

# RESPONSE OF COASTAL MACROPHYTES TO PRESSURES

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# Response of coastal macrophytes to pressures

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WATERS is a five-year research programme that started in spring 2011. The programme's objective is to develop and improve the assessment criteria used to classify the status of Swedish coastal and inland waters in accordance with the EC Water Framework Directive (WFD). WATERS research focuses on the biological quality elements used in WFD water quality assessments: i.e. macrophytes, benthic invertebrates, phytoplankton and fish; in streams, benthic diatoms are also considered. The research programme will also refine the criteria used for integrated assessments of ecological water status.

This report is a deliverable of one of the scientific sub-projects of WATERS focusing on macrophytes in coastal waters. The report presents analyses of a large set of macrophyte data from the entire Swedish coastline, showing how a number of candidate macrophyte indicators respond to changes in pressures across spatial gradients or over time. The results will provide a basis for development of refined macrophyte indicators.

WATERS is funded by the Swedish Environmental Protection Agency and coordinated by the Swedish Institute for the Marine Environment. WATERS stands for 'Waterbody Assessment Tools for Ecological Reference Conditions and Status in Sweden'. Programme details can be found at: <http://www.waters.gu.se>



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## Summary

This study tested the range of candidate indicators, identified by Blomqvist et al. (2012; D1), for their responsiveness to eutrophication. Identification of such responses demands that as much as possible of the total variation associated with the indicators is accounted for. Therefore, our analyses tested the response of the candidate indicators to variation in eutrophication variables as well as to overlapping gradients in other environmental and also to some extent considered methodological variability. The analyses were based on the large monitoring data set on benthic vegetation collected along the extended Swedish coastline and compiled and quality assured as part of the WATERS project. We here summarize our main findings regarding each of the tested candidate indicators.

*Distributional indicators - Depth limits:* The current Swedish assessment method, MSMDI (see description in Blomqvist et al 2012) is an example of an indicator based on depth limits, relying on a scoring of depth limits of selected eutrophication-sensitive perennial species. We explored the statistical properties of the MSMDI index and how the index responds to a eutrophication gradient in order to evaluate its usefulness as indicator for ecological status. Despite the strong theoretical basis for vegetation depth limits as a good indicator of eutrophication we identify major problems with the current indicator MSMDI including weak relationships with eutrophication-related variables, statistical limitations in the definition of the index, high uncertainty associated with the identified depth limits and a large fraction of unsuitable monitoring transects. However, the large dataset offers additional possibilities for testing the response of the depth distribution of selected species to eutrophication. Monitoring data have been prepared for such additional analyses and will be merged with data from gradient studies conducted in the Waters project for further analysis in the next phase of WATERS.

*Abundance indicators – cover of hard and soft bottom vegetation:* Vegetation cover responded to gradients in eutrophication as expressed by nutrient concentrations, shading and/or chlorophyll levels when taking into account variation due to other variability components such as salinity. On this basis we formulated empirical models predicting changes in vegetation cover in response to changes in nutrient concentrations, water clarity and/or chlorophyll levels in different water body types. Macroalgal cover showed highly predictable responses to eutrophication-related variables and therefore seems a promising indicator of ecological quality. By contrast, predictions of the cover of soft-bottom macrophytes was associated with large uncertainty and resulting limited predictive power and on this basis the cover of vascular plants and charophytes does not seem to be a promising indicator of ecological quality.

*Diversity and composition indicators – functional composition of macroalgae:* The proportion of opportunistic algae relative to the total algal cover did not show any strong relationship to eutrophication, and the physico-chemical variables included in the analyses only explained a limited fraction of the total variability in this candidate indicator. This is most likely due to 1) the interacting gradients of physico-chemical conditions affecting species composition across the extended Swedish coastline, probably in combination with 2) our coarse definition of opportunistic species that may fail to properly distinguish the true opportunistic species in the Gulf of Bothnia. Before drawing final conclusions on the responsiveness of this indicator to eutrophication in the Baltic Sea these identified limitations needs to be addressed, for instance by conducting separate analyses for 1) the medium-high saline west- and south coast and 2) the low saline Baltic Proper and the Bothnian Sea, thereby reducing the interacting effects of eutrophication and salinity.

*Diversity and composition indicators – Traits analysis of soft bottom vegetation:* Our analyses identified that some traits and trait combinations are correlated with gradients in eutrophication along the Swedish coast, but the pattern is relatively weak and other environmental factors such as salinity, interact with eutrophication to shape the trait composition of soft bottom vegetation. More studies on the effect of natural gradients on trait composition are needed before we can conclude on the possibility to use trait composition as indicator of the ecological status of coastal ecosystems. For instance, repeating the analyses in narrower salinity range may help isolate the response of traits to eutrophication.

One clear conclusion is, however, that a trait-based indicator for soft bottom vegetation is solely relevant for areas with low salinity and wave exposure, where the species pool is large enough to include a range of attributes and trait combinations. In the open, high-salinity parts of the Baltic Sea proper, as well as on the Swedish west coast, a more promising approach is to look specifically at the distribution and abundance of *Zostera marina*, and possibly the relative abundance of this species compared to the abundance of opportunistic macroalgal species. Such seagrass indicators are already in use for the WFD in several European countries, including areas in the Baltic Sea (Marbà et al. 2013).

*Species richness of macroalgae:* Species richness of macroalgae responded to anthropogenic pressures when accounting for natural gradients in salinity and physical exposure and normalising for sampling effort (area surveyed). This implies that macroalgal richness could be used as indicator of ecological status, except in the Bothnian Bay with constantly very low richness, but this requires careful consideration of how to handle the strong effect of salinity on the indicator and the development of a suitable monitoring method.

*Overall:* The clearest response of vegetation indicators to eutrophication has so far been identified for the cover of macroalgae and the species richness of macroalgae when accounting for, in particular, the strong effect of salinity across the steep Baltic Sea salinity gradient. Several of the other candidate indicators are also strongly affected by the influence of the steep salinity gradient on species composition, which interacts with the potential response to eutrophication, thereby likely contributing to their relatively weak response to eutrophication variables.

## Svensk sammanfattning

Ett viktigt kriterium för en bra indikator är att den svarar tydligt på påverkan. Vi har därför undersökt hur ett antal möjliga indikatorer på ekologisk status för vegetation svarar dels på övergödningsrelaterade variabler (näring- och klorofyllhalter samt siktdjup) och dels på naturliga gradienter i salthalt, vågexponering och latitud. Analyserna baserar sig på data från en stor mängd dyktransekter från hela den svenska kusten, samt sammanställts och kvalitetskontrollerats som en del i Waters-projektet. Vi summerar här våra huvudresultat för var och en av de möjliga indikatorer vi arbetat med.

*Djuputbredning:* Den nuvarande svenska bedömningsgrunden, MSMDI, är baserad på djuputbredningen av ett antal utvalda arter som är känsliga för övergödning. För att utvärdera hur väl MSMDI fungerar som indikator för ekologisk status undersökte vi dess statistiska egenskaper och hur indexet svarar på en eutrofieringsgradient. Det finns ett starkt teoretiskt stöd för att djuputbredningen av vegetation är en bra indikator på övergödning, men vi identifierade flera problem med den nuvarande indikatorn. Sambandet var svagt mellan MSMDI och övergödningsrelaterade variabler och dessutom identifierades problem med indexets statistiska egenskaper, med osäkerhet i skattningen av djuputbredning och med att en stor del av transekterna i databasen inte gick att använda för att beräkna MSMDI.

*Täckningsgrad av vegetation på hård- och mjukbotten:* Den kumulativa täckningsgraden av vegetation på hårdbotten var tydligt kopplad till övergödningsrelaterade variabler, när vi tog hänsyn till variation kopplad till naturliga gradienter i salthalt och vågexponering. En stor del av skillnaden i täckningsgrad mellan dyktransekter kunde förklaras av övergödning tillsammans med de naturliga gradienterna, vilket betyder att kumulativ täckningsgrad på hårdbotten är en lovande indikator på ekologisk status. För täckningsgraden av vegetation på mjukbotten var sambanden däremot svagare och förknippade med stor variation, vilket betyder att täckningsgraden av kärlväxter och kransalger på mjukbotten är en mindre lovande indikator.

*Funktionell sammansättning av makroalgssambällen:* Många studier har visat att opportunistiska arter gynnas av övergödning och andelen opportunistiska arter används i flera områden som indikator på ekologisk status. I vår studie uppvisade dock andelen opportunistiska arter inget starkt samband med övergödning och mycket av variationen i denna potentiella indikator kunde inte heller förklaras av de naturliga gradienterna i salthalt och vågexponering. Vår tolkning är att andelen opportunistiska arter styrs av en komplicerad kombination av salthalt, näringstillgång och fysisk störning, vilket gör det svårt att hitta tydliga samband. Det är också möjligt att vi använt en alltför grov definition av opportunistiska arter som inte är anpassad till de speciella förhållandena i Östersjön.

*Analys av funktionella egenskaper hos mjukbottenvegetation:* Vi identifierade ett antal egenskaper hos kärlväxter och kransalger som var mer eller mindre vanliga i eutrofierade områden längs Östersjöskusten. De samband vi hittade var dock relativt svaga och naturliga gradienter, exempelvis salthalt, var också viktiga för att förklara sammansättningen av egenskaper i vegetationen. Det behövs flera studier av hur naturliga gradienter påverkar sammansättningen av egenskaper innan det är möjligt att utvärdera potentialen för funktionella egenskaper som indikator på ekologisk kvalitet för kustvegetation. En tydlig slutsats är i alla fall att det bara är relevant att använda funktionella egenskaper som indikator i skyddade områden med låg salthalt där artrikedomen av kärlväxter och kransalger är hög. På västkusten och i öppna områden i egent-

liga Östersjön är det mer lovande att använda utbredning och abundans av den dominerande arten ålgräs (*Zostera marina*).

*Artantal av makroalger:* Artantalet av makroalger uppvisade som väntat framförallt ett starkt samband med salthalt, men när vi tog hänsyn till de naturliga gradienterna i salthalt och exponering samt normaliserade artantalet efter hur stor yta som undersökts i transekterna bidrog även övergödningsrelaterade variabler till att förklara en betydande del av variationen. Det betyder att artantalet av makroalger är en möjlig indikator på ekologisk status, men det kräver ett bra sätt att hantera den starka kopplingen mellan salthalt och artantal och utveckling av en lämplig övervakningsmetod som lämpar sig för att mäta artantal.

Sammanfattningsvis var det täckningsgrad och artantal av makroalger som uppvisade tydligast samband med övergödning. I båda fallen blev detta samband synligt när vi tog hänsyn till de starka naturliga gradienterna, speciellt salthaltsgradienten.

## 1. Introduction

This report follows up on the report ‘Potential Eutrophication Indicators Based on Swedish Coastal Macrophytes’ by Blomqvist et al. (2012), which suggested a set of candidate vegetation indicators for assessing the ecological status of Swedish coastal waters. The indicators represent the distribution, abundance, diversity and composition of macroalgal communities on rocky shores as well as of soft-bottom communities of vascular plants and charophytes along the extended Swedish coastline.

The candidate indicators fulfill fundamental criteria for good indicators, i.e. they 1) have a sound **scientific basis** with a conceptual understanding of their response to pressures, 2) have **ecosystem relevance**, i.e. are indicative of changes that reflect the status of the ecosystem in terms of structure and function, 3) are **supported by existing/ongoing monitoring data**, which 4) add to making them **cost-efficient** by profiting from the value of existing baseline data and ongoing monitoring, and 5) they are **concrete and measurable**.

In the present study we test the indicators against additional central quality criteria, namely **responsiveness to pressures** which is also affected by the **variability** associated with the indicators in terms of methodological variability/accuracy and the extent of random variation (noise) associated with the indicator. In order to be responsive to pressures an indicator must exhibit a high signal to noise ratio.

The criteria listed above, together with the **possibility to set targets** that will be addressed for the Swedish indicators in a future study, have been identified as some of the central criteria for selection of indicators in a number of studies (e.g. Mee et al. 2008, Elliott 2011, Ferreira et al. 2011, Rice et al. 2012), and are also represented in the latest recommendation of ICES on indicator criteria (ICES 2013). In order to test the responsiveness of indicators to pressures it is necessary to understand to the largest extent possible which factors contribute to the variability of the indicator across spatial and temporal scales, related to the methodology and to natural environmental gradients. The more of the variability associated with an indicator that is possible to explain and take into account, the better the chance of being able to identify responses of the indicator to changes in pressures.

## 2. Objective

The aim of the report is to explore to what extent the candidate indicators are able to reflect changes in pressures across spatial gradients or over time. This is done using large data sets that cover wide gradients in environmental variables including anthropogenic pressures. The report is initiated with an overview and description of the available data sets followed by chapters on analyses of different indicators. We tested both ‘distribution indicators’ (depth limit of selected macroalgae and soft-bottom macrophytes), ‘abundance indicators’ (cover of hard and soft bottom vegetation) and ‘diversity and composition indicators’ (functional composition of macroalgae, traits analysis of soft bottom vegetation and species richness of macroalgae). Throughout the report separate analyses are being conducted for ‘macroalgae on hard substratum’ and ‘soft-bottom vegetation’ as hard and soft substrates support fundamentally different plant communities.

## 3. Data

### 3.1. Vegetation data and study areas

Waters has made a major effort to compile and quality assure Swedish coastal vegetation data, and also to identify and link the vegetation data to environmental data. Quality assurance has been time consuming since our work, in many instances, represents the first thorough analyses based on these data. Many data providers have contributed with considerable amounts of work in this process. All together more than 6 man-months have been spent on quality assurance by Waters and the data providers during the project time. All corrections of data have been made in the original datasets and communicated to the data owners making it possible for the data owners to update the database at the national data host with the corrected data. In this way our work has resulted in a significant improvement of publicly available Swedish coastal vegetation data. Our dataset compiled from all these datasets is the most complete national dataset for Swedish vegetation data ever and forms the basis for the analyses presented in this report.

A number of methods have been used to collect vegetation data in Swedish coastal areas (see Blomqvist et al. 2012). In this study, we have chosen to include only data from diving transects and only from transects where both cover of vegetation and of substrate have been recorded (data type A, C and D in Blomqvist et al. 2012). Diving transects is the most common investigation method in the database, so this choice allowed us to derive a homogenous dataset that was still as large as possible. The vast majority of data follow the national standard method for the east coast (Kautsky 1992 and [www.havochvatten.se/hav/vagledning--lagar/vagledningar/miljoovervakningens-metoder-och-undersokningstyper-inom-programomrade-kust-och-hav.html](http://www.havochvatten.se/hav/vagledning--lagar/vagledningar/miljoovervakningens-metoder-och-undersokningstyper-inom-programomrade-kust-och-hav.html)), described below. Some (only few) transects were sampled using a 4 point scale instead of the 7 point scale prescribed by the standard method (data type D in Blomqvist et al. 2012). These were included in the dataset in order to get a larger dataset with better geographic coverage.

The diving transects were in most cases perpendicular to the shoreline and often reaching down to the deepest occurrence of vegetation. The cover of all macroscopic taxa and substrate was recorded in segments, more or less homogenous with respect to vegetation, substrate and slope, along the transects. In the vegetation surveys a diver swims from deeper to shallower depths and starts a new segment if a new species appears or if the composition of species or substrate changes. Segments thus have different lengths and span different depth intervals. In this way, the deepest depth of the deepest segment with a species represents the maximum depth of this species within a transect. In some few cases transects were divided into segments based on fixed lengths or fixed depth intervals (data type C in Blomqvist et al. 2012). In these cases notes of the deepest specimens are taken separately.

Cover estimates are made relative to the segment area regardless of substrate, i.e. they are not substrate specific. Since the substrate is an important determinant of vegetation composition, variations in substrate can be expected to introduce considerable variation in the vegetation data that decrease the chance to identify effects of other environmental variables. In order to reduce the effect of substrate we, therefore, only included transect segments with either homogenous hard or soft substrates in the analyses. We compiled one data set including segments dominated by hard substrate (at least 75 % solid rock, boulders or

non-mobile stones) and one data set including segments dominated by soft substrate (at least 75 % cover of sand or smaller fractions). Gravel was regarded as a mobile substrate and segments dominated by this substrate were not included in the analyses. Since substrate often was only recorded as presence/absence (0/1) before the year 2000 we have excluded data before this year from the analyses. Despite the large quality assurance effort there are still some inconsistencies within some datasets. To further reduce inconsistencies we excluded all segments where depth or length was missing and we also excluded segments where the sum of cover of the different substrate classes was less than 60 % since these were regarded as incomplete.

The resulting vegetation dataset includes a total of 3 433 diving transects with segments dominated by hard substrate, soft substrate or both from 1 788 sites ranging from Idefjorden on the northwest coast of Sweden southwards to Stavsten on the south coast and up along the east coast to Sävvisklubbarna on the north-east coast (Figure 1). The data thus covers the whole Swedish coast representing an 11 500 km long mainland coastline (the coastline including islands > 25 m<sup>2</sup> is 43 400 km which is longer than the circumference of the Earth) and spans a wide spatial gradient in salinity, exposure and eutrophication effects (see Table 3). The observations cover the time span from 2000 until today with the amount of data varying from 64 sites visited in 2000 to 641 sites in 2008 (Figure 2).

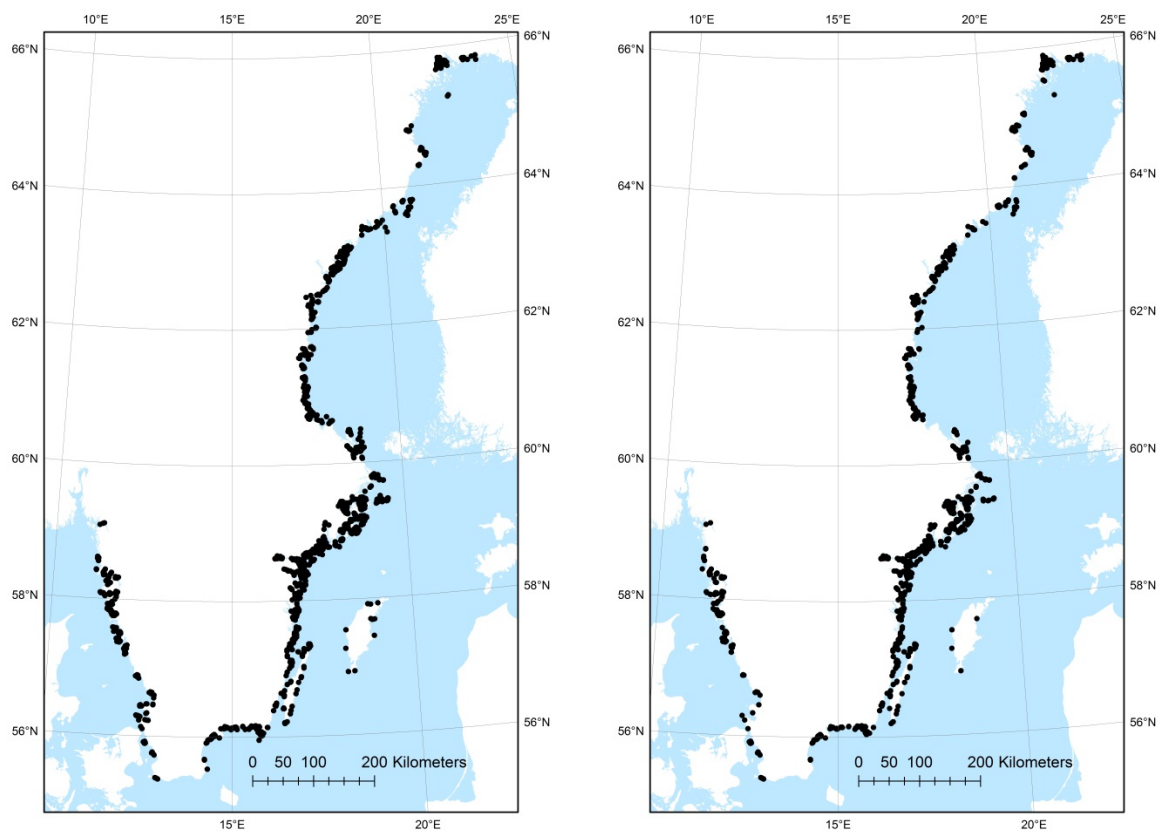


Figure 1. Sites with at least one transect segment with at least 75% cover of hard substrates (left) and soft substrates (right).



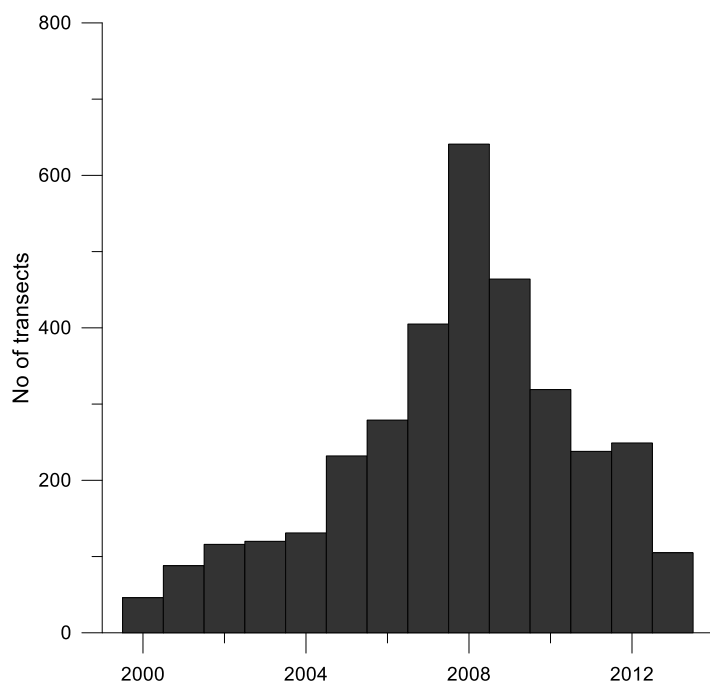


Figure 2. Number of diving transects per year used in this study.

