Local distribution patterns of macroalgae in relation to environmental variables in the northern Baltic Proper

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Abstract

The relationship between macroalgal assemblages and abiotic factors was quantified by gradient analyses in an area where long-term changes in macroalgal depth distributions have previously been documented. Biomass data from 4, 6, 8 and 10 m depth in an area of similar salinity (5) and substrate (rock) in the northern Baltic Proper was constrained by a set of environmental variables defining different aspects of abiotic control of species distributions (sediment cover, effective fetch, clarity index, the curvature and slope of the bottom, and direction of exposure) in multivariate analyses at different scales. \textit{Fucus vesiculosus} dominated the biomass at 4, 6 and 8 m depth, and \textit{Furcellaria lumbricalis} at 10 m. The applied models explained 30.7–53.3% of the total variance in community structure, and 49.3–60.9% when analysed separately for each depth. A separate analysis of species depth distributions demonstrated that effective fetch was most strongly related to upper limits of the algal belts, sediment cover to the lower limit and density of the \textit{F. vesiculosus} belt, and clarity index to the lower limits of \textit{F. vesiculosus}, perennial red algae, and of the red algal and \textit{Sphacelaria} spp. belts. The results show a strong correlation between environmental variables and vegetation structure even on a small, local scale in the northern Baltic Proper, indicating a high suitability of the phytobenthic zone for environmental monitoring. The results add to previous studies that show a strong importance of abiotic factors on large-scale variation in phytobenthic community composition in the Baltic Sea.

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1. Introduction

Whereas ecological processes are well recognised in marine intertidal communities (cf. Robles and Desharnais, 2002), considerably less is known about factors controlling sublittoral communities (Witman and Dayton, 2001). This is also true for the Baltic Sea, where tide is negligible and main part of the benthic community is permanently submerged.

In the Baltic Sea, biotic interactions are traditionally believed to have minor importance in controlling rocky shore community structure (Wern, 1952; Kautsky and van der Maarel, 1990). Due to its low salinity and short evolutionary history, species richness is low (Russel, 1985; Wallentinus, 1991). Most conspicuously, sessile animals and large herbivores are scarce, and rocky shore community structure is usually typified by vegetation structure (Kautsky, 1993). The phytal community is also simplified, as 70% of the macroalgal species present outside the Baltic Sea entrance do not extend into the Baltic Sea (Nielsen et al., 1995; Middelboe et al., 1997; Snoeijis, 1999). Due to prolonged unpredictable low water periods and ice-scraping, macroalgae that are
typically intertidal dislocate downwards into the sublittoral zone as they enter the Baltic Sea (Du Rietz, 1930; Wærn, 1952). This opportunity to extend their lower distribution limits presumably reflects decreased competition and grazing pressure with decreasing diversity (Wærn, 1965; Pedersen and Snoeijs, 2001). However, an increasing number of experimental studies suggest that grazing by small invertebrates and competitive interactions between macroalgae have significant effects on local community structure and macroalgal diversity in the Baltic Sea (Malm et al., 1999; Worm et al., 1999, 2001; Engqvist et al., 2000; Lotze et al., 2000, 2001; Hemmi and Jormalainen, 2002; Berger et al., 2003; Malm and Kautsky, 2003).

The relative effect of abiotic factors on community structure varies with scale and reveals a high predictability of large-scale vegetation patterns in the Baltic Sea. On a geographic scale, the strongest effect on both species composition and species biomass is that of salinity, enforced by a salinity decrease from 10 to 2 over the Baltic Sea area (Kautsky, 1993; Middelboe et al., 1997). Regionally, community type is mainly determined by type of substrate which is dependent on local geology, topology and wave action (Kautsky and van der Maarel, 1990; Kautsky et al., 1999). Within a site, depth is the most useful predictor of phytobenthic community structure (Kautsky, 1993). Water level, wave action and ice-scouring regulate the upper distribution limit of the vegetation, while the lower distribution limit is related to physiological constraints, such as light availability limiting photosynthesis and sediment cover limiting areas available for recruitment (Kautsky, 1993; Kiiikki, 1996a; Bäck and Ruuskanen, 2000; Eriksson and Johansson, 2003).

