the littoral fish communities in the middle archipelago collapsed when compared with data from the 1970s and 1980s. Although the present study can support these findings only indirectly, indications of the importance of trophic conditions to fish communities was demonstrated. However, a more precise comparison is strongly hampered by the nature of both types of gear used, as either method

cannot honestly be regarded as quantitative, at best only semi-quantitative.

The biotic factors that influence community composition in aquatic environment are (from bottom up to top down) productivity (e.g. Carpenter *et al.* 1985, MacQueen *et al.* 1986) competition (e.g. Hardin 1960), and predation (e.g. Paine 1966, Connell 1971, 1974, Menge 1978, Mills *et al.* 1987). Simultaneously environmental effects on species or communities depend on trophic levels and species-specific tolerance (e.g. Bottom & Jones 1990, Buhl-Mortensen & Hoisaeter 1993). More recently also physical disturbances have been demonstrated as important (e.g. Menge & Sutherland 1976, 1987), while the concept of competition (e.g. Hardin 1960) seems to have dropped somewhat out of focus. It was originally suggested that abiotic factors and the physical environment merely provide a “frame” within which interactions among organisms can modify the final ecosystem structure (for examples of the idea, see e.g. MacQueen *et al.* 1986, Carpenter 1988 and Gutierrez *et al.* 1994). Stable communities were thought to be organised largely through biotic interactions, while the role of the abiotic events have more been seen as to weaken the equilibrium of the communities. This concept has since then been developed largely in the lotic environment (for a recent contribution, see Thomson *et al.* (2002)) Based on these studies the role of predators is seen to decrease if the abiotic environment becomes more stressing. In a continuously disturbed environments the species richness is low, and the food web structure and trophic interactions are therefore simple (e.g. Menge & Sutherland 1987, McCann *et al.* 1998) as may be e.g. in the Baltic Sea, as a whole. According to our study the relative importance of these biotic and abiotic processes in structuring communities seems to be bipolar, with biotic control gaining more importance next to the coastline and physical control being important towards the open sea. However, in our study disturbed environment was found generally in the outer archipelago, but simultaneously also in relatively sheltered and shallow littoral (higher wind effect on (shallow) bottoms, more effect of variable water levels, intensive disturbance by ice movements) environments. Based on former,



the most disturbed outer archipelago and shallow littoral habitats would be influenced to a greater degree by abiotic factors, whereas biotic interactions play a bigger role in the inner archipelago and in more sheltered sites and deeper parts of the littoral zone, where also the structure-forming algal vegetation is concentrated.

In the Archipelago Sea, northern Baltic, the main reason for the impoverishment of the water quality and further deterioration of flora and fauna has been a massive eutrophication process over the last three to four decades. For example the upward lifting of the lower edge of sea grass and algal vegetation has been repeatedly shown to result in a diminution of the physical shelter as well as reproduction and feeding areas (e.g. Kautsky et al. 1986), a complete disappearance of the *Fucus* belt has been likewise recorded (HELCOM 1993). This has also led to changes in the nutrient budgets in the littoral zone-pelagial interface, especially so in the inner parts of the archipelago, which are more affected by human economy. Furthermore, we expect also changes in the littoral zonation due to eutrophication in similar manner that was found by O'Brien *et al.* (2003), who reported an outward shift of inner archipelago soft bottom animal communities. However, this study does not enable us to conclude nor speculate about possible effects of eutrophication on littoral biodiversity other than what is generally known already. The main sources of excess nutrients have been identified to be agricultural runoff, and industrial and municipal wastewater, forestry, and, during the last 20 years, fish farming (Bonsdorff *et al.* (1997a,b), Hänninen *et al.* 2000). Therefore the expected effects are more likely to occur where also other human impact is larger, i.e. in the inner and middle archipelago. Airborne and current-mediated nutrients in the water could extend the effect of eutrophication also to outer archipelago, but so far the knowledge about these is very limited. Only recently, the share of airborne nutrients and nutrients imported by currents from other parts of the Baltic Sea, Gulf of Finland, Bothnian Sea, Baltic Proper have been estimated (Jumppanen & Mattila 1994), Kirkkala *et al.* (1998), Helminen *et al.* (1998). The surface current coming from the Gulf of

Finland flows through the Archipelago Sea towards the Gulf of Bothnia (Palmén 1930), but the knowledge of wind-induced currents and water exchange is next to nil. Helminen *et al.* (1998) constructed a 3-d hydrographical model of water exchange between the outer archipelago and the Baltic Proper. One of the main conclusions was that the import of nutrients by surface currents from the Baltic Proper could be decisive for the eutrophication process of the Archipelago Sea. Precise data on water movement in the whole Archipelago Sea are still not available. One further complication is the internal loading of nutrients in low oxygen

conditions close to the bottom. Virtasalo *et al.* (2005) observed anoxia or low oxygen concentrations in all archipelago zones in a benthic mapping. Therefore protection of littoral or other aquatic biodiversity from the effects of eutrophication is not granted by concentrating the protective measures in the outer archipelago areas, where eutrophication is currently expected to have minor effects.

Concluding, the areas with highest biodiversity have also been under human-induced environmental change; therefore it seems not reasonable that the nature protection measures have been taken predominantly in the low biodiversity environment, in the outer archipelago. In a management point of view, if high biodiversity is taken as a value in itself, then the inner and middle parts of the archipelago should be preferred in the protection. We argue that measures to protect biodiversity should be aimed rather there than to the outer zones that are traditionally taken as the target for environmental protection work, and where most of nature protection and biosphere areas have been founded. Then, finally, if the natural or pristine biodiversity is valued high, then we should protect the outer archipelago, but that would actually mean protecting areas of lower biodiversity.

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