There are a total of 664 coastal water bodies in Sweden according to SVAR 2012:2 (Swedish water archive, a geodatabase at Swedish Meteorological and Hydrological Institute, SMHI). These water bodies are the assessment units in the Swedish implementation of the Water Framework Directive (WFD) (2000/60/EC). Each vegetation site was assigned a water body ID based on its coordinate by use of a GIS point in polygon join. A total of 300 water bodies have been investigated with at least one diving transect. The survey intensity, of both vegetation and environmental surveys, differs strongly between water bodies, both in terms of the number of study sites and the number of years that have been investigated.

Each coastal water body is assigned to a national water body type representing similar conditions in salinity, wave exposure, depth, stratification, water exchange and winter ice-cover. Swedish national regulation NFS 2006:1 (Naturvårdsverket 2006) defines 23 coastal and two transitional types. In most of the analyses, we have grouped the national water body types into regions according to large sea basins and inner and outer coastal waters (Figure 3, Table 1). The resulting nine regions represent the three basins of the Baltic Sea east of Sweden (the Baltic Proper, Bothnian Sea and Bothnian Bay) and the Swedish West coast (Kattegat + Skagerrak). The Öresund, south and east coast of Skåne was treated as a separate region (“Southern coast”) due to its special geology and coastal morphology. The monitoring effort in the different regions is shown in Table 1.

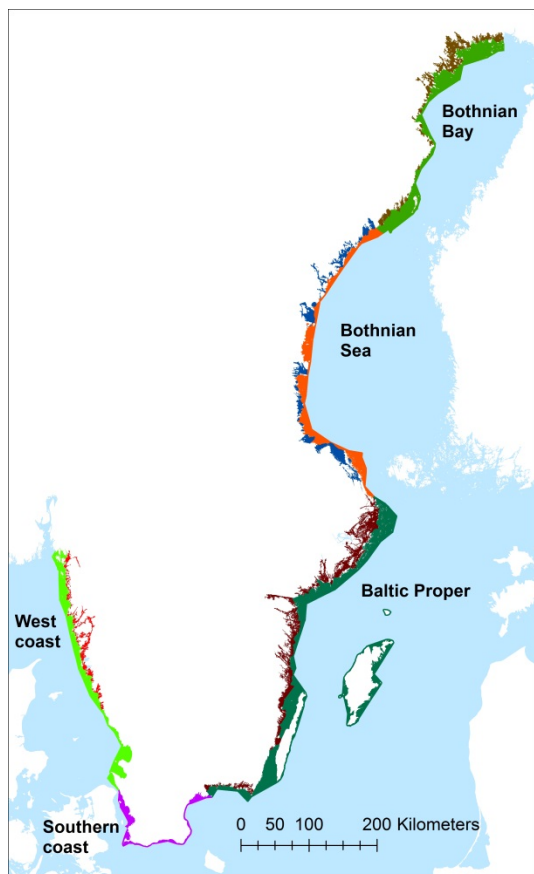


Figure 3. Grouping of national water body types into regions. Each large sea basin is divided into inner and outer coastal waters (not Southern coast). Colors represent the different regions listed in Table 1.

TABLE 1

The number of transects and number of segments dominated by hard and soft substrate in the different regions used in this study. See Figure 3 for geographic distribution of each region. Numbers represent data after filtering out incomplete substrate, length or depth information. National types according to the Swedish WFD typology are indicated by numbers (1-23).

Region	National types	Sites	Transects	Hard segments	Soft segments
Bothnian Bay inner	20, 22	107	165	347	1362
Bothnian Bay outer	21, 23	57	109	837	412
Bothnian Sea inner	16, 18, 20	275	405	2377	1137
Bothnian Sea outer	17, 19, 21	151	212	2155	260
Baltic Proper inner	8, 12, 13	542	1169	8576	3871
Baltic Proper outer	9, 10, 11, 14, 15	416	944	10013	1183
Southern coast	6, 7	63	119	969	268
West coast inner	1, 2	101	134	1269	326
West coast outer	3, 4, 5	76	176	2176	107
<b>Total</b>		<b>1788</b>	<b>3433</b>	<b>28719</b>	<b>8926</b>

The regions differ strongly in species composition, mainly due to the large span in salinity (Figure 4). The diversity of macroalgae (Chlorophyta, Phaeophyceae and Rhodophyta) is highest at the West coast and declines towards the Gulf of Bothnia. On the other hand, the Gulf of Bothnia has a high diversity of vascular plants (Magnoliophyta, Lycopodiophyta and Equisetophyta), stoneworts (Charophyceae) and freshwater mosses (Bryophyta) while these groups are represented by very few taxa on the West coast. Both vascular plants and stoneworts grow on soft bottoms and the highest number of taxa is found in the inner coastal regions that have a larger occurrence of shallow, sheltered areas with rich vegetation.

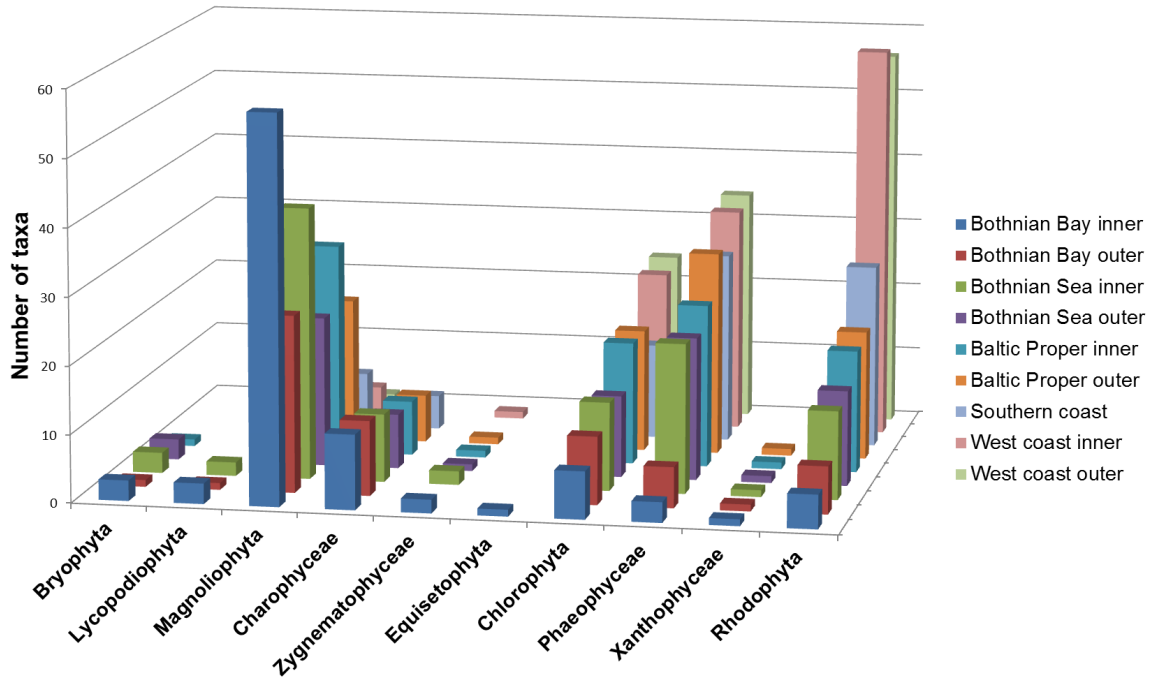


Figure 4. Number of taxa from different taxonomic groups in the regions used. The number of taxa is based on the dataset used in the analyses and does not reflect the total number of taxa possible to find in each region since the number of investigated sites differ between regions.

In order to reduce the effect of different taxonomic resolution and differences between divers taxonomical skills some taxa were grouped before calculations (Table 2).

TABLE 2

Taxa were grouped before calculations in order to reduce the effect of different taxonomic resolution and differences between divers.

Taxon	Grouped as
Bonnemaisonia hamifera	Bonnemaisonia hamifera/Spermothamnion repens
Spermothamnion repens	Bonnemaisonia hamifera/Spermothamnion repens
Chara globularis	Chara globularis/virgata
Chara virgata	Chara globularis/virgata
Chorda	Chorda filum
Coccotylus	Coccotylus/Phyllophora
Coccotylus truncatus	Coccotylus/Phyllophora
Phyllophora	Coccotylus/Phyllophora

TABLE 2 continued

<b>Taxon</b>	<b>Grouped as</b>
<i>Phyllophora pseudoceranoïdes</i>	Coccotylus/Phyllophora
<i>Cruoria</i>	<i>Cruoria pellita</i>
<i>Dictyosiphon</i>	Dictyosiphon/Stictyosiphon
<i>Dictyosiphon chordaria</i>	Dictyosiphon/Stictyosiphon
<i>Dictyosiphon ekmanii</i>	Dictyosiphon/Stictyosiphon
<i>Dictyosiphon foeniculaceus</i>	Dictyosiphon/Stictyosiphon
<i>Stictyosiphon</i>	Dictyosiphon/Stictyosiphon
<i>Stictyosiphon soriferus</i>	Dictyosiphon/Stictyosiphon
<i>Stictyosiphon tortilis</i>	Dictyosiphon/Stictyosiphon
<i>Ectocarpus</i>	Ectocarpus/Pylaiella
<i>Ectocarpus fasciculatus</i>	Ectocarpus/Pylaiella
<i>Ectocarpus siliculosus</i>	Ectocarpus/Pylaiella
<i>Pylaiella</i>	Ectocarpus/Pylaiella
<i>Pylaiella littoralis</i>	Ectocarpus/Pylaiella
<i>Furcellaria</i>	<i>Furcellaria lumbricalis</i>
<i>Halosiphon</i>	<i>Halosiphon tomentosus</i>
<i>Lithothamnion</i>	Lithothamnion/Phymatolithon
<i>Lithothamnion glaciale</i>	Lithothamnion/Phymatolithon
<i>Lithothamnion sonderi</i>	Lithothamnion/Phymatolithon
<i>Phymatolithon</i>	Lithothamnion/Phymatolithon
<i>Phymatolithon calcareum</i>	Lithothamnion/Phymatolithon
<i>Phymatolithon laevigatum</i>	Lithothamnion/Phymatolithon
<i>Phymatolithon lenormandii</i>	Lithothamnion/Phymatolithon
<i>Phymatolithon purpureum</i>	Lithothamnion/Phymatolithon
<i>Myriophyllum sibiricum</i>	<i>Myriophyllum spicatum</i>
<i>Nemalion</i>	<i>Nemalion helminthoides</i>
<i>Nitella flexilis</i>	<i>Nitella flexilis/opaca</i>
<i>Rhodochorton</i>	<i>Rhodochorton purpureum</i>
<i>Rhodomela</i>	<i>Rhodomela confervoides</i>
<i>Ruppia cirrhosa</i>	<i>Ruppia</i>
<i>Ruppia maritima</i>	<i>Ruppia</i>
<i>Scytosiphon</i>	<i>Scytosiphon lomentaria</i>
<i>Spongomorpha</i>	<i>Spongomorpha aeruginosa</i>
<i>Ulva clathrata</i>	<i>Ulva</i>
<i>Ulva compressa</i>	<i>Ulva</i>
<i>Ulva compressa/intestinalis</i>	<i>Ulva</i>
<i>Ulva flexuosa</i>	<i>Ulva</i>
<i>Ulva intestinalis</i>	<i>Ulva</i>
<i>Ulva linza</i>	<i>Ulva</i>
<i>Ulva procera/prolifera</i>	<i>Ulva</i>
<i>Ulva prolifera</i>	<i>Ulva</i>
<i>Vaucheria dichotoma</i>	<i>Vaucheria</i>
<i>Zannichellia</i>	<i>Zannichellia palustris</i>
<i>Zannichellia palustris</i> var. <i>major</i>	<i>Zannichellia palustris</i>
<i>Zannichellia palustris</i> var. <i>repens</i>	<i>Zannichellia palustris</i>

### 3.2 Environmental data

Physico-chemical data from field measurements of salinity, temperature, Secchi depths, chlorophyll a and nutrients (total nitrogen and total phosphorus) were achieved from the national data host SMHI. Data originates from Swedish national and regional monitoring. We have used data extracted by SMHI from the database Shark (Svenskt HavsARKiv) 2013-12-15. Similar data were also achieved from Svealands Kustvattenvårdsförbund ([www.skvvf.se](http://www.skvvf.se)) 2013-11-22 covering coastal regions of northern Baltic Proper. We have used data from surface waters (average of measurements 0-10 m depth) during the growth season (May – September) the same year as vegetation was sampled.

Environmental data was linked to each visit at a vegetation site by an iterative routine that selects all physico-chemical measurements from the same year within increasing distances from the vegetation site coordinate. For inner coastal waters the routine searched 1, 2 or 5 km away, primarily within the current water body and secondly within the current national type but still within the same distance from the vegetation site. For outer coastal waters the routine searched 1, 5, 20 or 55 km away, primarily within the current water body and secondly within any outer coastal water national types or open sea but still within the same distance from the vegetation site. After at least two physico-chemical sites were found the routine stopped and the vegetation site visit was associated with the median of the physico-chemical values found. The routine was run separately for all variables and all vegetation site visits. The distances used by the routine were selected visually by analysing maps of vegetation and physico-chemical sites. The logic of using physico-chemical data not only from the current water body but secondly also from adjacent waters is supported by the fact that vegetation sites on islands can be situated on the border between two water bodies. For a considerable part of the vegetation data it was not possible to link the site visit to a sufficient number of physico-chemical measurements, these data points had to be excluded from the analyses. This means that the actual number of observations that could be used for the analyses was lower than reported in Table 1 (the number is given for each analyses in the forthcoming chapters).

Modelled salinity, chl a and nutrient concentrations were also achieved from SMHI. Values are based on the coastal zone model (Sahlberg, 2009). The coastal zone model is divided into water bodies that are assumed to be horizontally homogeneous with high vertical resolution. Along the coast of Sweden, the model is applied to all marine water bodies according to SVAR version 2012:2. We have used modelled daily values from the model run 2013-04-09. We have used data from surface waters (average of measurements 0-10 m depth) during summer (June – August) for nutrients and chl a the same year as vegetation was sampled. For salinity the median of surface (0-10 m depth) values from one year (Oct-Sept) was used. Each visit at a vegetation site was associated with the modelled values of its water body the year of sampling. The modelled salinity, chl a and nutrient data were used instead of measured physico-chemical data in a separate set of analyses. This allowed inclusion of all vegetation data (also transects sections from sites lacking physico-chemical measurement stations in the vicinity) and thus complemented the analyses based on measured physico-chemical data.

Wave exposure was calculated in 25\*25 m resolution by a simplified wave model (SWM) (Isæus 2004). The model integrates the fetch in angular sectors around focal points by grid-based searches for nearby land, and local, mean wind speed from 16 directions. The mean wind speed was calculated for a 10 year period (1990 – 2000), using data from 13 wind stations along the coast. All vegetation sites were assigned the SWM value from the grid cell closest to the site coordinate (starting point for transects). We acknowledge that this value does not represent the correct value for the whole transect but believe that the relative differences between sites will be accounted for by this approach.

In Table 3 the range for each physical-chemical variable is shown together with latitude and wave exposure.

TABLE 3

Range of physical-chemical values used for analyses in this report. Values represent growing season (May – September) surface (0 – 10 m depth) values for all variables except latitude and exposure. Exposure is calculated according to a Simplified Wave Model SWM by Isæus 2004.

<b>Variable</b>	<b>Range</b>	<b>Unit</b>
Latitude	55.4 - 65.8	Degrees north
Secchi depth	1 - 12	Meter
Salinity	0.9 - 31	(PSU)
Total nitrogen (TN)	9.5 - 76	µmol/l
Total phosphorus (TP)	0.1 - 2.4	µmol/l
Chlorophyll a	0.5 - 41	µg/l
Exposure	1 - 1 333 000	

## 4. Depth limit of selected macroalgae and soft-bottom macrophytes

### 4.1 Introduction

Depth distributions of selected species were listed as potential distribution indicators for use in ecological status assessment by Blomqvist et al. (2012). In Appendix A we show a graphical representation of depth limits of 44 selected species in relation to national typology, natural gradients such as latitude, salinity and exposure and anthropogenic pressures illustrated by Secchi depth, chlorophyll a and nutrients. Further analyses of these data, together with data from Waters' gradient studies, will be performed at a later stage.

The current Swedish assessment method, MSMDI (see description in Blomqvist et al 2012) is an example of an indicator based on depth limits, relying on a scoring of depth limits of selected eutrophication sensitive perennial species. We here explore the statistical properties of the MSMDI index and how the index responds to a pressure gradient, in order to evaluate its usefulness as indicator for ecological status.

### 4.2 Methods

Geographic scope and general information on both vegetation and environmental data and method for extraction of depth limits from transect data used in this study is given in Ch. 3.

MSMDI is based on a scoring of maximum depth limits for single specimens of selected taxa. In this study we have made a slight deviation from the official calculation rules of MSMDI in order to increase the amount of data for analysis. This deviating calculation method is often used even in official WFD work and has been approved by the authorities (pers comm to M. Blomqvist). According to the official rules all transects that are not as deep as the deepest scoring boundary for all selected species within a national type are to be excluded from assessment. Another rule is that only transects with at least three scores are given a MSMDI-value. We used the modified depth rule that if the transect is sufficiently deep to include the deepest scoring boundary of at least three of the selected species, then the transect is included. An example, a transect in national type 1 has to be 18 meter deep according to the assessment method. However the highest scoring boundary for six of the selected species in this type is 12 meter or less making it possible to calculate a MSMDI value according to the modified rules if at least three out of these six species get a score even if the transect is between 12 and 18 meter deep.

Before calculation of MSMDI depth limits that were truncated (no observations below the depth limit) or substrate limited (the depth limit coincided with a shift to unsuitable seabed substrate) were excluded. We also excluded transects that lacked substrate information.

### 4.3 Results

MSMDI is the average score for the species depth limits that can be assessed in one transect. In the different national types there are different numbers (3 to 9) of species selected for assessment. At least three species have to get a score in order to calculate a MSMDI value for a transect. This means, for example,

TABLE 4

Number of theoretically possible values MSMDI can take based on the number of species used for assessment.

No of species in a type used for assessment	Possible number of scores used to calculate MSMDI	Theoretical number of possible MSMDI values
3	3	16
4	3-4	24
5	3-5	41
6	3-6	48
7	3-7	73
8	3-8	89
9	3-9	114

when five species are selected for assessment in a national type, MSMDI can be the average of 3, 4 or 5 score values depending on the number of species that are present in a certain transect. The score a species can get is 0.2, 0.4, 0.6, 0.8 or 1. In reality 0.2 never comes into play since this score is only given if a species have disappeared from an area due to anthropogenic factors and this is something we have no recording of in the database today. Scores can thus only be 0.4, 0.6, 0.8 or 1.

In order to examine the statistical properties of MSMDI, we ran simulations to study a theoretical distribution of MSMDI values. We ran simulations with different numbers of species selected for assessment, from 3 to 9 selected species, to show the effect of including a larger number of species in the assessment. For instance, for a case with 9 species selected for the assessment, 3 – 9 score values were randomly drawn with replacement from the possible scores (0.4, 0.6, 0.8 or 1). This represents fictive transects with 3 – 9 species. The drawn score values were averaged to calculate a MSMDI value for each fictive transect. The process was repeated 5 000 000 times, after which the number of unique MSMDI values was counted. This represents the theoretical number of MSMDI values that can occur in a water type with 9 species selected for assessment.

The resulting numbers of possible MSMDI values are shown in Table 4. The more species that are selected for the assessment, the more MSMDI values can occur, i.e. the higher is the resolution of MSMDI. In national types where only 3 species are selected for the assessment, there are only 16 values that MSMDI can take, while the index can take 114 values in national types with 9 species selected for the assessment.

The distribution of the simulated MSMDI values for the case with 9 species (and thus 114 theoretical MSMDI values) is shown in Figure 5. It is obvious that 0.6 and 0.8 are overrepresented. This is noteworthy since 0.6 and 0.8 represents the boundaries between good and moderate status and high and good status, respectively, in the current Swedish assessment method.



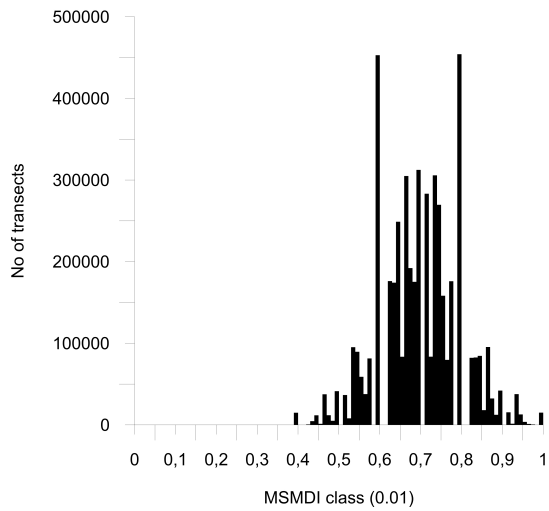


Figure 5. Distribution of 5 000 000 simulated MSMDI values.

The distribution of actual MSMDI-values calculated from monitoring data is shown in Figure 6. This distribution differs greatly from the simulated distribution with no overrepresentation of neither the score 0.6 nor 0.8 and is skewed with a high proportion of MSMDI value 1. The overrepresentation of 0.6 and 0.8 in Figure 5 and the high proportion of value 1 in Figure 6 make transformation to normality difficult and analysis of relationships with pressure data has not been done. As an overview of the relationships simple scatterplots of MSMDI against selected environmental factors along the entire Swedish coast and the east and west coasts separately are shown in Figure 7. Since selection of species and their scoring boundaries differ between national types MSMDI is in a way adjusted for the difference in salinity, exposure and latitude between national types and hence it is not possible to look at relationships between MSMDI and these factors on a larger scale than national type.