The amount of vegetation present determines ecological function and is directly related to the depth distribution. Studies on long-term changes in macroalgal communities show a general decline in the depth distribution of either whole vegetation or of important structural components (Rönnberg et al., 1985; Johansson et al., 1998; Rönnberg and Mathiesen, 1998; Jansson and Dahlberg, 1999; Cloern, 2001; Eriksson et al., 2002). The decrease has commonly been related to increased turbidity limiting primary productivity and/or increased deposition of organic sediments limiting recruitment, two effects that can be linked to large-scale nutrient enrichment and increased pelagic productivity (Jansson and Dahlberg, 1999; Cloern, 2001).

The aim of this study was to quantify the relationship between abiotic factors and macroalgal assemblages on a local scale, within an area of similar salinity and substrate. This was done by gradient analyses of macroalgal community composition in an area where long-term changes in macroalgal depth distributions have previously been documented (Wærn, 1952; Kautsky et al., 1986; Eriksson et al., 1998). Considering these changes, this study also evaluates the contribution of different environmental factors to explain the depth distribution of different species. The results provide a tool to derive hypotheses on factors regulating abundance patterns and compare previous experimental results with conditions in the field, but also to assess the suitability of using the phytobenthic zone for environmental monitoring.

2. Materials and methods

2.1. Study area

The study was carried out in the Singö archipelago on the east coast of Sweden, on the border between the Bothnian Sea and the Baltic Proper, consisting of more than 200 skerries (Fig. 1). The predominating bottom substrate in the area is rock, with some coarse moraine covering from 4–5 m depth. There are no larger freshwater outlets in the area and surface salinity (≤30 m depth) normally ranges between absolute values of 4.9 and 6.2 with monthly means of 5.0–5.5 in summer (minimum in August) and 5.5–6.0 in winter (maximum in December) (based on: Wærn, 1952, p.15; Baltic Environmental Database, 1991–1993, http://data.ecology.su.se/models/bed.htm; personal observations 1998). Total nitrogen concentrations commonly range between 12.3 and 24.1 (no seasonal pattern) with a mean of 17.7 and phosphorus concentrations range between 0.19 in summer and 0.68 in winter with a mean of 0.47 (μmol l⁻¹; based on Baltic Environmental Database, 1991–1993, http://data.ecology.su.se/models/bed.htm; personal observations 1998).
Sediment cover was estimated in situ for each biomass sample, according to a 5-level scale: 1 = no visible sediment, 2 = some visible sediment, 3 = substrate covered in part by flocks of sediment, 4 = substrate covered completely, and 5 = substrate and vegetation covered by sediment.

Exposure was modelled using a cartographic index, effective fetch, that is intended to reflect the physical impact of wave action on the shore, by estimating the area over which incoming waves potentially accumulate energy. It was calculated using the formula:

\[ \text{Fetch} = \frac{\sum x_i \cos z_i}{\sum \cos z_i} \]

where \( x \) is the distance from the site to the opposite shore at 15 evenly distributed directions within a sector of \( \pm 42^\circ \) from the central radius, and \( z \) is the angle of deviation from the central radius (Håkansson and Jansson, 1983). Effective fetch was obtained by placing the central radius in the direction giving the highest fetch value. The direction of exposure was decomposed into the north–south component and the east–west component of the compass direction, by incorporating the variables as the sinus and the cosinus of the angle of direction, respectively.

Light availability was modelled using a derivative of effective fetch, the clarity index, that is intended to describe the potential light penetration of the water column, by estimating the highest fetch value that can be acquired in any compass direction within 500 m from a site (Kiiikki, 1996a). The clarity index is less affected by local topography than effective fetch and therefore characterises properties of the water mass rather than wave force. To check the relationship between the clarity index and light penetration of the water, the Secchi depth was measured 1–2 times at each site during the sampling period. The results showed that clarity index correlated strongly with Secchi depth, but excludes the time dependency of Secchi depth measurements (Regression model of Secchi depth as a function of the clarity index and date of measurement, \( n = 12 \), \( R^2[adj.] = 0.91, p < 0.001 \)). Both fetch indexes were log-transformed before analysis.

The physiognomy of the bottom profiles was described as the curvature and the slope of transects. Curvature was calculated using a derivative of the form factor for lakes (Håkansson and Jansson, 1983) using the formula:

\[ \text{Curvature} = \frac{D_{\text{max}}}{(2 \times D_{1/2})} \]

where \( D_{\text{max}} \) is the maximum depth of the transect and \( D_{1/2} \) is the water depth at half-length of the transect. Slope was estimated by calculating the coefficient of inclination \( (k) \) of a straight line fitted onto the bottom profile.