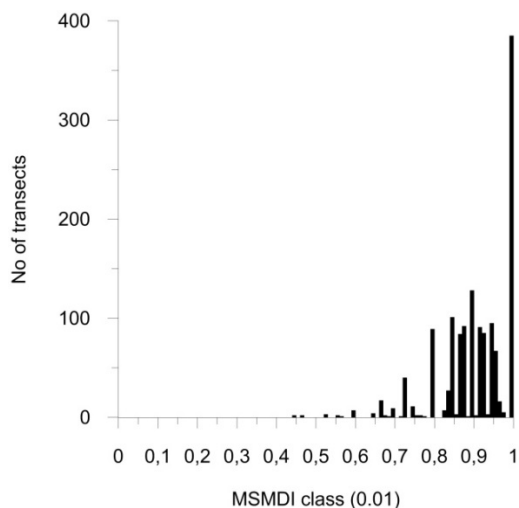


Figure 6. Distribution of 1 398 MSMDI values calculated from Swedish monitoring data from the Swedish coast.

RESPONSE OF COASTAL MACROPHYTES TO PRESSURES

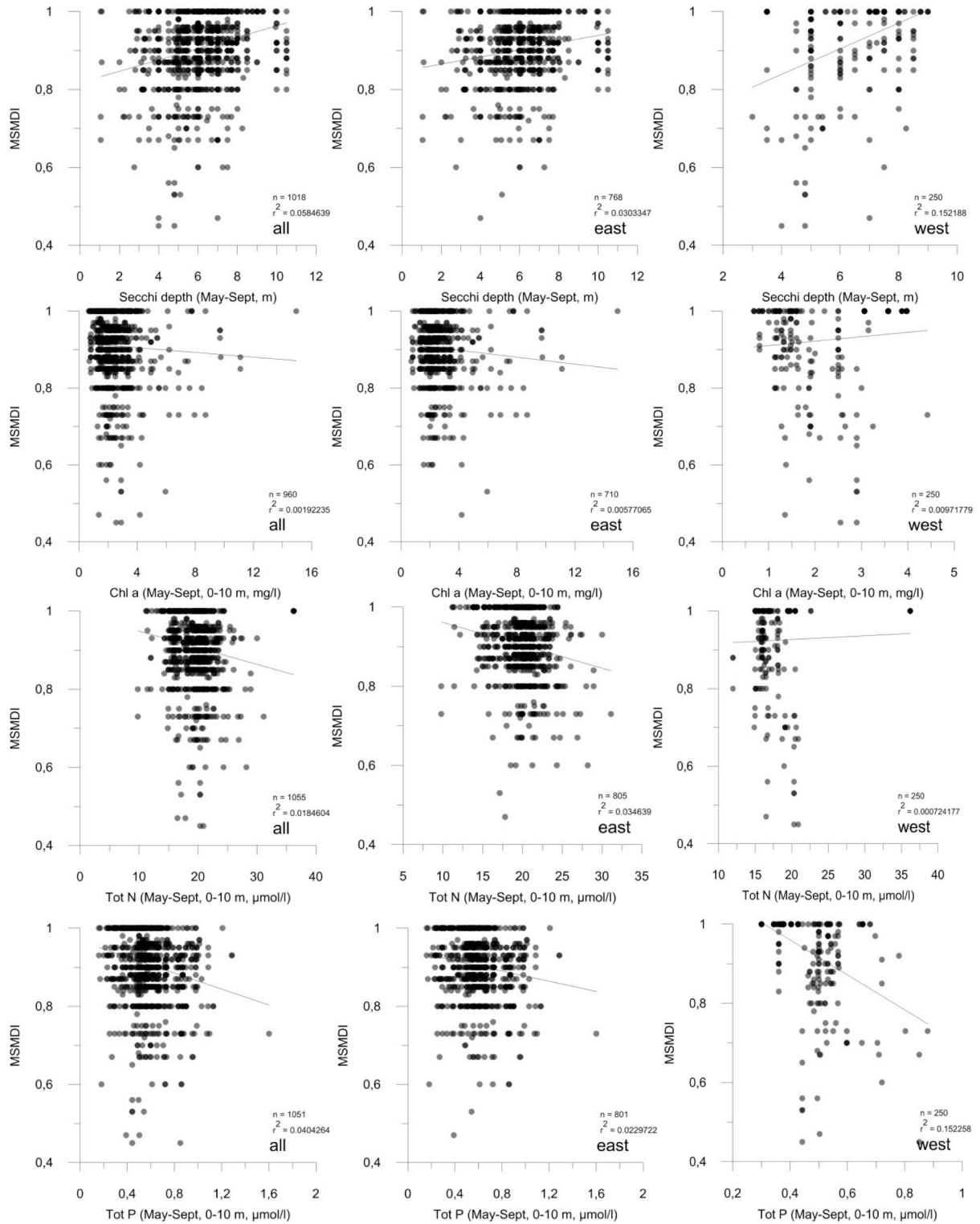


Figure 7. MSMDI values based on monitoring data from the entire Swedish coast, the east coast (type 7 – 24) and the west coast (type 1 – 6 and 25). A regression line is shown in each graph to illustrate the tendency in the relationship.

## 4.4 Discussion

Theoretical overrepresentation of some values in an indicator is problematic and even more problematic is the correspondence of these overrepresented values with ecological status class boundaries. This is a fact for MSMDI which together with low correlation with pressures, large scatter in pressure responses and high numbers of maximum values even at quite high pressure values makes the usability of MSMDI questionable. In the WFD intercalibration exercise a better correlation was found between MSMDI and pressures using only hard bottom data from Norwegian and Swedish parts of Skagerrak (MSMDI – total nitrogen  $r^2=0.43$ , Intercalibration technical report, in prep). This area is characterized by steeper fjords suggesting that this indicator might correlate better with pressures in certain habitats.

The purpose behind most of the surveys used in this study was not to measure depth limits per se but rather to give a general description of the vegetation along transects i.e. to monitor trends in a general way or make a one-time inventory of the vegetation in an area. Most transects are randomly positioned within the survey area which often gives high numbers of transects unsuitable for depth limit studies, e.g. too shallow, substrate limited, too steep or with scattered vegetation. Selection of transects suitable for depth limit studies, as well as selection of lowest depths of selected species, is difficult to do from data and should preferably be done in the field. To look for a light-limited lowest depth of a single specimen of a selected species in the field can result in other values than the extraction of data from a transect where these values have not been explicitly looked for in the field. This can be illustrated by the observation that depth distribution of the species included in current assessment system seemed to increase after publication of the system (Blomqvist et al. 2012). Thus the data we have based our study on is not ideal for the purpose or for assessment according to the present assessment method.

In the present Swedish assessment method the scoring boundaries for each selected species within each national type are based on an expert judgment deviation from the maximum observed depth limit value of each selected species within each national type. All transects that are not as deep as the deepest scoring boundary for all selected species within a national type are to be excluded from assessment. The effect of these cut-off values when used in calculation of MSMDI is a reduction of available transects by more than 50 % indicating that a large amount of the Swedish transect data is unsuitable for depth limit studies according to the principles of MSMDI.

Each MSMDI value is based on an average scoring of depth limits of at least three different species. Within a water body, depth limits for different species can be used to calculate MSMDI in different transects. This makes it hard to evaluate changes in MSMDI since different species can react differently to different factors. As an example there are both macroalgae and rooted plants selected for MSMDI calculation in national types 1, 2, 5, 6, 7, 14, 15, 18 and 21. These groups can react differently to pressures and also to other factors such as biotic interactions (e.g. grazing and competition) and climate.

Despite the strong theoretical basis for vegetation depth limits as a good indicator of eutrophication we see several problems with the current indicator MSMDI. Major problems are high numbers of unsuitable transects in the monitoring data, high uncertainty in many of the underlying depth limits, mathematical limitations and weak relationships with pressures.

## 5. Cover of hard and soft bottom vegetation

### 5.1 Introduction

Vegetation-covered belts of macroalgae and seagrasses occur on shallow illuminated sea floors along the Worlds' coast lines (Gattuso et al. 2006). Macroalgae dominate rocky coast lines where they in extreme cases may extend from the intertidal and down to maximum depths of 95 m in the case of kelps, and 268 m, in the case of shade tolerant encrusted red macroalgae (Lüning 1990, Steneck et al. 2002). On the Swedish west coast the macroalgal belt is generally restricted to water depths shallower than 30 m with the deepest occurrences in the open most saline areas (Pedersen & Snoeijs 2001). Seagrass meadows are dominant ecosystems of sandy coastal areas, potentially covering the seafloor down to depths of 5-15 m in North European waters and >40 m in clear Mediterranean waters (Duarte et al. 2007). In areas of low salinity seagrasses are often mixed with or even replaced by vascular plants of freshwater origin and such mixed meadows are common in the inner Baltic Sea (Boström et al. 2014).

Vegetation-covered habitats have important functional roles as they act as ecosystem engineers increasing the structural complexity and changing the physico-chemical environment, thereby facilitating colonization of other species and stimulating biodiversity of the coastal zone (Gutiérrez et al. 2011). They provide shelter and larder for a variety of species living on the vegetation, between the plants or in/on the seafloor below the canopy during shorter or longer periods of their life cycle (Bruno & Bertness 2001, Gutiérrez et al. 2011). They are also efficient primary producers providing an important input to the base of coastal food webs and affecting the cycling of carbon and nutrients; and by promoting sedimentation and stabilizing water flow they contribute to protecting sandy coasts from erosion and to keeping the water clear (Jones et al. 1994; Hemminga & Duarte 2000, Orth et al. 2006). These key ecological services make seagrass meadows and macroalgal beds rank among the most valuable ecosystems of the world (Costanza et al. 1997, Barbier et al. 2011). For sustainable management of the coastal seas it is therefore important to identify the main factors affecting the vegetation cover and their mutual effects on cover levels.

The rapid growth of the human population and the concentration of people and activities along the shores (Nicholls & Small 2002) have resulted in marked physical transformations of the coastline and substantial inputs of nutrients, organic matter and contaminants causing reduced coastal water quality and clarity and deterioration of coastal ecosystems (Nixon & Fulweiler 2009). Major reductions in the coastal vegetation have been reported on a global scale as a consequence of reduced water clarity forcing the belts closer to the shore (Lotze et al. 2006, Waycott et al. 2009). These challenges have prompted environmental policies such as the European water framework directive (WFD, 2000/60/EC) and the marine strategy framework directive (MSFD, 2008/56/EC) directed at assessing the status and ensuring a good quality of coastal ecosystems through management action. Consequently there is a large focus on identification and documentation of good indicators of coastal quality. Central criteria for good indicators are ecological relevance and scientific basis for response to pressures, and large-scale applicability is also an asset (ICES 2013).

Vegetation cover is a candidate indicator fulfilling these criteria. It represents a visual description of the structure of the coastal zone - i.e. distribution along horizontal and depth gradients and provides a quanti-

tative measure of vegetation abundance with clear links to the functioning of the coastal ecosystem. High vegetation cover is, therefore, generally considered a sign of a healthy coastal ecosystem. The European water framework directive defines good ecological status for coastal vegetation as a situation when ‘most disturbance sensitive macroalgal and angiosperm taxa associated with undisturbed conditions are present and the level of macroalgal cover and angiosperm abundance show slight signs of disturbance’ (WFD, 2000/60/EC). Vegetation cover is among the top-three most commonly used seagrass indicators in Europe (Marba et al. 2013). Macroalgal community cover (assessed as a total or by summing cover of individual species) is less commonly used for macroalgae (see database of Birk et al. 2010 and 2012) but makes part of macroalgae monitoring programmes in Denmark (Krause-Jensen et al. 2007ab, Carstensen et al. 2014), Norway, the Netherlands and France (database of Birk et al. 2010) and is available for other monitoring programs as well, such as the Swedish one. Cover or relative cover of functional groups (e.g. tolerant and sensitive species) is a more common indicator in macroalgal monitoring and is applied in many European countries (Birk et al. 2010).

Only few attempts have been made to identify relationships between macroalgal cover and environmental variables, including anthropogenic pressures, and explore whether relationships are area-specific or applicable across larger spatial scales. A variety of physico-chemical and biological variables affects the availability or use of resources, or imposes losses of biomass, thereby together controlling vegetation cover. Light, providing the energy source for macroalgae photosynthesis, is a key regulating factor, and cover declines predictably along depth gradients with fastest decline in the most turbid waters (e.g. Pedersen & Snoeijs 2001, Nielsen et al. 2002, Krause-Jensen et al. 2008). Eutrophication may induce negative effects on vegetation cover by leading to increased light attenuation as well as to further reduction in water and sediment quality via increased sedimentation of organic matter reducing the suitability of the sediments for supporting the vegetation and increasing the risk of anoxic events killing the vegetation (Duarte 1995, Pulido & Borum 2010). While moderate physical exposure to wind and waves potentially stimulates cover by ensuring renewal of water masses, strong exposure may cause loss of biomass and reductions in cover, particularly in shallow waters where physical forces are strongest (Kautsky & Kautsky 1989, Fonseca et al. 1983, Krause-Jensen et al. 2003). Ice cover is an additional important regulating factor in northern regions affecting the vegetation directly via scouring or via shading. Increased salinity may also exert positive effects on macroalgal cover as more saline areas have more species and, thus, potentially higher cumulated cover levels (Krause-Jensen et al. 2007a, Carstensen et al. 2014). Relationships between vegetation cover and eutrophication pressures are, therefore, likely to differ along environmental variables related to human pressure and natural settings.

This study aims to test the hypothesis that the cover of plants and macroalgae exhibits a negative relationship to eutrophication pressure which appears more distinct if effects of other potentially regulating factors such as salinity, exposure and large scale changes in climatic variables are accounted for. We test the hypothesis on a large monitoring data set of vegetation cover along the entire Swedish coastline spanning latitudes from 55.4 to 65.8 °N and representing wide gradients in eutrophication as well as in salinity, physical exposure, light and temperature from warmer almost fully marine salinities in Skagerrak to cold brackish conditions in the northern Bothnian Bay.

## 5.2 Methods

Overall information on the dataset and study area is provided in the Ch. 3 and key points of relevance for the present study provided below.

### Study area

The study area represents the entire Swedish coastline belonging to a total of nine regions. The nine regions represent the three basins of the Baltic Sea east of Sweden (the Baltic Proper, Bothnian Sea and

Bothnian Bay) and the Swedish West coast (Kattegat + Skagerrak). Each of these four large-scale regions was partitioned into inner and outer coastal waters, based on the typology of the WFD to form eight regions. The Öresund, south and east coast of Skåne was treated as a separate region (“Southern coast”) due to its special geology and coastal morphology. Within each region the data are grouped according to water body (see Ch. 3.1).

## Data

The vegetation data of the present study come from surveys along depth gradients and represents cumulated vegetation cover on hard seafloors, i.e. seafloors composed of >75% hard substratum, and cumulated vegetation cover on soft seafloors, i.e. seafloors composed of >75% soft substratum. The two data sets are analysed in two separate sets of analyses.

The environmental data include a set of physico-chemical variables measured in monitoring programmes; eutrophication-related variables (concentrations of nutrients, chlorophyll and Secchi depths) and salinity. We also ran complementing analyses using modelled nutrient concentrations, chl a and salinity which allowed inclusion of more water bodies with combined information of environmental variables and vegetation. The analyses based on modelled data are presented in the Appendix B.

The physical exposure of the vegetation sites was described by wave exposure calculated by a simplified wave model (SWM; Isaeus 2004). In short, the index is calculated from the distance to land (i.e. fetch) in 16 directions, multiplied with the mean wind speed over 10 years in the corresponding direction. The vegetation sites were further characterised by their geographical latitude.

## Statistical analyses

The overall aim of the statistical analyses was to model and partition the most significant variations affecting observations from the monitoring program and describe these for the different regions in Sweden. These analyses generated comparable estimates of the vegetation variables in the different water bodies, which were analysed in relation to environmental variables computed in a similar way for the water bodies.

We initially discarded observations from shallow depths, where physical exposure is the most important regulating factor of vegetation rather than nutrient enrichment/shading. Plots of cumulative cover versus depth for seven exposure classes ranging from ultra-sheltered to very exposed were used to determine a cut-off depth, and observations above this cut-off were not used in this study. Cut-off values ranged from 0.5 m in the very sheltered areas to 7 m in the highly exposed areas. Two different variables were analysed: cumulative cover of macroalgae and cumulative cover of soft-bottom vegetation (vascular plants and charophytes). The models for macroalgae were estimated on transect segments with at least 75% hard substrates, and similarly the model for cumulative cover of soft-bottom vegetation was estimated on segments with at least 75% soft substrates. After log-transformation the variables showed an approximate normal distribution.

These monitoring variables representing different segments of the transects, were analysed using generic mixed models describing monitoring-specific variations with respect to time, space and diver. These variations are spatial differences between water bodies, spatial differences between transects within waterbodies, depth-specific differences, temporal differences between years and months of observations, and differences between divers investigating the transect. Spatial differences between transects within areas and differences between divers were considered random factors in the analysis, since they represent a subset of the larger population of possible transects within a waterbody and the divers investigating a region represent only a subset of the larger population of possible divers. Thus, for each region (nine in total) a generic statistical model was employed assuming the mean of the log-transformed variables to depend on:

$$\mu_{ijk} = \text{area}_i + \text{year}_j + \text{month}_k + \text{depth} \quad , \quad \text{Eq. (1)}$$

where  $\text{area}_i$  describes the differences between water bodies (hereafter areas),  $\text{year}_j$  describes differences between years,  $\text{month}_k$  describes differences between months of sampling, and  $\text{depth}$  describes differences in observations with depth. For cumulative cover of macroalgae and soft-bottom vegetation the depth relationship was linear for the log-transformed observations (i.e. modelling an exponential decrease with depth for the cumulative cover as would be expected from the overall attenuation of light), whereas the depth relationship was categorical (dividing depths into classes of 2 m, i.e. 0-2 m, 2-4 m, etc.) because the nature of the relationship was unknown and therefore had to be estimated for specific depth intervals separately. In addition to the parameters describing variations in the mean, three sources of random variation was estimated: 1) random spatial variation between transects, 2) random variation between divers, and 3) residual variation around the depth relationship.

For each region marginal means for areas, years and months were computed from the parameter estimates of Eq. (1) by averaging over the other factors in the equation and choosing a standard depth of 5 m for cumulative cover of soft-bottom vegetation and 7 m for cumulative cover of macroalgae. For example, the area-specific marginal mean for macroalgae cumulative cover represents an average of all years and months with data from that region at a depth of 7 m. There were also differences in years and months with monitoring data between regions, but the seasonal and interannual variations were generally small, compared to depth variations, and these differences would only influence the estimated area-specific means marginally.

The potential regulation of environmental factors was investigated by modelling the area-specific means as a function of average salinity, TN or TP, chlorophyll and Secchi depth from monitoring data and modelled wave exposure (SWM). In addition, latitude was included as incoming light conditions were also hypothesised as a potential governing factor. We employed a Generalized Additive Model (GAM) approach testing for higher-order relationship in addition to a linear, since the exact nature of the putative relationships was not known. To reduce the curvature of the relationships a maximum of 3 degrees of freedom was imposed on all terms in the GAM model. The environmental factors were included only if they explained a significant proportion of the variation in addition to the other explanatory factors (i.e. by comparing the model with and without the given factor). This model selection approach reduced the potential effect of inter-correlation between the environmental factors. If the higher-order relationship was not significant, the relationship with the explanatory variable was reduced to a linear relationship and tested again. Through this backward elimination procedure non-significant non-parametric smoothers and linear relationships were iteratively excluded until all factors included in the model were significant.

Similar GAM models were also run using modelled salinity, TN or TP and chlorophyll a, together with wave exposure and latitude, and the results from this analysis are presented in Appendix B.

## 5.3 Results

### Macroalgae cumulative cover

There were large differences in the number of transect segments (i.e. monitoring effort, Table 1) between the nine regions, ranging from 106 transect segments in the Southern coast region and Bothnian Bay inner to 4037 transect segments in Baltic Proper inner (Table 5). These differences in number of observations naturally affected the significance of the factors in the mixed model. The cumulative cover of macroalgae decreased significantly with depth in all regions, except for the two in the Bothnian Bay where the number of macroalgae species is low and the vegetation is often dominated by benthic diatoms. For most regions the spatial variation was also significant, both for variation between areas and variation between transects within areas. However, it should be stressed that this spatial variation was highly significant for all regions

TABLE 5

Test of fixed and random factors for modelling cumulative cover of macroalgae. P-values less than 0.05 are highlighted in bold. In the Bothnian Bay the seasonal variation could not be tested as most of the transects were monitored in August with relatively few observations from July and September.

Region	Number of observations	Fixed factors				Random factors	
		Area	Year	Month	Depth	Transect	Diver
Bothnian Bay inner	106	<b>0.0018</b>	0.5018	N/A	0.1000	0.1296	0.4773
Bothnian Bay outer	269	0.2177	0.6692	N/A	0.7609	<b>0.0157</b>	0.3145
Bothnian Sea inner	1042	<b>&lt;0.0001</b>	0.2788	0.1783	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.0858
Bothnian Sea outer	954	0.3684	0.6820	0.8536	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0405</b>
Baltic Proper inner	4037	<b>&lt;0.0001</b>	<b>0.0005</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0117</b>
Baltic Proper outer	3775	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0149</b>
Southern coast	106	0.2629	0.4706	<b>0.0255</b>	<b>&lt;0.0001</b>	<b>0.0474</b>	1.0000
West coast inner	606	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.1757	<b>&lt;0.0001</b>	<b>0.0006</b>	0.2999
West coast outer	1331	0.2046	<b>0.0049</b>	0.9923	<b>&lt;0.0001</b>	<b>0.0001</b>	0.1743

of inner coastal waters, where differences are presumably larger. The variation between divers was the smallest of the three random factors and only significant in the Bothnian Sea outer and Baltic Proper. Hence, although diver-specific variation typically contributes 20-50% (6 of the 9 regions) uncertainty to each segment observation, the spatial variation between transects and in particular residual variation around the depth relations are considerably larger (Table 6).

The interannual variation in macroalgae cumulative cover was significant in four regions only, and two of these displayed a significant trend over time (Figure 8). The cumulative cover increased in Baltic Proper inner (linear regression,  $P=0.0010$ ) and West coast inner (linear regression,  $P=0.0302$ ). The seasonal pattern was significant for Baltic Proper only, showing an expected higher cumulative cover during summer decreasing towards the winter months (Figure 8). It should also be noted that the macroalgae cumulative cover was substantially higher in the outer regions and that estimates from regions, year or months with few data were associated with a considerable uncertainty.

TABLE 6

Variance estimates for the random factors and their relative contribution to the uncertainty associated with individual segment observations of macroalgae cumulative cover.

Region	Number of observations	Variance estimates			Relative uncertainty		
		Transect	Diver	Residual	Transect	Diver	Residual
Bothnian Bay inner	106	0.3358	0.0030	3.0904	79%	6%	480%
Bothnian Bay outer	269	1.3100	0.0579	12.1016	214%	27%	3142%
Bothnian Sea inner	1042	0.4974	0.0989	2.7271	102%	37%	421%
Bothnian Sea outer	954	0.6815	0.4280	2.4820	128%	92%	383%
Baltic Proper inner	4037	0.4422	0.1082	2.4025	94%	39%	371%
Baltic Proper outer	3775	0.4620	0.0369	2.6130	97%	21%	404%
Southern coast	106	0.0598	0	0.9842	28%	0%	170%
West coast inner	606	0.2972	0.0551	0.8282	72%	26%	148%
West coast outer	1331	0.1310	0.1860	0.7839	44%	54%	142%



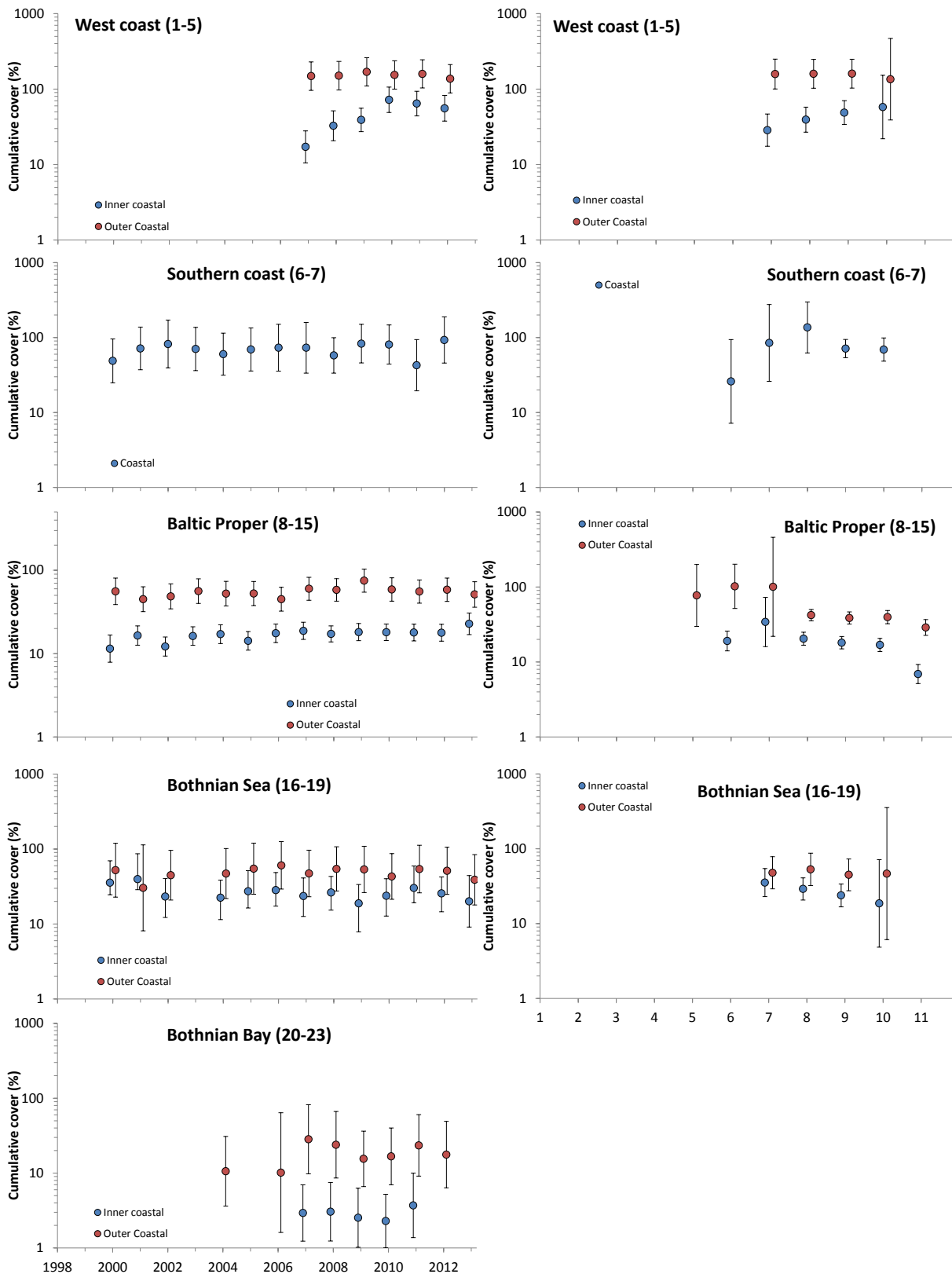


Figure 8. Estimated interannual (left panel) and seasonal variation (right panel) in macroalgae cumulative cover for the nine regions. Seasonal variation was not estimated for the two regions in the Bothnian Bay. Numbers after the inserted regional name refer to the Swedish WFD typology. Error bars mark the 95% confidence interval for the geometric means. Note the log-scale on the y-axes.

The area-specific marginal means of macroalgae cumulative cover were significantly related to a combination of several environmental variables (Figure 9). The log-transformed cumulative cover increased linearly with salinity (slope=0.0296;  $P=0.0057$ ), suggesting that the macroalgae cumulative cover is expected to increase by factor 2.5 over the entire salinity gradient, i.e. an expected cumulative cover at 7 m ranging from 23% to 57%. Macroalgae cumulative cover also increased with light conditions (slope=0.183;  $P<0.0001$ ) with a predicted increased of the expected cumulative cover at 7 m depth from 13% at Secchi depth of 1.1 m to 48% at Secchi depth of 8 m. Physical exposure had a significant positive effect on macroalgae cumulative cover (slope=0.307;  $P<0.0001$ ), when depths with detrimental physical exposure were excluded (see methods). At 7 m depth, the effect of physical exposure from the most sheltered to the most exposed areas ranged from 8% to 83% cumulative cover. Macroalgae cumulative cover had a higher-order relationship to both TN ( $P=0.0002$  for linear component and  $P<0.001$  for smoother) and latitude ( $P<0.0001$  for linear component and  $P<0.0001$  for smoother). The effect of TN was relatively constant for concentrations below 20  $\mu\text{mol/l}$  ( $\sim 3$  on the log-scale) with an expected cumulative cover of approximately 34% and decreased for higher TN levels to about 8% for TN concentrations around 30  $\mu\text{mol/l}$ . Similarly, the expected macroalgae cumulative cover was relatively constant ( $\sim 25\%$ ) for latitudes below  $63^\circ\text{N}$ , thereafter decreasing rapidly by a factor of 5-7. This rapid latitudinal change in cumulative cover matches the transition from the Bothnian Sea to the Bothnian Bay. Similar results were obtained using modelled environmental variables with chlorophyll substituting for Secchi depth and TN (Figure A1 in Appendix B).

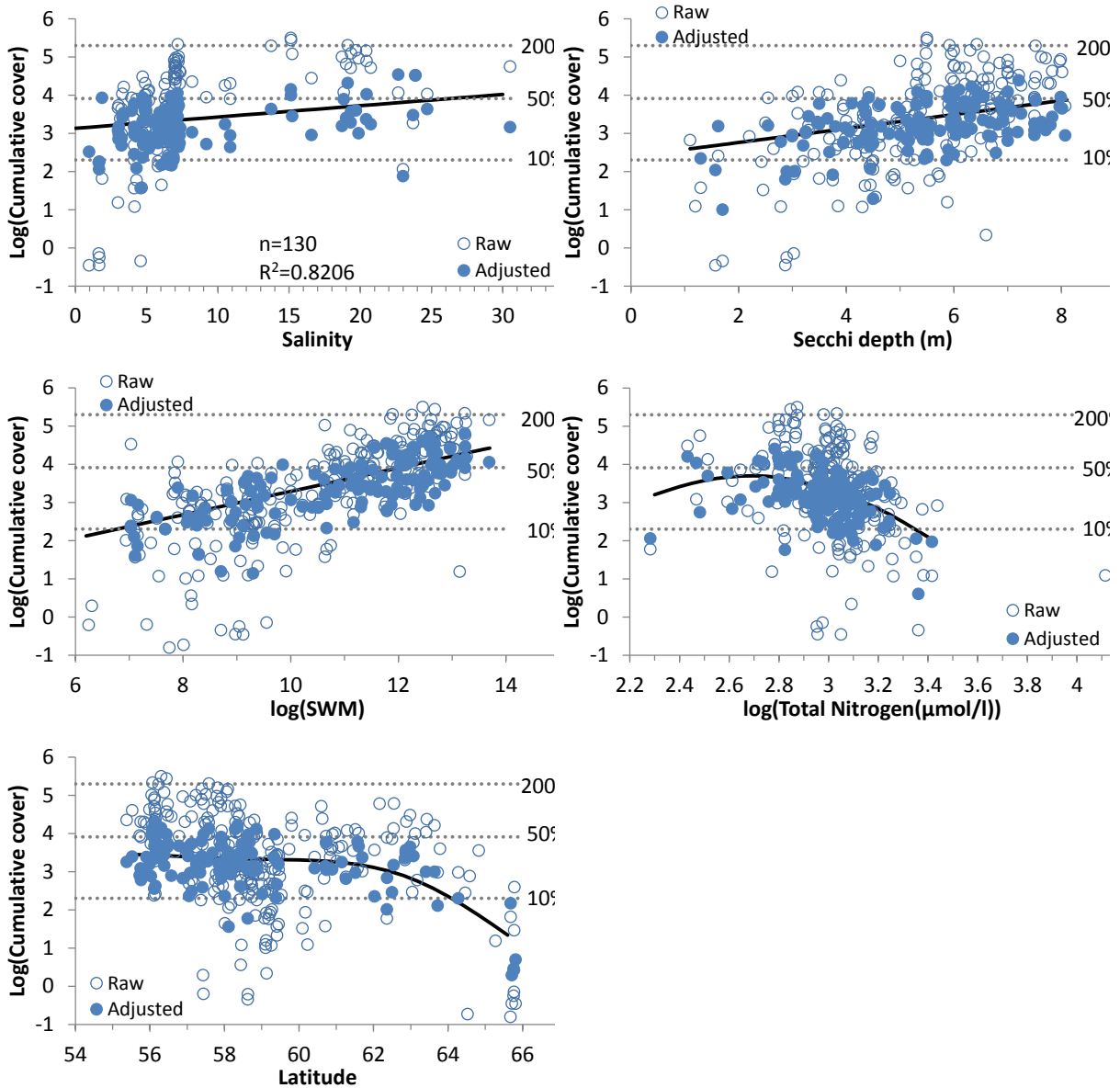


Figure 9. GAM relationships between area-specific means of macroalgae cumulative cover (log-transformed) and environmental variables obtained from monitoring data. Open symbols show the area-specific means (raw) and filled symbols show the means adjusted for variations explained by the other four factors in the GAM model. Expected mean cumulative cover was adjusted to average salinity of 6.5, Secchi depth of 5.1 m, log(SWM) of 10.1, log(TN) of 3, and latitude of 59°N. Adjusted means for cumulative cover could only be calculated for areas where data on all environmental variables were available. Statistics for the GAM are inserted in the salinity plot.

**Cumulative cover of soft-bottom vegetation**

Cumulative cover of soft-bottom vegetation (vascular plants and charophytes) was analysed for eight of the nine regions, because there were only three segments with angiosperm data in the West coast outer. Overall, compared to the macroalgae cumulative cover there were less data available for partitioning the different sources of variation in cumulative cover of vegetation (Table 7). The fewer observations and the larger random variation in data (Table 8) resulted in less significant sources of variations (Table 7). The

TABLE 7

Test of fixed and random factors for modelling cumulative cover of soft-bottom vegetation. P-values less than 0.05 are highlighted in bold. In the Bothnian Bay the seasonal variation could not be tested as most of the transects were monitored in August with relatively few observations from July and September. For the Southern coast the number of observations was so low that interannual variation was confounded with variation between areas and the interannual variation was therefore not included. For West coast outer there were almost no recordings of soft-bottom vegetation.

Region	Number of observations	Fixed factors				Random factors	
		Area	Year	Month	Depth	Transect	Diver
Bothnian Bay inner	106	<b>&lt;0.0001</b>	<b>0.0018</b>	N/A	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.1113
Bothnian Bay outer	214	<b>0.0120</b>	0.1757	N/A	<b>&lt;0.0001</b>	<b>0.0332</b>	0.2966
Bothnian Sea inner	935	<b>0.0011</b>	0.1826	0.1688	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.3117
Bothnian Sea outer	218	0.8385	0.8068	0.8051	<b>&lt;0.0001</b>	<b>0.0016</b>	1.0000
Baltic Proper inner	3562	<b>0.0003</b>	0.7129	0.0907	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.0583
Baltic Proper outer	918	0.7454	<b>0.0179</b>	0.2500	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.2598
Southern coast	75	0.1978	N/A	0.8497	<b>&lt;0.0001</b>	<b>0.0263</b>	1.0000
West coast inner	134	0.1425	0.9595	0.5191	0.0617	<b>0.0416</b>	1.0000
West coast outer	-	-	-	-	-	-	-

TABLE 8

Variance estimates for the random factors and their relative contribution to the uncertainty associated with individual segment observations of cumulative cover of soft-bottom vegetation.

Region	Number of observations	Variance estimates			Relative uncertainty		
		Transect	Diver	Residual	Transect	Diver	Residual
Bothnian Bay inner	106	0.4577	0.0687	6.147	97%	30%	1093%
Bothnian Bay outer	214	0.4431	0.0645	8.128	95%	29%	1630%
Bothnian Sea inner	935	0.3929	0.0342	8.160	87%	20%	1640%
Bothnian Sea outer	218	0.6231	0	7.729	120%	0%	1512%
Baltic Proper inner	3562	0.7079	0.0406	6.614	132%	22%	1209%
Baltic Proper outer	918	0.8378	0.0472	6.970	150%	24%	1301%
Southern coast	75	1.2352	0	10.095	204%	0%	2298%
West coast inner	134	0.5942	0	13.715	116%	0%	3958%
West coast outer	-	-	-	-	-	-	-

most important factors were the declining relationship with depth and random variation between transects within areas, which were consistently significant except for depth in West coast inner that was marginally significant. The variation between areas was also significant for half of the regions. Differences between areas were larger for inner coastal regions. Variation between divers was not significant for any of the eight regions, despite contributing 20-30% uncertainty, because spatial variation between transects and residual variation, expressing the patchiness in the angiosperm cumulative cover, were much larger. The random variation between transects within areas was similar to that for macroalgae, but the residual variation was much higher, indicating that the “noise” on angiosperm cumulative cover is much higher and therefore more data are needed to obtain sufficient certainty in area-specific estimates.

The interannual variation in macroalgae cumulative cover was significant in Bothnian Bay inner and Baltic Proper outer only; however, none of these regions displayed a consistent trend pattern (Figure 10). The seasonal variation was not significant for any of the eight regions and the monthly estimates were generally associated with large uncertainties.

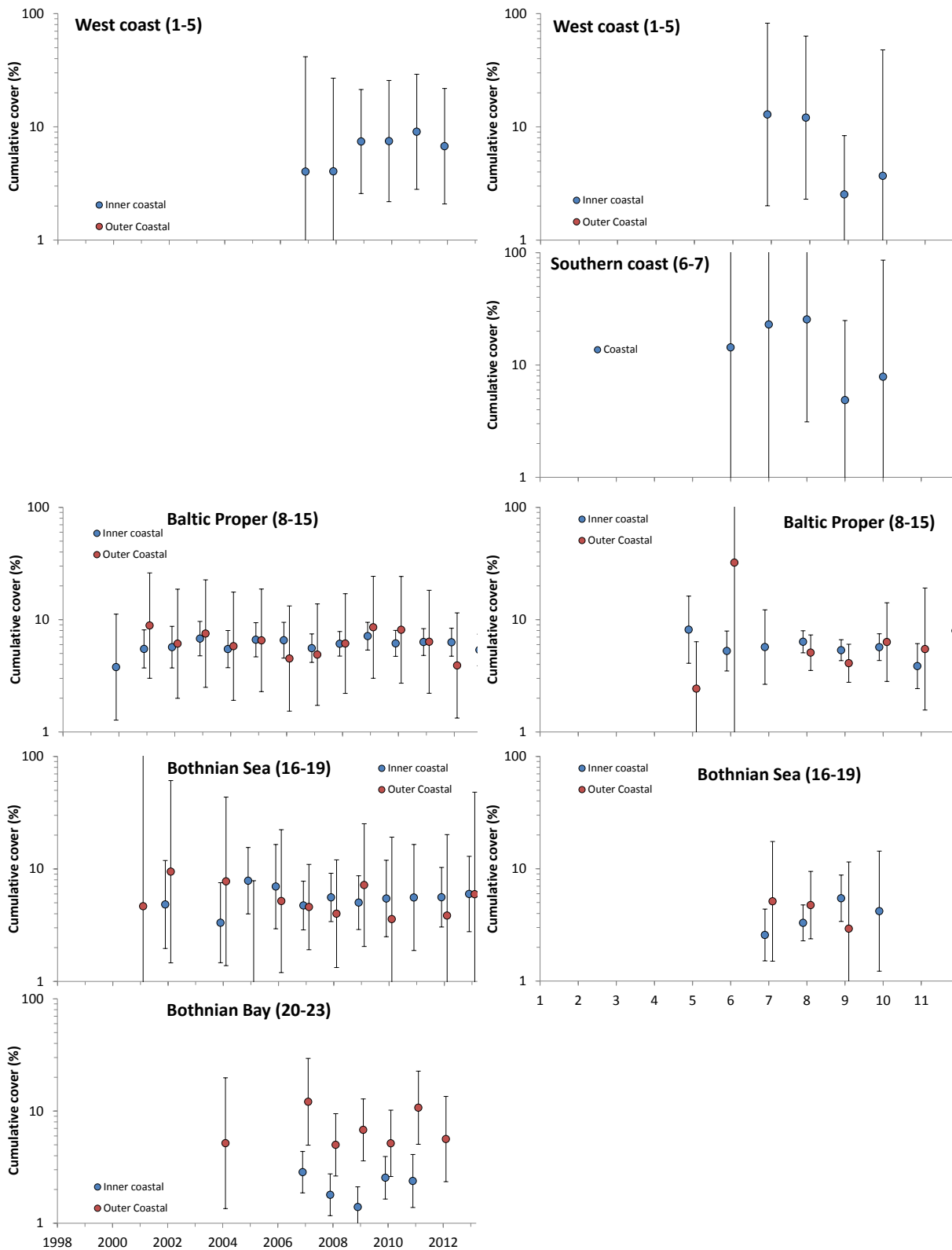


Figure 10. Estimated interannual (left panel) and seasonal variation (right panel) in macroalgae cumulative cover for the nine regions. Seasonal variation was not estimated for the two regions in the Bothnian Bay and interannual variation was not estimated for the Southern coast. Numbers after the inserted regional name refer to the Swedish WFD typology. Error bars mark the 95% confidence interval for the geometric means. Note the log-scale on the y-axes.

The area-specific marginal means of angiosperm cumulative cover were significantly related to Secchi depth and latitude (Figure 11). Overall, the GAM model only explained 25% of the variation among the 183 areas, which gives a considerably lower predictability compared to macroalgae cumulative cover. The log-transformed cumulative cover decreased linearly with latitude (slope=-0.1266;  $P<0.0001$ ), yielding a difference in expected cumulative cover at 5 m from 8% in the south to 3% in the north. The relationship with Secchi depth was non-linear displaying a positive and gradually flattening curve from an expected cumulative cover of 1% at low Secchi depth to about 8% for Secchi depths above 5 m. Similar results were obtained using modelled environmental variables with chlorophyll replacing Secchi depth as proxy for the level of eutrophication (Figure A2 in Appendix B).

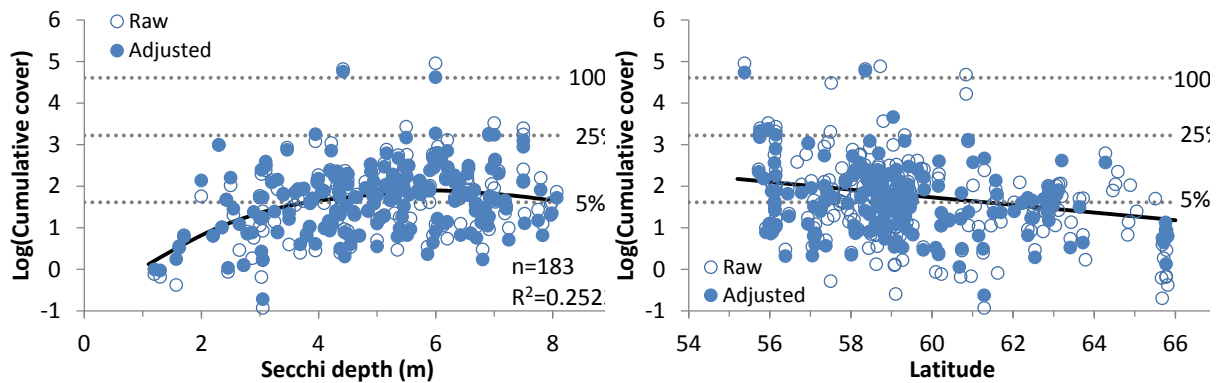


Figure 11. GAM relationships between area-specific means of angiosperm cumulative cover (log-transformed) and environmental variables obtained from monitoring data. Open symbols show the area-specific means (raw) and filled symbols show the means adjusted for variations explained by the other four factors in the GAM model. Expected mean cumulative cover was adjusted to average Secchi depth of 5.1 m and latitude of 59°N. Adjusted means for cumulative cover could only be calculated for areas where data on all environmental variables were available. Statistics for the GAM are inserted in the Secchi depth plot.