2.4. Data analysis

The relationship between community structure and incorporated environmental variables was explored by three sets of gradient analyses (CANOCO 4.0), regarding different characteristics the vegetation: (1) the
total community structure; (2) the community structure at specific depths; and (3) the depth distribution of the vegetation. All data sets were first analysed by detrended correspondence analyses (DCA), as suggested by ter Braak and Šmilauer (1998) to explore the gradient length of the data set and to decide on approach for subsequent direct gradient analyses. Canonical correspondence analysis (CCA) was applied for gradient lengths >2 SD, and redundancy analysis (RDA) for gradient lengths <2 SD. Statistical significance of the generated ordination axes was tested for each analysis using Monte Carlo permutation tests. All species biomass data (dw m⁻²) was log-transformed prior to use.

In analysis 1 (total community structure), species biomass data was related to all environmental variables, including depth in order to assess its overall importance for community structure. Two separate analyses were performed, incorporating (a) original sample units (n = 200), and (b) samples units pooled within each site and depth (n = 40). Estimates of sedimentation for each sampling unit were also incorporated separately and pooled, respectively.

In analysis 2 (community structure at specific depths), species biomass data was related to the environmental variables separately at each sampled depth, or 4, 6, 8 and 10 m, using redundancy analysis (RDA). Original sample units where used, but due to its strong dominance, Fucus vesiculosus was not included in the analyses (n = 50 at each depth).

In analysis 3 (depth distribution of the vegetation), the distribution limits of individual species and algal belts were related to one environmental variable at the time using redundancy analysis. The analysis was performed separately for each environmental variable, and only environmental variables that generated a statistically significant output on the first ordination axis were considered. The statistical significance of the correlation between distribution limits and the environmental variable was determined from t-value biplots (ter Braak and Šmilauer, 1998). Sedimentation was included as the total sum of estimates in each transect.

3. Results

3.1. General pattern of the vegetation

At all sites a belt of annual, filamentous species, mainly Cladophora glomerata (L.) Kützing dominated the uppermost layer. A belt of permanently submerged Fucus vesiculosus began at 1.3–3.8 m depth, indicating the beginning of the true sublittoral zone. Below 4.6–6.8 m depth, semi-annual and perennial filamentous algae dominated, most typically with red algae (Polysiphonia fucoides (Hudson) Greville, Rhodomela confervoides (Hudson) P.C. Silva and Furcellaria lumbricalis (Hudson)) higher up and with the brown alga Sphacelaria spp. (mainly Sphacelaria arctica Harvey) from 7.1 to 12.3 m depth. Maximum depth distribution of the conspicuous vegetation was 11–20 m, coinciding with the lower distribution limit of belt-forming Sphacelaria spp. The deepest specimens of Sphacelaria spp. were not accurately detectable since they grew sparsely and were often covered by sediment. Likewise, the lower limits of P. fucoides and R. confervoides were indistinguishable in situ, as the two species were evenly mixed and morphologically very similar at their lower distribution. F. vesiculosus strongly dominated the biomass samples at 4, 6 and 8 m depth (>50% of total biomass), while F. lumbricalis dominated at 10 m depth. In total 19 macroalgal species were found.

3.2. Total community structure

Canonical correspondence analysis (CCA) explained a high degree of the variation in species biomass data among depths. Using each biomass sample as the lowest unit of replication total explained variance was 30.7%. This increased to 53.3% when using pooled biomass samples from each site and depth (Table 2). Accordingly, the fit of the included species also increased, especially for common ephemerals such as Cladophora glomerata, Ectocarpus siliculosus (Dillwyn) Lyngbye, Enteromorpha spp. and Pilayella littoralis (L.) Kjellman (Table 3). When pooled samples where used, 34.1% of the variance was attributed to axis 1, which was strongly correlated with depth (inter-set correlation coefficient, c₁ = 0.88). However, the correlation between axis 1 and estimated sedimentation was of the same level (c₁ = 0.81). The second axis was mainly correlated with effective fetch (c₂ = 0.64), and also with the clarity index (c₂ = 0.42), distinguishing predominantly ephemeral species at the point of the arrow and predominantly perennial species in the opposite direction (Fig. 2).