## 5.4 Discussion

### The cover of coastal vegetation of hard and soft seafloors declines along gradients of eutrophication

Vegetation cover of hard and soft seafloors reflected gradients in eutrophication as expressed by nutrient concentrations, shading and/or chlorophyll levels across the Swedish coastline. Vegetation cover thus increased significantly towards nutrient poor areas with high water clarity. This relationship appeared after accounting for variation due to other environmental variables such as salinity, exposure and/or large-scale climatic variables as well as variation caused by differences in water depth, substrate characteristics, sampling season and differences between divers. Thorough knowledge on variability components affecting vegetation cover thus facilitated the identification of responses of the indicator to pressure, in this case eutrophication.

The empirical models describing vegetation cover as functions of environmental variables were stronger and more robust for macroalgal vegetation than for soft bottom vegetation. The models thus explained 82% of the variation in macroalgal cover by a combination of variables related to eutrophication, salinity, exposure and latitude. By contrast, only 25% of the variation in soft bottom vegetation could be explained by the environmental variables, and in this case solely Secchi depth and latitude contributed to explaining the variation. Cover of soft bottom vegetation was, thus, connected with much more noise than macroal-

gal cover. The reason for this is probably larger patchiness of soft bottom vegetation inducing additional small-scale spatial variability in the data which the large-scale explanatory variables could not resolve. Higher levels of cumulated cover of hard bottom vegetation as compared to soft bottom vegetation also increase the possibility of identifying significant relationships as a larger range in cover levels potentially gives a better graduation of the response.

Variations in Secchi depth (1.1-8 m) across the Swedish coastline were reflected by an increase in algal cover at 7 m depth from 13% to 48%. By contrast, the cover of soft-bottom vegetation increased only from 1% at low Secchi depth to 8% at Secchi depths above 5 m and, surprisingly, remained at this level even if the Secchi depth was further improved. This suggests that regulating factors in addition to those included in the study play important regulating roles in the clearest waters or that the data contains so much noise that a possible further light-response cannot be detected. The clearest soft bottom sites are predominantly located along outer/open coasts, suggesting that currents or high exposure may play a regulating role.

The response of macroalgal cover similarly stabilized at TN levels around 2.8  $\mu\text{M}$  and did not improve any further with additional reductions in TN. This suggests that alternative regulating factors are in operation at low nutrient levels. In the most brackish waters furthest north in the Baltic Sea the influence of terrestrial runoff with high concentrations of dissolved organic matter may lead to brownification and, thus, cause reduced light levels even though bioavailable nutrient levels are low (Tolvanen et al. 2013, Fleming-Lehtinen & Laamanen 2012).

The positive response of vegetation cover to reduced nutrient concentrations and improved water clarity confirmed our hypothesis and is promising in terms of using the vegetation cover as an indicator of ecological quality. The relationship of cover to eutrophication appeared despite variations in many other factors that influence cover levels. The additional environmental variables that contributed to explain the variation in cover also showed overall similarities between hard and soft bottom vegetation and will be further discussed below.

### **Large scale climatic variables affect vegetation cover**

Cover of macroalgae as well as soft bottom vegetation responded to large scale climatic variables related to latitude by showing declining trends towards higher latitudes. The decrease in macroalgal cover occurred at latitudes  $< 63^\circ\text{N}$  at the border to the Bothnian Bay while cover of soft-bottom vegetation declined linearly from 8% in the south to 3% in the north (at 5 m depth). We interpret this decline in cover with latitude as reflecting large scale differences in light levels with longer dark periods in the north due to longer winters in combination with longer periods of ice cover. The extent of ice cover differ between years, but the Bothnian Bay is covered every year and has the longest duration of ice cover (on average  $>150$  days; Al-Hamdani and Reker 2007). Increased algal cover and broader vegetation belts have also been reported in the Arctic as a response to longer ice-free periods (Krause-Jensen et al. 2012, Kortsch et al. 2012). Brownification in the brackish waters furthest north may, as already mentioned also contribute to causing poorer light availability for the vegetation.

The analyses thereby identified 3 spatial scales of light-regulation of vegetation cover: small scale effects along depth gradients, and for given depths medium scale effects between water bodies differing in concentrations of light attenuating components and large-scale latitudinal effects related to differences in the ice-free period and insolation.

### **Large-scale differences in exposure and salinity affect vegetation cover**

Increased exposure also stimulated macroalgal cover whereas no significant effect was identified for cover of soft-bottom macrophytes. The positive effect of exposure may be due to more efficient supply of mi-

cro- and macronutrients, carbon dioxide and oxygen along with reduced risk of sedimentation of particles in the more exposed waters.

Salinity also had a positive effect on macroalgal cover whereas no such effect was identified for soft bottom vegetation. The stimulating effect of salinity on macroalgal cover may be related to the increase in species number of macroalgae, particularly large canopy-forming species such as kelps, along the gradient of increasing salinity from the inner parts of the Baltic Sea to the Kattegat area along the Swedish west coast (Ch. 3 of this report, Nielsen et al. 1995). The presence of kelps and other large engineering species in the marine areas tend to increase habitat diversity and stimulate species diversity (Gutiérrez et al. 2011). More species potentially result in large cover levels as the cumulated cover is the summed cover of all individual species which often form a multi-layered structure with canopy and understorey macroalgal vegetation. By contrast, the species number of vascular plants and charophytes typically increases from marine waters where solely seagrasses occur towards more brackish waters where freshwater macrophytes play an increasing role (Boström et al. 2014). This increase in species number of soft-bottom macrophytes towards brackish areas had no significant effect on cumulated cover of macrophytes, likely because the soft bottom vegetation tends to grow in a relatively uniform layer (when not considering the epiphytic part of the community).

### **Use of modelled versus measured environmental data**

As measured environmental data were not available for all water bodies, use of environmental data modelled for the entire coast line allowed inclusion of more water bodies with combined information of environmental variables in a parallel, comparable set of analyses. These analyses showed similar overall response patterns of vegetation cover as the models based on measured data, i.e. they identified significant responses of the vegetation to eutrophication-related variables, large scale climatic variables and to differences in salinity and exposure. With regard to eutrophication-related variables, no modelled Secchi depths were available and chl a became the most significant eutrophication-related variable taking the place of nutrients and Secchi depth in the relationships. Macroalgal cover increased significantly in response to modelled decreases in chlorophyll levels (Figure A1) thus paralleling the increase in macroalgal cover in response to measured decreases in nutrient concentrations and increases in water clarity. Similarly, the cover of soft-bottom vegetation increased significantly in response to modelled decreases in chlorophyll levels (Figure A2) thus paralleling the increase in soft-bottom macrophyte cover in response to measured increases in water clarity. On this basis we can conclude that modelled environmental data are useful supplements to measured data which can help increase the available datasets for analysis.

### **Temporal vs spatial responses in vegetation response - predictions for the future**

The Swedish coastline covers huge spatial gradients in vegetation cover and environmental variables and the large data set covering these gradients allowed identification of general patterns of vegetation response to a range of regulating factors. The data set also included quite a long time series but temporal gradients in environmental variables were much smaller than spatial gradients, and inter-annual responses of macroalgae were only significant in few regions (macroalgae: inner and outer parts of Baltic Proper with only inner parts showing significant trends (positive), soft-bottom macrophytes: inner Bothnian Bay, outer Baltic Proper but showing no trends). However, the relationships established based on the entire spatio-temporal data set can be used to form predictions on vegetation response to future changes in e.g. eutrophication levels (e.g. Fukami & Wardle 2005).

Temporal responses of ecosystem status to changes in pressures can exhibit considerable complexity e.g. related to resilience of ecosystem states which may result in some divergences between predictions and reality and may introduce lags in response (Duarte et al. 2009, Carstensen et al. 2013). Responses are, for example, likely to differ between periods of increasing and decreasing pressure. A dense vegetation can to some extent buffer and delay potential negative effects of increased nutrient concentrations by sequester-



ing nutrients, stimulating sedimentation which tends to improve water clarity and through their role as habitat (Gutiérrez et al. 2011) stimulate top-down controls on epiphyte cover. By contrast, recovery of lost vegetated habitats may be delayed because of resilience of the bare state where nutrients are primarily taken up by phytoplankton, sediments are easily resuspended and contribute to maintain reduced water clarity, and top-down controls may be disrupted (Krause-Jensen et al. 2012, Carstensen et al. 2013, Duarte et al. 2013). The predictive models established via the current study include ecosystems in various stages and should thereby provide a good overall indication of expected responses which can possibly be improved in the future when longer time series become available and potentially allow identification of threshold levels of pressures prompting ecosystem response in different types of ecosystems.

In conclusion, vegetation cover responded to gradients in eutrophication as expressed by nutrient concentrations, shading and/or chlorophyll levels when taking into account variation due to other variability components. On basis of these relationships the established empirical models allows predictions of general changes in vegetation cover in response to changes in nutrient concentrations, water clarity and/or chlorophyll levels in different water body types. Macroalgal cover showed highly predictable responses to eutrophication-related variables associated with relatively limited uncertainty and therefore seems a promising indicator of ecological quality. By contrast, predictions of the cover of soft-bottom macrophytes were associated with large uncertainty and resulting limited predictive power. On this basis the cover of vascular plants and charophytes does not seem to be a promising indicator of ecological quality.

## 6. Functional composition of macroalgae

### 6.1. Introduction

Changes in nutrient enrichment affect the functional composition of marine primary producers rather than the total primary production of aquatic ecosystems (Sand-Jensen & Borum 1991, Borum & Sand-Jensen 1996; Krause-Jensen et al. 2012). As nutrient enrichment increases, large, slow-growing and long-lived macroalgae and plants (late-successionals) are often replaced by smaller, fast-growing and ephemeral species with simpler tissues (opportunists) and eventually by phytoplankton (Duarte 1995, Valiela 1997). Such change in the balance between phototrophs reflects a shift from selection pressure directed at efficient and stable use of environmental resources (K-selection) towards selection directed at high productivity rates (r-selection) with variable population sizes and changed energy flow as a consequence (Pianka 1970). R-selected, opportunistic species contain less structural tissue and more nutrient-rich tissue than K-selected late-successionals (Littler & Littler 1980, Littler et al. 1983) and are, therefore, more readily grazed and decomposed, so their dominance is associated with faster turnover of the organic matter and increased risk of oxygen depletion (Sand-Jensen & Borum 1991, Cebrian & Duarte 1995).

The basis for a nutrient-generated shift in the functional composition of the vegetation is that nutrient requirements of late-successionals are lower than those of opportunists because of lower specific productivity rates, higher internal C: N: P ratios and nutrient-conserving mechanisms in combination with more long-lived and grazer-resistant tissue giving them competitive advantages at low nutrient levels. When nutrient levels increase, opportunistic species can realize their large growth potential, out-grow grazers, and out-shadow late-successional species (Pedersen & Borum 1996, Cloern 2001). Increased abundance of opportunists at the expense of late-successionals has been recorded in response to increased nutrient loadings across spatial gradients (Littler & Murray 1975) and also as a function of increased nutrient loadings over time in individual systems (Middelboe & Sand-Jensen 2000).

As the dominance pattern of phototrophs responds to changes in eutrophication pressure and also reflects the ecological quality of coastal ecosystems, it has the potential to be a useful quality indicator in coastal monitoring programs. The dominance of opportunistic versus late-successional macroalgae already makes part of the coastal monitoring programs of eg. Greece, Italy, Spain and Portugal (Diez et al. 2012, Juanes et al. 2008, Neto et al. 2012 Orfanidis et al. 2003, Sfriso et al. 2009).

However, it is not only nutrient loading that affects the functional composition of macroalgae. In a broader perspective, the functional composition depends on both the productivity potential of the environment (e.g. nutrients and light conditions) and the disturbance potential (including disturbance from herbivory, storms and ice scouring) which cause direct losses of biomass (Steneck and Dethiers 1994). Reduction in the productivity potential, eg. sub-optimal light or nutrient levels or suboptimal salinity and temperature, can be characterized as stress (Steneck & Dethiers 1994). The ability of macroalgae to occupy different niches along such gradients of environmental conditions is to a large extent related to a few key functional traits such as productivity, longevity and reproductive strategy which are closely related to thallus form (Littler & Littler 1980, Littler et al. 1983, Steneck & Dethiers 1994). This is the basis for dividing the macroalgae into a number of functional-form groups ranging from thin filamentous and foliose algae

typically possessing opportunistic r-strategic traits to large leathery macroalgae possessing late-successional, K-strategic traits, and using these groupings in ecological analyses (Littler et al. 1983, Steneck & Dethiers 1994).

Even though functional form/group models for marine macroalgae have received some criticism and suggestions to base groupings on specific functions rather than morphology (Phillips et al. 1997, Padilla and Allen 2000) there is solid documentation for close relationships between macroalgal structure and function. Key plant features such as metabolic rates, nutrient uptake rates and growth rates scale to species size and demonstrate large-scale relationships between key functional traits and organism size across plant species (Nielsen & Sand-Jensen 1990, Hein et al. 1995, Enriquez et al. 1996, Nielsen et al. 1996, Reich et al. 2006, de los Santos et al. 2009).

In this study we aim to identify how the functional composition of macroalgae responds to marked natural and anthropogenic gradients in water quality and their interactions. We wish to explore these responses across the extended Swedish coastline from fully marine waters in Skagerrak to brackish or almost fresh waters in the northernmost part of the Gulf of Bothnia which also covers large gradients in exposure, sea bottom characteristics, water temperatures and human pressures such as eutrophication (Korpinen et al. 2012, Boström et al. 2014). Earlier studies have documented that macroalgal diversity declines markedly and the composition changes from the entrance to the inner part of the Baltic Sea along with changes in salinity (Nielsen et al. 1995) and possibly also due to increasing distance from the source area (North Sea) of the marine macroalgae (Middelboe et al. 1997). A number of studies have also documented effects of nutrients and exposure on the composition of the algal community in various areas of the Baltic Sea (eg. Kautsky & Kautsky 1989, Middelboe & Sand-Jensen 2004, Krause-Jensen et al. 2007b) but no studies have yet explored responses of the functional composition of macroalgae on the large geographical scale of the Swedish coastline.

We test the hypothesis that opportunistic species, here coarsely defined as those with simple morphology, are more dominant in nutrient-rich areas and in naturally stressed and/or disturbed environments with e.g. low salinity or high exposure. We do so based on a large monitoring data set on marine macroalgae and associated environmental conditions along the Swedish coastline. We will apply the functional group approach and define the opportunists as those belonging to the groups of thin filamentous and foliose algae (Steneck and Dethiers 1994). The results will be evaluated with regard to the use of functional macroalgal composition as an indicator of coastal water quality.

## 6.2 Methods

### Data

Overall information on the dataset and study area is provided in Ch. 3. The dataset extracted for analysis is basically the same as for analysis of cumulative cover of macroalgae (Ch. 5).

### Analysis

For the analyses of how the functional composition of macroalgae responds to marked natural and anthropogenic gradients in water quality and their interactions, the macroalgal species were classified into functional groups based on morphology.

The assignment of macroalgal taxa recorded in Swedish waters to morphological functional groups is mainly based on a classification done by Karsten Dahl and Steffen Lundsteen, Aarhus University (AU) (Carstensen et al. 2008) according to Steneck and Dethiers (1994). However, some modifications to the AU classification have been made based on literature and other classifications according to morphology (mainly Kraufvelin et al. 2009, Eriksson et al. 2002, Kautsky unpubl. and several floras and algal web pages with photographs). Also, the original group 4-‘Corticated algae’ was divided into two: soft and stiff

corticated algae. The taxa are classified into the following groups: 2-Filamentous algae (uniseriate, uncorticated), 2.5-Filamentous algae (sparsely corticated, polyseriate), 3-Foliose algae (leaf shaped), 3.5-Corticated foliose algae (leaf shaped, sturdy), 4- Soft corticated algae (soft, coarsely branched), 4.5-Stiff corticated algae (rigid/tough, coarsely branched) 5-Leathery algae, 6-Calcareous algae or 7-Crustose algae. Most (167) of the 179 recorded algal taxa were assigned to a functional group according to morphology.

Each classification into morphological functional group is coupled with a confidence value to indicate how reliable the group determination is (Appendix C). For the analyses the classifications were used without regard to the confidence values.

The groups identified for analyses were 'opportunists', coarsely defined as those with simple tissues classified into the functional morphology groups 2, 2.5 and 3 (Table 9) and 'late-successionals', coarsely defined as those with complex tissues and belonging to the remaining functional morphology groups (i.e. 3, 3.5, 4, 4.5, 5 and 6; Table 10)

We further attempted to characterize the longevity of the various taxa based on information extracted from articles, floras, databases and other work (mainly Wallentinus 1979, Tolstoy and Österlund 2003, the MarLIN database online). We applied the following six groups: Annual, Perennial overwintering parts, Persistent perennial (whole or most of the plant overwinters), Perennial, A/P (literature states it can be both annual and perennial) and biennial. The group perennial includes perennial taxa which could not be further classified, i.e. into either of the groups Perennial overwintering parts or Persistent perennial, due to lack of information. The perennial group can thus include taxa that overwinter as whole plants and taxa that have overwintering parts. The longevity of 137 of the 179 macroalgal taxa recorded in Swedish waters could be determined. Similar to the functional group classification, each longevity classification is coupled with a confidence value in order to provide some information on how reliable the group determination is (Appendix C).

The proportion of opportunistic macroalgae was calculated as the cumulative cover of opportunistic species divided by the cumulative cover of the entire macroalgal community. Moreover, the proportion of opportunistic macroalgae was only calculated when cumulative cover was more than 10%, since the proportion was not well-determined for lower values of cumulative cover. The variable was approximately normal distributed after logistic transformation.

Analyses were conducted as described for analyses of cumulative cover (Ch. 5), except that the depth relationship was categorical instead of linear (dividing depths into classes of 2 m, i.e. 0-2 m, 2-4 m, etc.) because the nature of the relationship was unknown and therefore had to be estimated for specific depth intervals separately. Since maximum depths varied from 10 m in inner coastal areas of the Bothnian Bay to 30 m in other regions, the area-specific marginal means for the proportion of opportunists were computed for depths up to 10 m only.

TABLE 9

Taxa considered 'opportunists', coarsely defined as those with simple tissue (classified into the Functional morphology groups: 2-Filamentous algae (uniseriate, uncorticated), 2.5-Filamentous algae (polyseriate, sparsely corticated) and 3-Foliose algae (leaf shaped). The Longevity (Long.) of the various taxa is also indicated (A = Annual, POW = Perennial overwintering parts, P = Perennial, PP = Persistent perennial, A/P = literature states it can be both annual and perennial).