3.3. Community structure at specific depths

Redundancy analysis (RDA) performed separately for each depth explained 49.3% of species variance at 4 m depth, increasing to 60.9% at 10 m depth. At all depths, the two first ordination axes were most important, explaining 46.3–53.8% of total variation in species data (Table 4). At 4 m depth, axis 1 was mainly correlated with aspects of wave exposure (effective fetch and the clarity index) and axis 2 with slope of the transect. At 6 m depth, axis 1 was mainly correlated with sediment cover and axis 2 with the south-north component of direction. However, at 8 and 10 m depths there was no clear relationship between the axes and any single environmental variable (Table 5).
3.4. Depth distribution of the vegetation

The environmental variables effective fetch, sediment cover and clarity index contributed to statistically significant RDA models (Monte Carlo Permutation tests, \( p < 0.05 \)). Each of these variables contributed to explain some aspect of the vegetation’s depth.

Table 3

Life-history of the included species and variation in biomass explained (%) by canonical correspondence analysis of total community structure

<table>
<thead>
<tr>
<th>Species</th>
<th>Original</th>
<th>Pooled</th>
<th>Life-history</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aglaothamnion sp.</td>
<td>10.6</td>
<td>29.6</td>
<td>Ephemeral</td>
</tr>
<tr>
<td>Ceramium tenuicorne</td>
<td>24.9</td>
<td>37.5</td>
<td>Ambiguous</td>
</tr>
<tr>
<td>Cladophora glomerata</td>
<td>1.9</td>
<td>11.9</td>
<td>Ephemeral</td>
</tr>
<tr>
<td>Cladophora rupestris</td>
<td>21.7</td>
<td>41.1</td>
<td>Perennial</td>
</tr>
<tr>
<td>Chorda filum</td>
<td>1.3</td>
<td>16.1</td>
<td>Ephemeral</td>
</tr>
<tr>
<td>Coccotylus truncatus/</td>
<td>22.7</td>
<td>40.8</td>
<td>Perennial</td>
</tr>
<tr>
<td>Phyllophora pseudoceranoides</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Enteromorpha spp.</td>
<td>3.9</td>
<td>19.2</td>
<td>Ephemeral</td>
</tr>
<tr>
<td>Fucus vesiculosus</td>
<td>50.0</td>
<td>76.0</td>
<td>Perennial</td>
</tr>
<tr>
<td>Furcellaria lumbricalis</td>
<td>63.9</td>
<td>77.5</td>
<td>Perennial</td>
</tr>
<tr>
<td>Pilayella littoralis/</td>
<td>26.0</td>
<td>56.7</td>
<td>Ephemeral</td>
</tr>
<tr>
<td>Ectocarpus siliculosus</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polysiphonia fibrillosa</td>
<td>5.6</td>
<td>34.0</td>
<td>Ephemeral</td>
</tr>
<tr>
<td>Polysiphonia fucoides</td>
<td>50.1</td>
<td>76.4</td>
<td>Perennial</td>
</tr>
<tr>
<td>Rhodochorton purpureum</td>
<td>13.6</td>
<td>24.8</td>
<td>Ambiguous</td>
</tr>
<tr>
<td>Rhodomela confervoides</td>
<td>26.0</td>
<td>38.3</td>
<td>Perennial</td>
</tr>
<tr>
<td>Sphacelaria spp.</td>
<td>51.1</td>
<td>75.7</td>
<td>Perennial</td>
</tr>
<tr>
<td>Stictyosiphon tortillis</td>
<td>8.9</td>
<td>35.6</td>
<td>Ephemeral</td>
</tr>
</tbody>
</table>

Results for original sampling units of 0.04 m² (0.25 m² for F. vesiculosus at 4 m depth) and for five pooled sampling units within each depth.

Table 4

Ordination results obtained by redundancy analyses (RDA) of the community structure at separate depths (\( p < 0.001 \) for all analyses)

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Axis 1</th>
<th>2</th>
<th>3</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>Eigenvalue</td>
<td>0.39</td>
<td>0.07</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Species-environment correlation</td>
<td>0.79</td>
<td>0.58</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>Cumulative explained variance (%) in species data by the RDA axes</td>
<td>39.1</td>
<td>46.3</td>
<td>48.5</td>
</tr>
<tr>
<td>6</td>
<td>Eigenvalue</td>
<td>0.41</td>
<td>0.09</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Species-environment correlation</td>
<td>0.93</td>
<td>0.74</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>Cumulative explained variance (%) in species data by the RDA axes</td>
<td>41.1</td>
<td>50.6</td>
<td>54.0</td>
</tr>
<tr>
<td>8</td>
<td>Eigenvalue</td>
<td>0.41</td>
<td>0.11</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Species-environment correlation</td>
<td>0.85</td>
<td>0.73</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>Cumulative explained variance (%) in species data by the RDA axes</td>
<td>40.5</td>
<td>51.7</td>
<td>54.0</td>
</tr>
<tr>
<td>10</td>
<td>Eigenvalue</td>
<td>0.39</td>
<td>0.15</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Species-environment correlation</td>
<td>0.85</td>
<td>0.85</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td>Cumulative explained variance (%) in species data by the RDA axes</td>
<td>39.0</td>
<td>53.8</td>
<td>57.2</td>
</tr>
</tbody>
</table>

For explanations of terminology, see Table 2.
distribution. However, some distribution limits were significantly related to more than one variable (Table 6).