OPPORTUNISTS - COARSELY DEFINED AS THOSE WITH SIMPLE MORPHOLOGY			
	Long. 2 Filamentous algae	Long. 2.5 Filamentous algae	Long. 3 Foliose algae
ANNUAL OR WITH PERENNIAL OVERWINTERING PARTS	A Acrosiphonia	A Bonnemaisonia asparagoides	A Monostroma
	A Acrosiphonia arcta	A Ceramium tenuicorne	A Monostroma balticum
	A Aglaothamnion	A Chaetopteris plumosa	A Monostroma grevillei
	A Aglaothamnion roseum	A Dasya baillouviana	A Porphyra purpurea
	A Batrachospermum	A Dictyosiphon	A Porphyra umbilicalis
	A Bonnemaisonia hamifera	A Dictyosiphon chordaria	A Ulva
	A Bonnemaisonia hamifera/Spermothamnion repens	A Dictyosiphon foeniculaceus	A Ulva compressa
	A Bryopsis	A Dictyosiphon/Stictosiphon	A Ulva compressa/intestinalis
	A Bryopsis hypnoides	A Polysiphonia fibrillata	A Ulva flexuosa
	A Bryopsis plumosa	P Stictosiphon	A Ulva intestinalis
	A Callithamnion	POW Brongniartella byssoides	A Ulva lactuca
	A Callithamnion corymbosum	POW Heterosiphonia plumosa	A Ulva linza
	A Callithamnion tetragonum	POW Plocamium cartilagineum	A Ulva procera/prolifera
	A Chaetomorpha	POW Polysiphonia fucoides	A Ulva prolifera
	A Chaetomorpha linum	POW Polysiphonia stricta	
	A Cladophora fracta	POW Ptilodermis	
	A Ectocarpus	POW Stictosiphon tortilis	
	A Ectocarpus siliculosus		
	A Ectocarpus/Pylaiella		
	A Elachista		
	A Elachista fucicola		
	A Mougeotia		
	A Pterothamnion plumula		
	A Pylaiella		
	A Pylaiella littoralis		
	A Spermothamnion		
	A Spermothamnion repens		
	A Spirogyra		
	A Spongomorpha		
	A Spongomorpha aeruginosa		
	A Spongonema tomentosum		
	A Ulothrix		
A Ulothrix flexa			
A Ulothrix zonata			
POW Cladophora glomerata			
POW Griffithsia callirodes			
PERENNIAL OR ANNUAL/PERENNIAL	P Rhodochorton purpureum	PP Battersia arctica	- Porphyra
	P Vaucheria	PP Battersia plumigera	- Prasiola stipitata
	PP Aegagropila linnaei	PP Ceramium virgatum	- Ulva clathrata
	PP Chaetomorpha melagonium	PP Plumaria plumosa	
	PP Cladophora rupestris	PP Polysiphonia elongata	
	A/P Cladophora	PP Protohalopteris radicans	
	- Acrochaetum	PP Rhodomela	
	- Aglaothamnion hookeri	PP Rhodomela confervoides	
	- Antthamion cruciatum	PP Sphacelaria	
	- Audouinella	PP Sphacelaria cirrosa	
	- Cladophora albida	A/P Ceramium	
	- Cladophora pachyderma	A/P Polysiphonia	
	- Derbesia marina	- Heterosiphonia japonica	
	- Ectocarpales	- Polysiphonia brodiei	
	- Erythrotrichia	- Pterosiphonia parasitica	
	- Hincksia ovata	- Sphaceloderma caespitula	
	- Rhizoclonium riparium	- Stictophora tenella	
	- Rhodochorton	- Striaria attenuata	
	- Seirospora interrupta		
	- Urospora		
	- Urospora penicilliformis		
	- Vaucheria dichotoma		

TABLE 10

Taxa defined as 'late-successionals', coarsely defined as macroalgae with complex morphology (classified into the Functional morphology groups: 3.5-Corticated foliose algae (leaf shaped, sturdy), 4- Soft corticated algae (soft, coarsely branched), 4.5-Stiff corticated algae (rigid/tough, coarsely branched), 5-Leathery algae and 6-Calcareous algae). The Longevity (Long.) of the various taxa is also indicated (A = Annual, POW = Perennial overwintering parts, P = Perennial, PP = Persistent perennial)

		LATE SUCCESSIONALS - COARSELY DEFINED AS THOSE WITH COMPLEX MORPHOLOGY								
		Long. 3.5 Cort. foliose algae	Long. 4 Cort. algae (soft)	Long. 4.5 Cort. algae (stiff)	Long. 5 Leathery algae	Long. 6 Calcareous algae	Long. not classified			
PERENNIAL	PP	Chondrus crispus	PP	Cystoclonium purpureum	PP	Ahnfeltia plicata	PP	Ascophyllum nodosum	PP	Corallina officinalis
	PP	Coccolytus truncatus			PP	Codium fragile	PP	Fucus		
	PP	Coccolytus/Phyllophora			PP	Desmarestia aculeata	PP	Fucus radicans		
	PP	Dilsea carnosa			PP	Furcellaria	PP	Fucus serratus		
	PP	Membranoptera alata			PP	Furcellaria lumbricalis	PP	Fucus vesiculosus		
	PP	Odonthalia dentata			PP	Polyides rotundus	PP	Halidrys siliquosa		
	PP	Phyllophora			P	Osmundea	PP	Laminaria hyperborea		
	PP	Phyllophora crispa					PP	Saccharina latissima		
	PP	Phyllophora pseudoceranoides								
ANNUAL OR WITH PERENNIAL OVERWINTERING PARTS	POW	Delesseria sanguinea	POW	Dumontia contorta	POW	Gracilaria gracilis	POW	Laminaria digitata	-	Acrochaetaceae
	POW	Palmaria palmata	A	Eudesme virescens	A	Chorda	POW	Sargassum muticum	-	Callithamniaceae
	POW	Phycodrys rubens	A	Leathesia marina	A	Chorda filum	-	Fucus spiralis	-	Chlorophyceae
	A	Apoglossum rusCIFolium	A	Lomentaria clavellosa	A	Chordaria flagelliformis	-	Laminaria	-	Chlorophyta
	A	Asperococcus bullosus	A	Nemalion	A	Desmarestia viridis			-	Floriideophyceae
	A	Petalonia fascia	A	Nemalion helminthoides	A	Halosiphon			-	Phaeophyceae
	A	Petalonia zosterifolia	A	Scytosiphon	A	Halosiphon tomentosus			-	Polysiphonia hemisphaerica
	A	Punctaria tenuissima	A	Scytosiphon lomentaria	-	Gracilaria vermiculophylla			-	Pseudolithoderma/Hildenbrandia rubra
			A	Spermatochnus paradoxus					-	Rhodophyta
			-	Leathesia					-	Ulotracheae
			-	Sphaerotrichia divaricata					-	Vaucheriales
									-	Zygnematales

## 6.3 Results

### Proportion of opportunistic macroalgae species

The number of observations used for modelling the proportion of opportunistic species was 10-20% lower than for macroalgae cumulative cover, because observations with less than 10% cumulative cover were not used (Table 11). In the Bothnian Bay the macroalgae community was almost entirely composed of opportunistic species and consequently, there were essentially no variations in these data to model. The proportion of opportunistic macroalgae had a depth-dependent pattern in all seven regions, where the model was estimated. Spatial differences were also significant, both among transects within areas as well as between areas. The only exception was from the Southern coast, where the amount of data was small. The variation between divers was the smallest of the three random factors (Table 12) and only significant in the Baltic Proper inner. The estimates for the diver variation were not consistent across regions, which could indicate that this source of variation, although small compared to other random factors, could be dependent upon specific divers monitoring specific regions.

TABLE 11

Test of fixed and random factors for modelling the proportion of opportunistic macroalgae. P-values less than 0.05 are highlighted in bold. In the Bothnian Bay the proportion could not be modelled. Note that depth is a categorical factor in this model.

Region	Number of observations	Fixed factors				Random factors	
		Area	Year	Month	Depth	Transect	Diver
Bothnian Bay inner	-	-	-	-	-	-	-
Bothnian Bay outer	-	-	-	-	-	-	-
Bothnian Sea inner	912	<b>0.0220</b>	<b>&lt;0.0001</b>	0.9936	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	1.0000
Bothnian Sea outer	893	<b>&lt;0.0001</b>	0.1319	0.5522	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.0609
Baltic Proper inner	3390	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0118</b>
Baltic Proper outer	3385	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.6044	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.0782
Southern coast	106	0.1195	0.1100	<b>0.0032</b>	<b>0.0305</b>	<b>0.0152</b>	1.0000
West coast inner	537	<b>&lt;0.0001</b>	<b>0.0010</b>	0.1990	<b>&lt;0.0001</b>	<b>0.0012</b>	0.2380
West coast outer	1302	<b>0.0104</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0014</b>	0.3608

TABLE 12

Variance estimates for the random factors and their relative contribution to the uncertainty associated with individual segment observations of proportion of opportunistic macroalgae.

Region	Number of observations	Variance estimates			Relative uncertainty		
		Transect	Diver	Residual	Transect	Diver	Residual
Bothnian Bay inner	-	-	-	-	-	-	-
Bothnian Bay outer	-	-	-	-	-	-	-
Bothnian Sea inner	912	1.6821	0	7.177	266%	0%	1357%
Bothnian Sea outer	893	0.5555	0.4580	6.472	111%	97%	1173%
Baltic Proper inner	3390	1.4446	0.2992	6.278	233%	73%	1125%
Baltic Proper outer	3385	0.8931	0.0315	7.897	157%	19%	1561%
Southern coast	106	0.4703	0	3.888	99%	0%	618%
West coast inner	537	0.3220	0.0677	1.549	76%	30%	247%
West coast outer	1302	0.1035	0.0310	2.095	38%	19%	325%

A diverse set of depth patterns were estimated for the proportion of opportunistic macroalgae (Figure 12). The highest proportions were found in the Bothnian Sea with more than 90% opportunistic macroalgae at all depths in the inner coastal regions and an increasing proportion with depth towards the same level for the outer coastal areas. In the Baltic Proper, the proportion was typically around 50-80% for most depths with the exception of the 0-2 m depth interval. In this depth interval the proportion of opportunistic macroalgae was higher in the outer coastal area than the inner. In all other regions and depth intervals there were relatively fewer opportunistic macroalgae in the outer coastal regions. The depth pattern for the Southern coast resembled that of the Baltic Proper inner. In the West coast regions the proportions of opportunistic macroalgae were highest at intermediate depths and decreased at deeper depths, most pronounced for the outer coastal region.

The interannual variation in the proportion of opportunistic macroalgae was significant in five of the seven regions (Figure 13). However, a significant trend was found only for Baltic Proper inner (linear regression,  $P=0.0441$ ) suggesting an increasing proportion of opportunistic macroalgae over time. Three of the seven regions had a significant seasonal pattern, showing a tendency towards decreasing proportions from summer to winter (Figure 13). The seasonal patterns also confirmed that the proportion of opportunistic macroalgae is generally lower in the outer coastal regions.

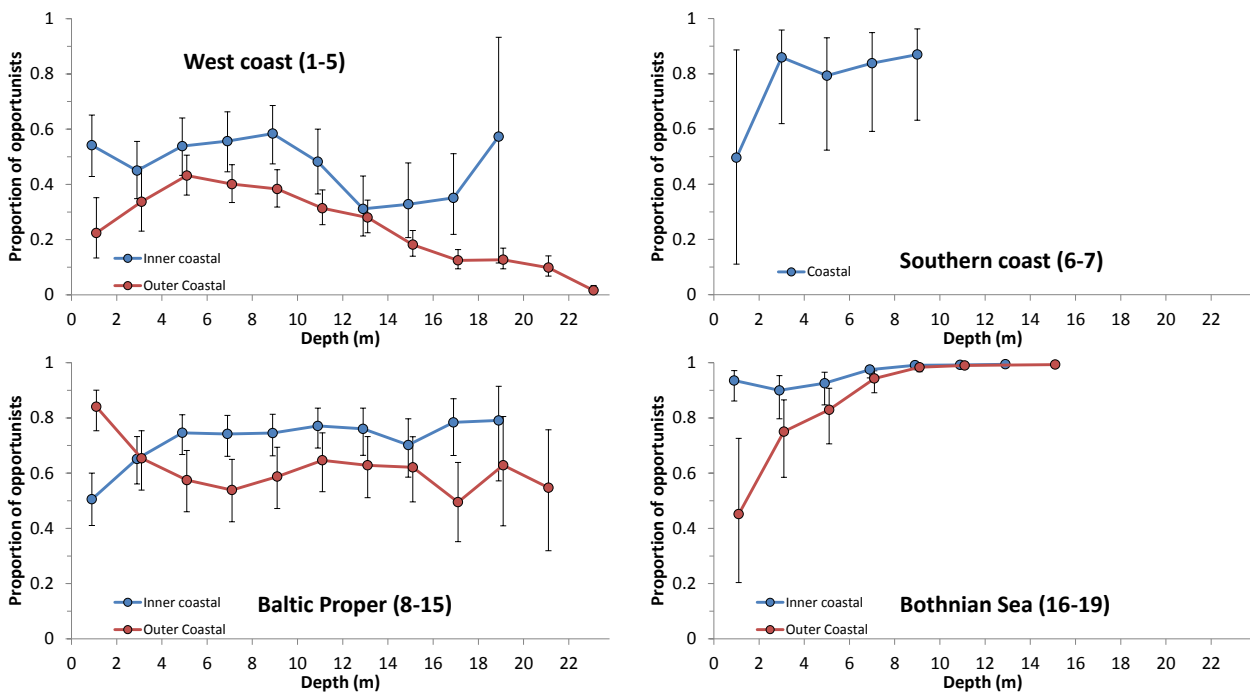


Figure 12. Estimated depth relationships for the proportion of opportunistic macroalgae for the seven regions. The proportion was not modelled for the Bothnian Bay. Numbers after the inserted regional name refer to the Swedish WFD typology. Error bars mark the 95% confidence interval for the geometric means



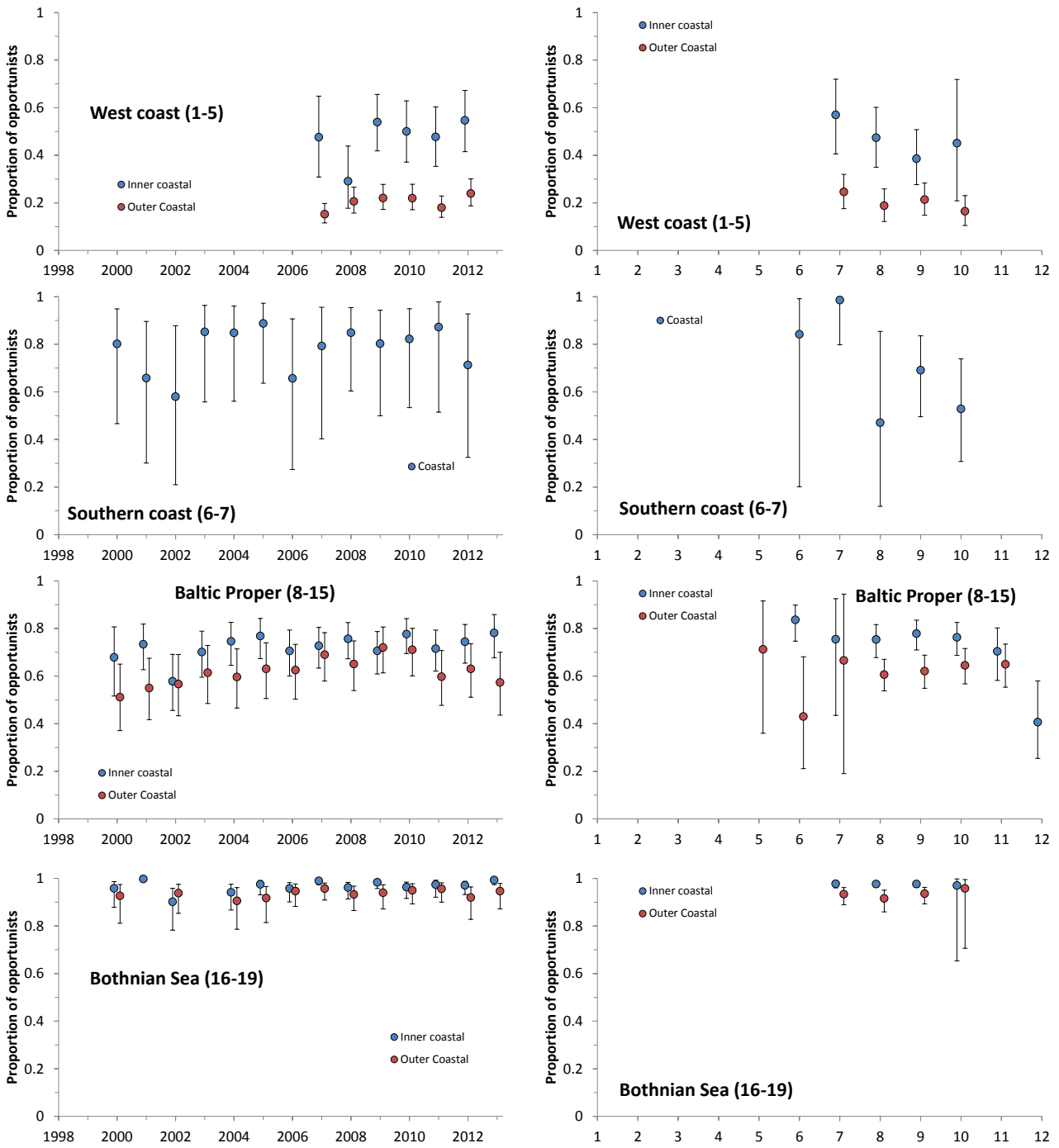


Figure 13. Estimated interannual (left panel) and seasonal variation (right panel) in the proportion of opportunistic macroalgae in seven regions. The proportion was not modelled for the Bothnian Bay. Numbers after the inserted regional name refer to the Swedish WFD typology. Error bars mark the 95% confidence interval for the geometric means.

The area-specific marginal means for the proportion of opportunistic macroalgae were significantly related to a combination of four environmental variables (Figure 14). The logistic transformed proportions had a non-linear relationship with salinity ( $P < 0.0001$  for linear component and  $P < 0.0001$  for smoother), decreasing from more than 90% at low salinities ( $< 5$ ) to a plateau of 35% for salinities above 10. The relationship to Secchi depth was also non-linear ( $P = 0.0011$  for linear component and  $P = 0.0003$  for smoother), decreasing from more than 90% to a plateau of 70% for Secchi depths above 4 m. The differences in the levels of the two relationships is because the relationship with salinity is predicted for Secchi depth (6.5 m) that has a relatively low proportion and the relationship with Secchi depth is predicted for a salinity (6.5) that has a relatively high proportion of opportunistic macroalgae.

In addition, the logistic transformed proportions were linearly related to physical exposure and TN. The proportion of opportunistic macroalgae increased with physical exposure (slope=0.157;  $P = 0.0213$ ), although the relationship was relatively weak. This could indicate that the waves occasionally disturb the vegetation also below the depth where we could see a clear signal in the cumulated cover of algae (that we used as cut-off depth in the analyses), favoring opportunistic species. Surprisingly, the proportion of opportunists decreased with  $\log(\text{TN})$  (slope=-1.74;  $P = 0.0041$ ), but the relationship was relatively weak and driven by a few areas with low  $\log \text{TN}$ .

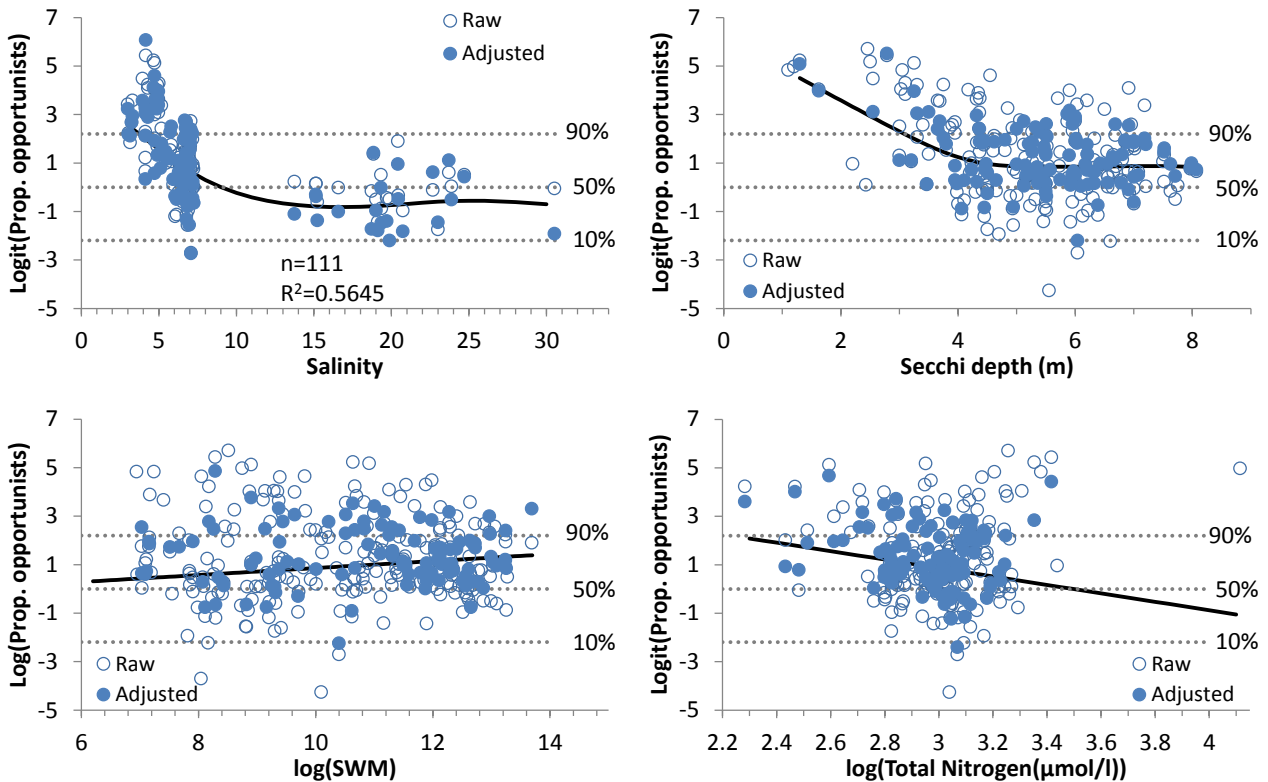


Figure 14. GAM relationships between area-specific means of proportion of opportunistic macroalgae (logit-transformed) and environmental variables obtained from monitoring data. Open symbols show the area-specific means (raw) and filled symbols show the means adjusted for variations explained by the other three factors in the GAM model. Expected mean proportion of opportunistic macroalgae was adjusted to an average salinity of 6.5, Secchi depth of 5.1 m,  $\log(\text{SWM})$  of 10.1, and  $\log(\text{TN})$  of 3. Adjusted means could only be calculated for areas where data on all environmental variables were available. Statistics for the GAM are inserted in the salinity plot

Similar results were obtained using modelled environmental variables (with chlorophyll substituting for Secchi depth and TN; Figure A3 in Appendix B). The relationship with modelled chlorophyll was positive, consistent with the relationship for Secchi depth obtained with monitoring data, but relatively weak and the model explained only 38% of the variation between areas. Thus, our analyses show ambiguous results with respect to the response of opportunists (as defined here) to eutrophication level. As expected the proportion decreased with decreasing chlorophyll levels (modelled data) and also decreased with increasing Secchi depth in the lower range of measured Secchi depths. On the other hand, the proportion of opportunists increased with decreasing TN concentrations. So the pattern is complex and a large part of the variation could not be explained by the factors included in the models.

## 6.4 Discussion

The results show that opportunistic macroalgae, as defined here, play a very significant role in the Baltic Sea and represent the all-dominant growth form in regions with low salinity. This is the case along the southern coast of Sweden, in the Baltic Proper and, particularly, in the Bothnian Sea where >90% of the macroalgal community, except in shallow outer coastal waters, is composed of such algae (Figure 12). In contrast, the proportion of opportunistic algae is markedly lower in the most saline region along the west coast of Sweden. These results are in line with a Baltic-wide study of macroalgae in the Baltic Sea which also documented an increased proportion of algae with simple morphology, such as green algae, as the total species number declines towards the low saline inner Baltic Sea (Nielsen et al. 1995). Moreover, our analysis clearly showed that the proportion of opportunistic macroalgae was consistently larger in inner coastal waters than in outer coastal waters of all study regions – a pattern that might be related to a combination of lower salinity, more nutrients and less exposure in inner coastal waters. These patterns were consistent over the entire study-period (2000–2012) and with the inner Baltic Proper even showing an increase in the proportion of opportunistic macroalgae over time.