Generally, the upper limits of algal belts were most strongly correlated with effective fetch, and the lower limits of species with the clarity index. The lower limit of the red algal belt and the Sphacelaria belt were also most correlated with the clarity index, while the lower limit of the *Fucus vesiculosus* belt, as well as its depth of maximum coverage, was most strongly correlated with sediment cover.

### 4. Discussion

#### 4.1. Predictability of the system

The results from this study indicate a high level of predictability of macroalgal distribution patterns on a local scale in the sublittoral phytobenthos of the northern Baltic Proper. According to correlations produced by the applied multivariate models, environmental variables explained 30.7–53.3% of the observed vegetation structure when depth was included and 49.3–60.9% when vegetation structure was analysed within each depth. The results add to previous studies that show a strong correlation between environmental variables and large-scale variation in phytobenthic community composition in the Baltic Sea (Kautsky, 1993; Kautsky and van der Maarel, 1990; Middelboe et al., 1997).

Comparing with results from adjacent studies that included a similar set of environmental variables, a study of soft-bottom vegetation in a shallow bay archipelago system ca. 100 km south of the present study area (n = 44) (Eriksson et al., 2004) and a study of rocky-shore macroalgal vegetation in the Gullmar Fjord on the Swedish Atlantic coast (n = 68) (Eriksson et al., 2002; unpublished data) generated cumulative explained species variances of 28.4 and 28.9%, respectively, using CCA. The latter indicates that the strong correlation between environmental variables and vegetation structure may be related to low species richness. In a comparable study of a species rich macroalgal community at the western Basque coast (northern Spain), a CCA including the environmental variables pollution, wave exposure, sediment load, depth and slope explained 52% of vegetation structure along a 108 km coastline, with main part of the variation attributed to a pollution gradient (Diez et al., 2003).

#### 4.2. Scale dependent effects on biomass

After pooling samples within each depth and site in analysis 1, the cumulative explained variance increased from 30.7 to 53.3%. Pooling primarily improved the fit of ephemeral algae to the CCA model, while the fit of perennials was already generally high. Ephemeral algae are probably more stochastic in their occurrence than perennial algae (Kautsky, 1989; Kiirikki and Blomster, 1993; Kiirikki and Lehvo, 1997), but the results may also reflect possible physical interference from *Fucus vesiculosus* on its surrounding. Although *F. vesiculosus*
was sampled in larger sampling units, interaction effects were probably not adequately represented in the smaller sampling units used to sample the undergrowth. *F. vesiculosus* may control surrounding vegetation either directly through a whiplash effect (Kiirikki, 1996b) and shading, or indirectly through a higher presence of grazers in the *Fucus* zone (Svensson et al., 2004; Råberg, 2004; but see Merilaita and Jormalainen, 2000).

4.3. Environmental variables

The vegetation was clearly structured with depth. In the analysis of pooled data (analysis 1), 34.1% of the biomass variance was attributed to axis 1, which was strongly correlated with depth. As sediment cover increases with depth, the correlation between axis 1 and estimated sedimentation was also strong. However, all included environmental variables represent some aspect of depth regulation of the vegetation.

Effective fetch and curvature of the transects affect resuspension processes, and provide additional indirect estimates of sedimentation independent of sampling time. Light penetration was modelled by the clarity index, but since this is a derivate of effective fetch the two indices are correlated along some axes in ordination space. This is evident in the analysis of total community structure, where effective fetch and the clarity index correlate similarly with axis 2 (Fig. 2). The similar assignment of these two fetch indices is probably confounded by the fact that they do not have any resolution along the depth gradient in this analysis and the resolved variation is the shared variation that relate to differences between sites. However, effective fetch and the clarity index were not linearly correlated and should have separate and varied effects on the vegetation with depth.

Due to strong interrelationships between the included environmental variables, it is not possible to single out any variable most likely to determine overall biomass patterns. This may not even be desirable at the community level, since differential responses among species in relation to their physiological constraints may be expected.