The analyses showed ambiguous results regarding the use of the proportion of opportunists, as defined here, as an indicator of eutrophication. Within regions, the proportion of opportunistic macroalgae was consistently larger in inner coastal waters than in outer coastal waters – a pattern that may partly be related to more nutrients and reduced Secchi depths in inner regions, favoring opportunistic algae (eg. Duarte 1995, Cloern 2001) but which also may reflect lower salinity in inner coastal waters. In the large scale-analyses across all four regions, the proportion of opportunists increased towards areas with reduced Secchi depths (at least in the low range of Secchi depths) and increased chlorophyll levels, i.e. at light and chlorophyll conditions typically representing more eutrophic locations. However, in opposition to expectations, the large scale analysis showed declining proportions of opportunists towards areas with higher TN concentrations. The structuring role of low salinity, favoring ‘opportunistic macroalgae’ particularly in the inner Baltic Sea, represents an important confounding factor that complicates the identification of isolated responses of these algae to eutrophication.

The sheltered nature of inner coastal waters may also contribute to favoring opportunistic algae relative to the situation on the outer coasts where waves and currents may detach algae with simple tissue. Drifting opportunistic algae are, thus, often transported by wind and currents to sheltered locations where they accumulate (Pihl et al. 1999). However, the pattern is not straight-forward because while the inner, most protected (but also more nutrient-rich and less saline) coastal waters of a given region indeed had larger proportion of opportunistic algae, exposure seemed to play a stimulating role for this group of algae relative to late-successional species on the Baltic-wide scale (Figure 14). Other studies have also identified exposure as a strong structuring factor for the functional composition of macroalgae in the Baltic Sea and identified finely branched and crust-forming algae as those being best able to resist wave exposure (Kautsky & Kautsky 1989). The sturdier of the finely branched algae grouped as opportunistic species in this study may have the capacity to resist wave exposure and contribute to explain the increase in opportunists as a function of increasing exposure on the Baltic-wide scale. Kautsky &

Kautsky (1989) also underline that exposure may cause an increased dominance of opportunistic algae, probably through suppression of late-successionals, which allows the opportunistic algae to develop. Again, the collinearity of regulating factors complicates the interpretation of the results.

The patterns becomes even more complex when considering how the proportion of opportunistic algae changes along depth gradients from shallow, exposed (and clearer, fresher) waters to deeper, more protected (and darker, more saline) waters. The two most distinct changes in the proportion of opportunistic algae with depth occurred along depth gradients in the low saline outer Bothnian Sea and the high saline outer coastal waters of the Swedish west coast. These areas showed contrasting depth patterns, i.e. an increased proportion of opportunistic macroalgae with depth in the outer Bothnian Sea as opposed to a declining proportion with depth in outer coastal waters along the Swedish west coast. Competition from other algae likely plays a part in explaining these patterns. In the Bothnian Sea the competition from other algae is very limited and the simple algae can proliferate towards deeper waters where they are the only macroalgae present. By contrast, the competition is considerably stronger along the Swedish west coast where the algal community is much more diverse and macroalgae with complex morphology can exert a significant competition pressure. The tendency of reduced competition pressure and associated increased depth penetration of Baltic-wide species in response to declining salinity was first identified by Reinke (1889), described as the 'downward process' by Waern (1952) and further explored by Pedersen & Snoeijs (2001). A striking example of this phenomenon is that a pan-Baltic species, such as *Fucus vesiculosus*, is an intertidal species in the North Sea region, but becomes sublittoral and grows to larger depths towards the inner Baltic Sea, paralleling the declining salinity (Pedersen & Snoeijs 2001, Torn et al. 2006). These contrasting depth-patterns of opportunistic algae between the Swedish west coast and the Bothnian Sea further complicates the identification of general patterns in the control of opportunistic algae at the Baltic-wide scale.

Seasonality of the opportunistic algae also exhibited markedly different patterns from the high-saline Swedish west coast and the south coast with intermediate salinity to the low-saline Bothnian Sea. Whereas the regions with high-intermediate salinity exhibited a pronounced seasonal pattern with declining proportion of opportunistic algae during autumn, this group maintained a high proportion throughout autumn in the low-saline Bothnian Sea. This pattern suggests that the simple algae in high-saline regions have a more ephemeral nature than those in the inner Baltic Sea. The literature survey of the longevity of the various algae (Table 9 & Table 10) allowed us to test whether the group we defined as opportunists was characterized by a larger fraction of perennial species in the Bothnian Sea as compared with the Swedish west coast. This was, however, not the case, and only 10% of the opportunistic algae of the Bothnian Sea had perennial overwintering parts. An important point is still that all the morphologically simple algae present in the inner Baltic Sea are defined as 'opportunistic species' in our analysis, even though this region, because of the low salinity, practically solely supports macroalgae with simple tissue. And many of the simple macroalgae of the inner Baltic Sea may not possess the same opportunistic traits as those on the Swedish west coast.

Overall, the interacting gradients of physico-chemical conditions across the very large study area along with our coarse definition of opportunistic species, that may fail to properly distinguish the true opportunistic species in the Bothnian Sea, are likely main reasons why our analyses only explained a limited fraction of the total variation in the proportion of opportunistic algae. In order to address these limitations and reduce the interacting effects of eutrophication and salinity we recommend conducting separate analyses for 1) the medium-high saline west- and south coast and 2) the low saline Baltic Proper and the Bothnian Sea in a future study.

## 7. Traits analysis of soft bottom vegetation

### 7.1 Introduction

The ability of organisms to occupy different niches along environmental gradients is to a large extent related to biological traits. For aquatic plants and macroalgae, traits such as productivity, longevity and reproductive strategy, which are also coupled to thallus form have been related to habitat use (e.g. Littler & Littler 1980, Littler et al. 1983, Steneck & Dethiers 1994, Kautsky 1988, Wilby et al. 2000). Furthermore, as biological traits such as productivity reflect the ecological function of a species, grouping of species based on biological traits translates directly to ecosystem function and thereby possesses an advantage in functional ecosystem studies relative to or as a supplement to classic taxonomic grouping.

A number of studies have evaluated the possibility to use trait composition of biotic assemblages to assess the effects of human impacts in aquatic environments. Most work has been done for invertebrate communities in streams, where the trait composition has been suggested as an important tool for biomonitoring (e.g. Dolédec et al. 1999, Usseglio-Polatera et al. 2000). A number of studies have also shown that the trait composition of marine benthic invertebrates respond to disturbance from bottom-trawling (e.g. Bremner et al 2006, Tillin et al 2006) and pollution (Oug et al. 2012). For freshwater plants, previous studies have focused on the relationship between traits and habitat utilization along natural gradients in productivity and disturbance (Bornette et al. 1994, Willby et al. 2000). These studies have shown a clear relationship between biological traits and habitat utilisation, indicating that these traits can be a useful tool for assessment of the response of freshwater hydrophyte communities to anthropogenic pressures. However, no study has previously attempted to relate trait composition of coastal plant communities to natural or anthropogenic gradients. In the present study we explore coastal vegetation along wide environmental gradients with the use of biological trait analysis (BTA). In order to do this we compile a database of morphological and life-history traits for soft-bottom macrophytes (vascular plants and charophytes) present in monitoring data from Swedish marine and brackish waters. This database is used to explore the relationship between species traits and to run BTA by coupling the defined traits with abundance estimates of the species and with information on physiochemical growth conditions along environmental gradients. Based on the results, we evaluate whether traits of soft-bottom macrophytes can be used as indicators of the ecological status of coastal ecosystems.

### 7.2 Methods

#### Study area

The study area represents the Swedish coastline of the Baltic Proper and Gulf of Bothnia. The Swedish west coast (Kattegat and Skagerrak) was excluded from the analyses due to the very low diversity of vascular plants and charophytes in this area (Figure 4).

### Traits and categories

The choice of morphological and life-history traits was modified from the attribute-based classification of European hydrophytes by Willby et al. 2000, who classified vascular plants in freshwater habitats into 17 traits such as growth form, leaf type, fruit size etc (Table 13). The selections of biological traits relevant to survival in freshwater environments were based on literature, but the final choice of traits was determined by the availability of information. Lack of information also excluded physiological traits (e.g. photosynthetic mechanism) and some other potentially important traits (e.g. period of germination and seed weight). In order to account for variation within the traits (e.g. growth form), Willby et al. (2000) subdivided most of the traits into categories (“attributes”) resulting in a total of 58 categories for the 17 traits (Table 13). Each hydrophyte was then given a score for each category. Categorical scores were used to account for the heterogeneity of available information, where '0' indicated absence of the category, '1' indicated occasionally but not generally exhibited and '2' indicated presence of the category.

We assigned trait scores to all 63 taxa of vascular plants and characeans recorded on soft substrate in transect surveys in Swedish coastal waters during 2000-2012 (Table 14). The scoring of most vascular plants was based on the classifications by Willby et al. (2000) but was revised based on literature (mainly Wallentinus 1979, Idestam-Almqvist 1998, Mossberg & Stenberg 2003) and expert knowledge, to account for ecological differences between fresh and brackish water conditions. Vascular plants that were not classified by Willby et al. (2000), as well as characeans, were assigned scores based on literature (Schubert & Blindow 2003, Tolstoy & Österlund 2003, Blindow et al. 2007 for charophytes) and expert knowledge. A compilation of trait and category scoring for the taxa is given in Appendix D.

TABLE 13

Traits and categories used in the analyses of trait composition. The abbreviation is used in the ordination plots.

Trait	Category	Abbreviation
Amphibious	-	Amphibious
High below-ground:above-ground biomass	-	Biomass
Body flexibility	High	BodyflexHigh
	Intermediate	BodyflexInterm
	Low	BodyflexLow
Evergreen leaf	-	Evergreen leaf
Fruit size	< 1mm	FruitszS
	> 3 mm	FruitszL
	1-3 mm	FruitszM
Gamete vector	Air bubble	GamVectAirBubble
	Insect	GamVectInsect
	Self	GamVectSelf
	Water	GamVectWater
	Wind	GamVectWind
Growth form	Anchored, emergent leaves	GfAnchEmerg
	Anchored, floating leaves	GfAnchFloat
	Anchored, heterophylly	GfAnchHetero
	Anchored, submerged leaves	GfAnchSubm
	Free-floating, submerged	GfFreeSubm
	Free-floating, surface	GfFreeSurf

TABLE 13. Continued.

<b>Trait</b>	<b>Category</b>	<b>Abbreviation</b>
Leaf area	Extra large (> 100 cm <sup>2</sup> )	LeafAreaXL
	Large (20-100 cm <sup>2</sup> )	LeafAreaL
	Medium (1-20 cm <sup>2</sup> )	LeafAreaM
	Small (< 1 cm <sup>2</sup> )	LeafAreaS
Leaf texture	Non-waxy	LeafTxNonWaxy
	Rigid	LeafTxRigid
	Soft	LeafTxSoft
	Waxy	LeafTxWaxy
Leaf type	Capillary	LeafTyCapill
	Entire	LeafTyEntire
	Tubular	LeafTyTubu
Perennation	Annual	Annual
	Biennial/short lived perennial	Biennial
	Perennial	Perennial
Mode of reproduction	Seeds	SeedsSpores
	Budding	Budding
	Fragmentation	Fragmentation
	Rhizome	Rhizome
	Stolons	Stolons
	Tubers	TubersBulbils
	Turions	Turions
Morphology index (score) (height + lateral extension of the canopy)/2	(1) 2	MorphInd1
	(2) 3-5	MorphInd2
	(3) 6-7	MorphInd3
	(4) 8-9	MorphInd4
	(5) 10	MorphInd5
Number of reproductive organs per year and individual	Very high (>1000)	ReprOrgVeryHigh
	High (100-1000)	ReprOrgHigh
	Medium (10-100)	ReprOrgMedium
	Low (<10)	ReprOrgLow
Period of production of reproductive organ	Early (March-May)	ReprPerEarly
	Mid (June-July)	ReprPerMid
	Late (August-September)	ReprPerLate
	Very late (post-September)	ReprPerVeryLate
Rooting at nodes	-	RootingAtNodes
Vertical shoot architecture	Multiple apical growth point	VertShootMult
	Single apical growth point	VertShootSingApic
	Single basal growth point	VertShootSingBasal

TABLE 14

Taxa of vascular plants and charophytes included in the analysis, with abbreviations used in ordination plots.

Division	Taxon name	Abbrev.	Division	Taxon name	Abbrev.
Lycopodio- phyta	<i>Isoetes lacustris</i>	Iso.lac		<i>P. natans</i>	Pot.nat
Magnolio- phyta	<i>Alisma wahlenbergii</i>	Ali.wah		<i>P. obtusifolius</i>	Pot.obt
	<i>Callitriche hamulata</i>	Cal.ham		<i>P. pectinatus</i>	Pot.pec
	<i>C. hermaphroditica</i>	Cal.her		<i>P. perfoliatus</i>	Pot.per
	<i>C. palustris</i>	Cal.pal		<i>P. praelongus</i>	Pot.pra
	<i>Ceratophyllum demersum</i>	Cer.dem		<i>P. pusillus</i>	Pot.pus
	<i>C. submersum</i>	Cer.sub		<i>P. vaginatus</i>	Pot.vag
	<i>Elatine hydropiper</i>	Ela.hyd		<i>Ranunculus aquatilis</i>	Ran.aqu
	<i>E. orthosperma</i>	Ela.ort		<i>R. circinatus</i>	Ran.cir
	<i>Eleocharis acicularis</i>	Ele.aci		<i>R. confervoides</i>	Ran.con
	<i>E. parvula</i>	Ele.par		<i>R. peltatus</i>	Ran.pel
	<i>Elodea canadensis</i>	Elo.can		<i>R. reptans</i>	Ran.rep
	<i>Hippuris × lanceolata</i>	Hip.lan		<i>Ruppia cirrhosa</i>	Rup.cir
	<i>Hippuris tetraphylla</i>	Hip.tet		<i>R. maritima</i>	Rup.mar
	<i>H. vulgaris</i>	Hip.vul		<i>Sagittaria sagittifolia</i>	Sag.sag
	<i>Lemna trisulca</i>	Lem.tri		<i>Sparganium</i>	Sparg
	<i>Limosella aquatica</i>	Lim.aqu		<i>Subularia aquatica</i>	Sub.aqu
	<i>Myriophyllum alterniflorum</i>	Myr.alt		<i>Utricularia vulgaris</i>	Utr.vul
	<i>M. sibiricum</i>	Myr.sib		<i>Zannichellia palustris</i>	Zan.pal
	<i>M. spicatum</i>	Myr.spi		<i>Zostera marina</i>	Zos.mar
	<i>M. verticillatum</i>	Myr.ver	Strepto- phyta	<i>Chara aspera</i>	Cha.asp
	<i>Najas marina</i>	Naj.mar		<i>C. baltica</i>	Cha.bal
	<i>Nuphar lutea</i>	Nup.lut		<i>C. canescens</i>	Cha.can
	<i>Nymphaea alba</i>	Nym.alb		<i>C. connivens</i>	Cha.con
	<i>Persicaria amphibia</i>	Per.amp		<i>C. globularis/virgata</i>	Cha.glo
	<i>Plantago uniflora</i>	Pla.uni		<i>C. horrida</i>	Cha.hor
	<i>Potamogeton alpinus</i>	Pot.alp		<i>C. tomentosa</i>	Cha.tom
	<i>P. berchtoldii</i>	Pot.ber		<i>C. virgata</i>	Cha.vir
	<i>P. filiformis</i>	Pot.fil		<i>Nitella flexilis/opaca</i>	Nit.fle
	<i>P. friesii</i>	Pot.fri		<i>N. wahlbergiana</i>	Nit.wah
	<i>P. gramineus</i>	Pot.gra		<i>Tolypella nidifica</i>	Tol.nid
	<i>P. gramineus × perfoliatus</i>	Pot.gxp			

The relationship among species traits was analysed with fuzzy correspondence analysis (FCA; Chevenet et al. 1994) of the species trait table (Appendix D). FCA is an extension of normal correspondence analysis developed for the analyses of fuzzy-coded data, such as the categorical scores of the trait categories. Since FCA can only handle traits with at least two categories, we excluded four traits that only had one category from the analyses (amphibious, high below-ground/above-ground biomass, evergreen leaf and rooting at nodes). FCA was performed using the ade package (Dray & Dufour 2007) in R version 3.1 (R Core Team 2014).



### Trait-environment data

We analysed the relationship between the trait composition and a number of environmental variables describing natural (salinity, wave exposure and latitude) and anthropogenic (Secchi depth, chlorophyll a, TN and TP) gradients. Salinity, Secchi depth, chl a and nutrient concentrations were derived from field measurements and wave exposure from a fetch-based wave model, as described in Ch. 3.

Vegetation data for the analyses were extracted from diving transects from the Baltic Proper and the Gulf of Bothnia, excluding transitional waters, i.e. waters close to the city of Stockholm. We only included transect sections with  $\geq 75\%$  cover of sand or finer sediment (see Ch. 3). The transect data was collected between 2000 and 2012 and between April-November, with 90 % of the transects from July-September when the vegetation is most fully developed. Initial analysis showed that there was a significant difference in multivariate trait composition between months when including all months, but no differences between the months July-September or between years. The analyses are therefore based on data from July-September.

For each transect ( $n=375$ ) we calculated the mean cover of all registered taxa, as the mean of the cover in the transect sections between 0.5 m and 4.5 m depth, weighted for the length of the sections. The depth interval 0-0.5 m was excluded since the shallowest plant communities are strongly affected by disturbance from water level fluctuations and ice. The lower depth limit was set since only few transects had vegetation below 5 m depth and we expected the species and trait composition to change with depth. Only transect sections with at least 10 % mean cumulative cover of vascular plants and charophytes were included in the analyses.

Trait composition in each transect was achieved by multiplying the cover of each species with the trait category scores for that species and then summing the trait category scores across all species that were found in the transect. The score sums were then normalised for differences in vegetation cover between transects by dividing with the total cumulative cover of vascular plants and charophytes in the transect.

Principal component analysis (PCA) was used to describe the trait composition in the field transects and assess which traits were associated in the field. The relationship between trait composition and the environmental variables was analysed with redundancy analysis (RDA). We first ran RDA with all environmental variables except Latitude, which was excluded due to its strong correlation with salinity and resulting high variation inflation factor in the RDA model. Secondly we ran partial RDA, extracting the variation explained by the pressure variables (TN, TP, chl a and Secchi depth) while removing the effects of the natural gradients (salinity and wave exposure). The significance of the models relating the trait composition to the environmental variables was tested with permutation test, restricting the permutations within years to account for that some sites were sampled more than one year.

The analyses were performed in the vegan package (Oksanen et al. 2013) in R version 3.1 (R Core Team 2014).

## 7.3 Results

### Relationship among traits

The distribution of the trait categories along the first and second axis of correspondence analysis, (explaining 18 and 12 % of the total inertia respectively), are shown in Figure 15. The first axis was mainly related to leaf type, leaf area, plant size (morphology index), and fruit size, separating small species with small, tubular leaves and small fruits (to the left) from large species with large, entire or capillary leaves and medium or large fruits (to the right). The second axis was mainly related to vertical shoot architecture, separating species with single basal shoots (lower part of the graph) from species with single apical and multiple shoots). Also body flexibility and leaf texture were to some extent separating along the second axis, with rigid and waxy species in the lower part of the graph.

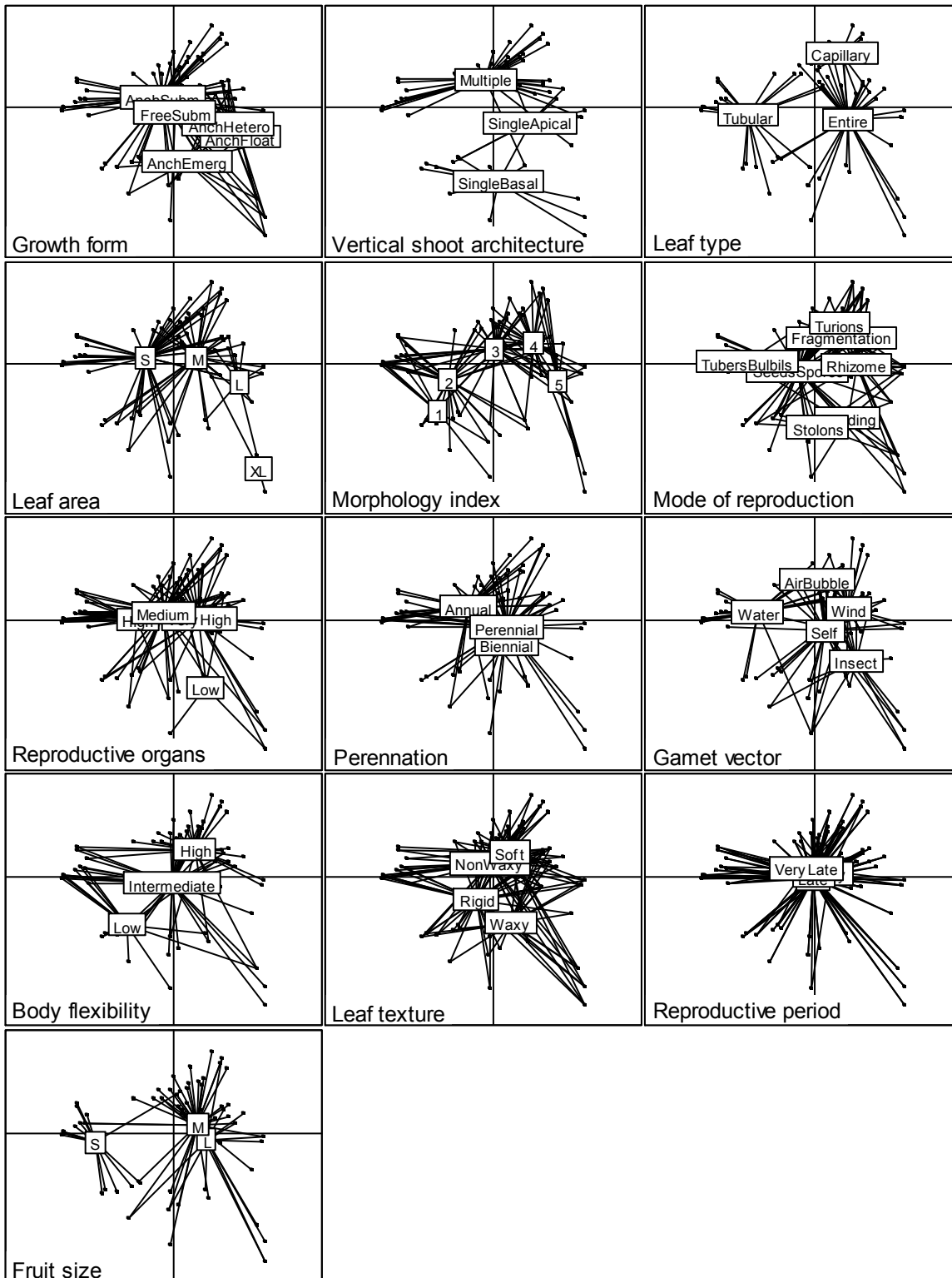


Figure 15. Ordination of species traits by fuzzy correspondence analysis. The graphs show the distribution of categories for the different traits on the first two ordination axes, explaining 18 and 12 % of the total inertia. The categories are positioned at the weighted average of species (represented by small squares) that possess that category of a trait and lines link species to their categories. Species labels are shown in Figure 16.