4.4. Depth distributions

In the analysis of single species and algal belts depth limits (Analysis 3), effective fetch best described the upper limit of the *Fucus* belt and the red algal belt. Clarity index best described the lower limits of perennial species and of the red algal and *Sphaecelaria* belts. The strong correlation (75.5%) between the clarity index and the lower limit of *F. vesiculosus* agrees with observations in the Gulf of Finland that light availability at the depth limit of *Fucus* coincides with its photosynthetic compensation point (Bäck and Ruuskane, 2000). A correlation between upper distribution limits and effective fetch, and between deeper growing species and the clarity index was also observed by Kiirikki (1996a) in the Gulf of Finland. In the present study a negative relationship between sedimentation and the density of *Fucus* was also observed, as both the depth of maximum coverage and the lower belt limit of *Fucus vesiculosus* were significantly correlated with sediment cover. This observation is supported by a field experiment demonstrating a ca. 50% increase in the density of *Fucus* juveniles when loose-lying sediment was removed from the settling substrate during its time of reproduction (Eriksson and Johansson, 2003).

Since the 1940s, the lower distribution limit and average depth of *Fucus vesiculosus* have decreased in the study area (Kautsky et al., 1986; Eriksson et al., 1998). The results from the present study support previous suggestions that this decline is due to a documented decrease in the light penetration of the water and an increase in sedimentation during the past 60 years in the area (Sandén and Håkansson, 1996; Jonsson and Carman, 1994).

4.5. Possible effects of biotic factors

A large part of the observed variation in macroalgal biomass and depth distribution co-varied with the incorporated environmental variables, indicating that abiotic factors may have a strong influence on macro-algal assemblages in the study area. However, as mechanistic links were not studied, this does not rule out the possible role of biotic interactions in mediating these effects, or their possible influence on the part of variation not correlating with abiotic factors. Several studies have shown that grazing may have major effects on macroalgal abundance patterns in the Baltic Proper (Malm et al., 1999; Worm et al., 1999, 2001; Engqvist et al., 2000; Lotze et al., 2000, 2001), including areas with a salinity regime and species composition similar to those of the study area (Kangas et al., 1982; Hemmi and Jormalainen, 2002; Honkanen et al., 2002).

The main grazers in the northern Baltic Proper are small crustaceans and gastropods (cf. Kautsky, 1993; Hemmi and Jormalainen, 2002) that are often highly mobile and potentially found at all depths. However, the relative importance of environmental variables may be expected to increase with depth (cf. Wittman and Dayton, 2001). The probable main effect of grazers on vegetation structure in the Baltic Proper is by modifying the competitive outcome between species at their early life stages (Lotze et al., 2000, 2001; Worm et al., 2001). This effect is most prominent on shallow depths highly structured by disturbance from wave action, ice-scouring and changes in water level, where high reproductive efficiency is crucial for survival. The sublittoral zone is more stable in this respect, the
macroalgal community is dominated by perennial and semi-perennial algae, and the ability to cope with physiological constraints is probably more important than the ability to quickly utilise space. Also, specifically for the study area, many species with alternative life strategies shift to predominance of vegetative reproduction in low salinity, and stress-tolerant mechanisms of propagation such as reproduction by fragmentation are common in the sublittoral in the study area (Eriksson, 2002; Bergström et al., 2003). This should further decrease the significance of small reproductive stages for population maintenance.

Temporal disturbance may occur in the sublittoral zone as intensified grazing by the isopod *Idotea baltica*, which has probably caused a rapid reduction of *Fucus* populations on a local scale in the Baltic Proper (Kangas et al., 1982; Rönnberg et al., 1985; Engqvist et al., 2000; Hemmi and Jormalainen, 2002). *Idotea baltica* is found in the study area, but grazing damages on the *Fucus* were not readily observed in the present study.

4.6. Environmental monitoring

The study indicates a high suitability of the phyto-benthic zone for environmental monitoring, due to a strong association between macroalgal assemblages and ecologically relevant environmental factors even on a small scale. The level of predictability differed among species and sampling depths, suggesting that monitoring efforts should be directed towards perennial species with a sufficient depth distribution. In particular, *Furcellaria lumbricalis*, *Fucus vesiculosus*, *Polysiphonia fucoides*, *Rhodomela confervoides* and *Sphacelaria* spp. are suggested as suitable focal species in the study area and its ecological vicinity.

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