The first two axes separated five groups of species based on their traits, where group 2 and 3 were less well separated from each other than the other groups (Figure 16). Group 1 contains exclusively the characeans, which are separated from the vascular plants by combining small size, tubular leaves and small fruits (shared with group 4) with multiple vertical shoots (shared with group 2 and 3). Group 2 and 3 contain a large number of species that are characterised by medium-large plant and fruit size and entire or capillary leaves. The two groups overlap in trait composition, but all species in group 2 have entire leaves and all species in group 3 have shoots with multiple growth points. Group 4 contains small species, typically with a single basal growth point and rigid or waxy leaves. Most species in this group are traditionally classified as isoetids. Group 5 contains the emergent, large-leaved water lilies (*Nuphar lutea* and *Nymphaea alba*) and *Sagittaria sagittifolia*.

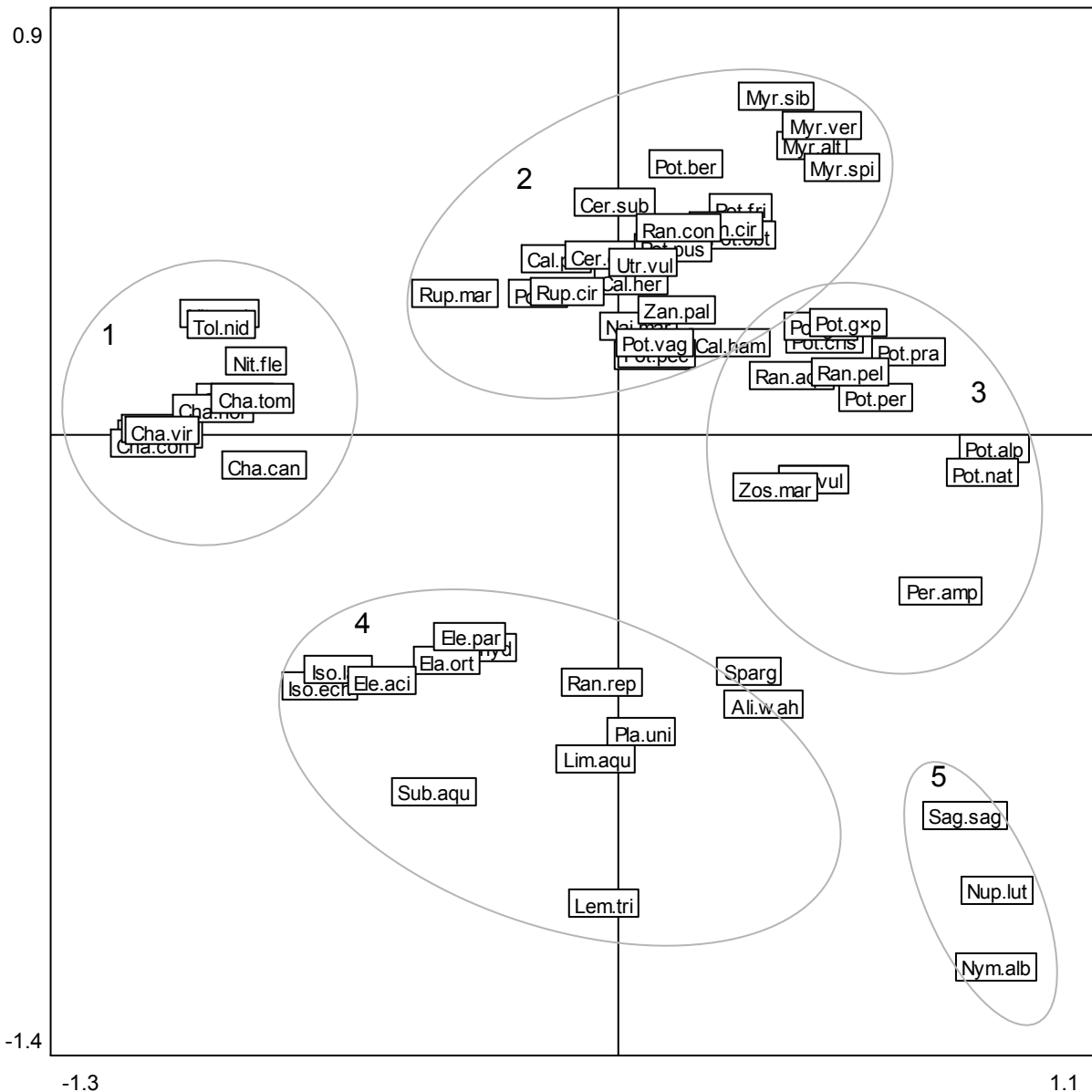


Figure 16. Ordination of species on the first two axes of the species trait correspondence analysis (0). Abbreviation of species names are given in Table 14.

### Trait-environment relationship

The strongest pattern in trait composition in the vegetation transects are shown in Figure 17A. The first two axes of the PCA display 65 % of the variation in trait composition of vegetation transects. The first axis mainly separates a small group of transects with distinct trait composition (left part of Figure 17A) from the remaining transects. This group is characterised by a large fraction of plants with single basal growth point, large leaf area and medium-sized fruits. The FCA of trait associations (Figure 15) show that this is an unusual combination of traits that is unique to eelgrass (*Zostera marina*). Figure 17B shows the environmental factors fitted as vector onto the ordination of traits, which shows that sites with this characteristic trait composition are found in low-latitude areas with high salinity and wave exposure and a large Secchi depth. This represents relatively exposed sites of the open coast of southern Sweden and the outer parts of the archipelagos and the Baltic Proper. These sites are in most cases characterised by a strong dominance of *Zostera marina* and occurrence of a few other species with a relatively similar set of traits (including *Ruppia* sp., *Potamogeton pectinatus* and *Zannicbellia palustris*).

The remaining transects are mainly separated along the second axis, where one part of the gradient is characterised by large-sized plants (morphology index 4-5) with single apical shoots, soft, intermediate-sized leaves and large seeds (upper part of Figure 17A). Wind- or self-pollination is also characteristic for plants in these transects, as is reproduction through rhizomes and fragmentation. The other part of the gradient is characterised by small plants (morphology index 2-3) with small and often tubular leaves and small seeds or spores (lower part of Figure 17A). Water pollination and an annual life cycle are also common among plants that occur in this part of the gradient. The environmental variables that are mainly correlated with the second axis are TN and chl a, both with high values in upper part of the graph (Figure 17B). This indicates that nutrient and chlorophyll concentrations can explain part of the trait composition in vegetation transects, with large-sized plants (morphology index 4-5) being more common in areas with high TN and chl a concentration. This effect is, however, only seen in sites that are not dominated by *Z. marina*.

RDA was used to test how much of the variation in trait composition that could be explained by the environmental variables. Latitude was not included in the model due to the high variation inflation factor (VIF>9) when this variable was included together with salinity in the model. The remaining environmental factors together extracted 24 % of the total variation in the trait composition and the relationship was significant according to permutation analysis. The first axis extracted the largest part of the variation (19 %) and represented the gradient in salinity and wave exposure, with both salinity and wave exposure increasing with decreasing latitude (Figure 18). Also Secchi depth and TP were correlated with this axis. A number of traits showed a clear pattern to this gradient, including vertical shoot structure, leaf area and texture, morphology index, body flexibility, mode of reproduction and fruit size. As was also shown in the PCA, communities in high salinity and wave exposure had a larger fraction of plants with single basal growth point, while communities at the other end of the gradient instead were dominated by plants with single or multiple apical growth points. The trait categories large and soft leaves, intermediate plant and seed size and reproduction with rhizomes were also more common in high salinity and exposure, whereas the characteristic traits for low salinity and exposure included small and rigid leaves and small fruit size.

The second axis represented a gradient in TN and chl a, and to some extent TP. The trait categories associated with nutrient and chlorophyll concentrations included large size (morphology index 4 and 5), intermediate leaf area, large fruits and reproduction through rhizome or fragmentation. Traits categories associated with low concentrations were instead small size, small fruits and, unexpectedly, an annual life cycle. This axis represents a much weaker gradient and explained only 4 % of the total variation in trait composition. Still, Partial RDA showed that the pressure variables (TN, TP, chl a and Secchi depth) were significantly related to the trait composition when accounting for the effect of salinity and wave exposure.

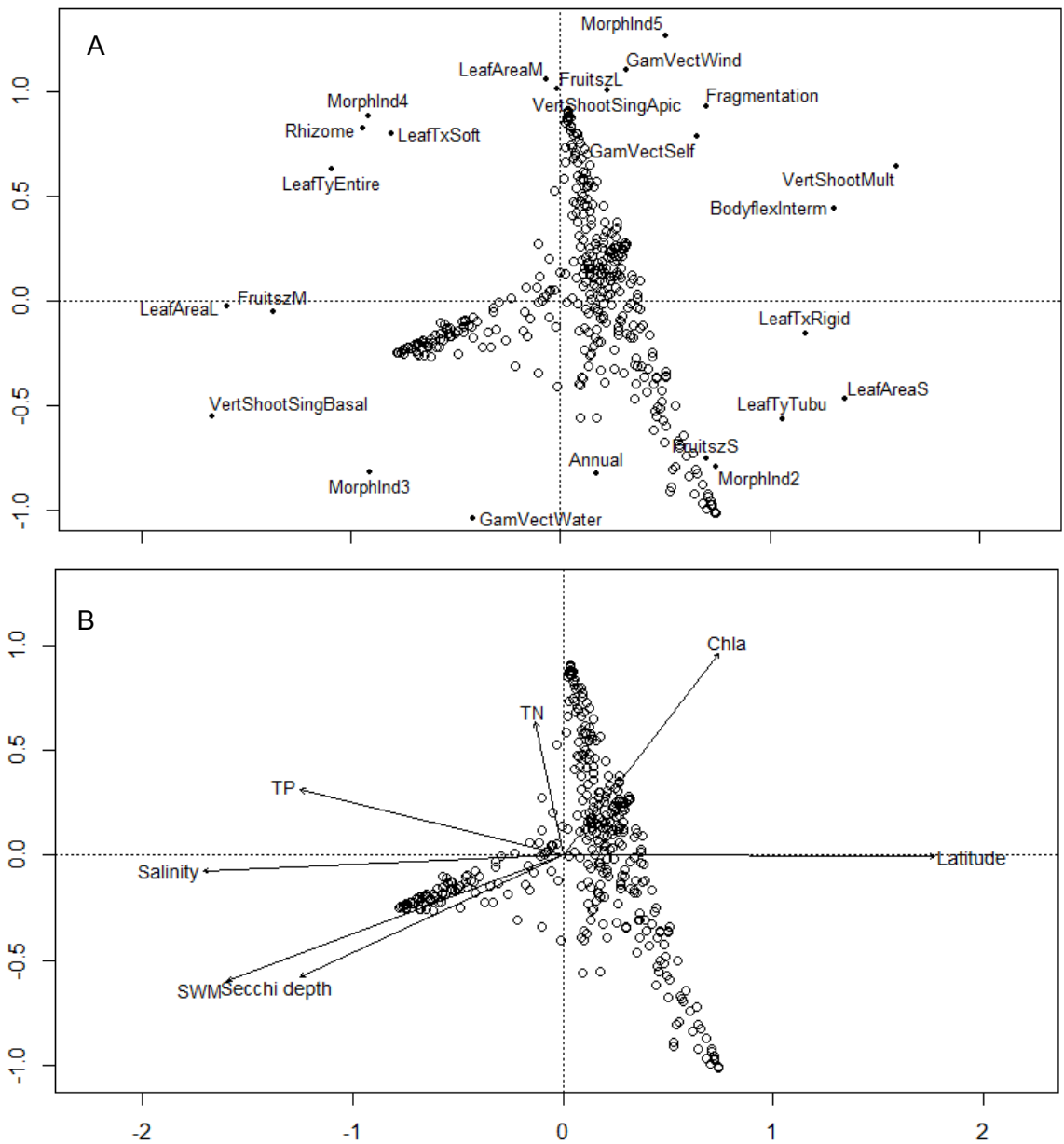


Figure 17. Principal component analysis (PCA) of trait composition in vegetation transect from the Baltic Sea and Gulf of Bothnia. A) Biplot of trait categories and transects for the first two PCA axes. For clarity, only traits that show a clear pattern to these two axes are shown. B) Plot of sites with the environmental variables fitted.

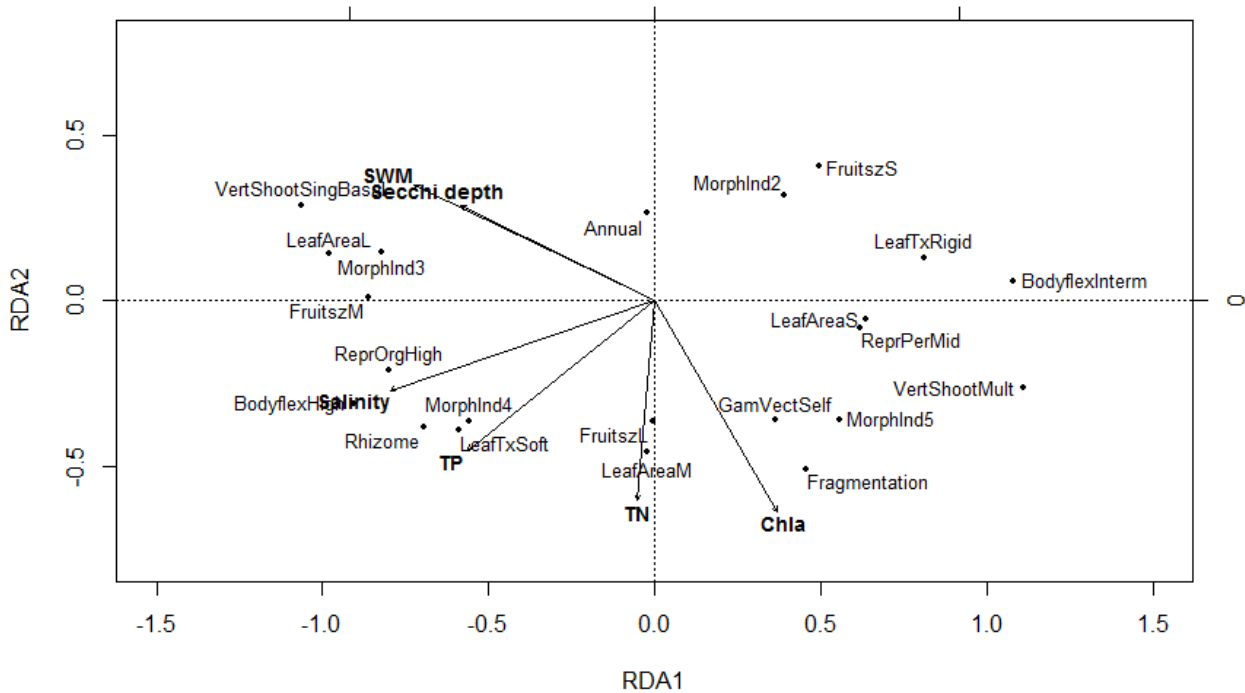


Figure 18. Relationship between trait composition in vegetation transects and environmental factors from redundancy analysis (RDA).

## 7.4 Discussion

### Relationship among traits

The main patterns in association of traits within species can be interpreted within the classical framework of plant life history-strategies, separating between “competitors”, “stress tolerators” and “ruderals” (Grime 1977). The first ordination axis separated small-sized plants with small, often tubular leaves and small seeds from large-sized plants with large leaves and larger seeds. This can be recognised as on the one hand “ruderals”, opportunistic species adapted to disturbed habitats and on the other “competitors”, adapted to stable habitats with high resource availability. The second axis largely separates the isoetids. This group is regarded as stress-tolerators with a number of adaptations to survive low resource availability, including small size, evergreen leaves and CAM photosynthesis.

The grouping of species corresponds to some extent to previous classification of freshwater macrophytes based on morphological characteristics. All isoetids grouped together and one group consisted only of nympheids (species with floating leaves). All elodeids (completely submerged non-rosette plants) were included in the poorly separated groups 2 and 3. The characeans form, not surprisingly, a group on their own with a distinct set of traits. These species are generally poor competitors, confined to environments with low resource availability or physical disturbances (e.g. Baastrup-Spohr et al. 2013). The seagrass *Zostera marina* and the estuarine *Ruppia* sp. are grouped with the freshwater plants with similar growth form (the elodeids).

### Trait-environment relationship

The trait composition of vegetation transects was correlated with both the natural and anthropogenic gradients. The most distinct pattern, which was expressed by the first axis both in the PCA and RDA, correlated with the gradient in salinity and wave exposure. This pattern was to a large extent driven by the special trait composition of communities dominated by *Zostera marina*. This is the only true seagrass species that is found in the study area, i.e. the only species able to complete its entire life cycle in the sea and tolerate oceanic conditions, and differ in ecology from the other soft substrate macrophytes that originate from brackish or freshwater. Most notably, it is excluded from areas with low salinity and is the dominating species in sandy areas with relatively high wave action. The distinct ecology of the species was only in part reflected by the set of morphological and life-history traits included in this study. In the analysis of species-trait relationships, *Z. marina* grouped with a number of species of which only a few can also be found in salinities around 6 psu and moderate wave exposure and thus typically co-occur with *Z. marina* (mainly *Ruppia* species, *Potamogeton pectinatus* and *Zannichellia palustris*). Instead, its distribution pattern is likely to a large extent explained by ecophysiological traits related to its marine origin (e.g. salinity tolerance). It also has a number of traits related to energy storage, including rhizomes, vegetative spread and a large overwintering biomass, which makes it well adapted to low light and nutrient availability (Kautsky 1988). This unique combination of functional traits and ecology highlights that *Z. marina* plays a special role in the Baltic Sea that cannot easily be replaced by any other species.

Most of the other soft sediment macrophyte species occurring at the Swedish Baltic Sea coast are confined to areas with lower salinity and/or wave exposure. Three of the groups identified in the traits analysis (groups 1, 4 and 5) were only found in low salinity and wave exposure. Accordingly, transects in this part of the gradient varied more in trait composition, separating along the second axis of the PCA. The traits that were correlated with this axis were to a large extent similar to those correlated with the first axis of the species-trait analysis, i.e. plant, leaf and seed size, depicting a gradient in Baltic Sea plant communities from domination of small to domination of large-growing species. This gradient was partly correlated with the gradient in nutrient load. As expected short, often rosette-forming species dominated at low TN and chlorophyll concentrations, while tall species dominated at high TN and chlorophyll concentrations. Such change in community composition from small to large species along a productivity gradient has been documented from freshwater systems (e.g. Chambers 1987, Baastrup-Spohr et al. 2013) and supports the general notion that large size and possession of large seeds give a competitive advantage when resource availability is high. In aquatic systems, species that concentrate a large part of their biomass close to or at the surface are also less sensitive to reduced light availability due to phytoplankton blooms.

However, the environmental factors connected to human disturbance could only explain a few percent of the total variation in trait composition between transects. This could either indicate a large random variability in trait composition or that other factors are more important in determining trait composition. We know that salinity is an important factor for species distributions in the Baltic Sea and although salinity tolerance was not included among the investigated traits it could act on trait composition if some traits or trait combinations are more or less common in species with different salinity tolerance. Previous studies of brackish water or freshwater macrophytes have also emphasised the importance of disturbance (Kautsky 1988) or temporal and spatial variability (e.g. Bornette 1994, Willby et al. 2000) for the distribution of species with certain trait combinations or life-history strategies. Since we were most interested of the effects of water quality, we tried to reduce the effect of natural disturbance on trait composition by excluding data from the shallowest depths that are frequently disturbed by ice and emersed during low water. Still, disturbance by water level fluctuations and ice may have influenced the results. Wave exposure may also be an important factor, acting both by disturbing the plant communities and affecting sediment composition, although we could not clearly separate the effects of salinity and wave exposure in our data.

Thus, our results show that some traits and trait combinations are correlated with the gradient in human pressures, but that the pattern is relatively weak and other environmental factors are likely to interact with human pressures to shape the trait composition of soft bottom vegetation. More studies on the effect of natural gradients on trait composition are needed before we can conclude on the possibility to use trait composition as indicator of the ecological status of coastal ecosystems. For instance, it would be interesting to investigate the trait composition in a more narrow salinity range and include more data on natural disturbances.

One clear conclusion is however that a trait-based indicator for soft bottom vegetation could only be developed for areas with low salinity and wave exposure, where the species pool is large enough to include a range of attributes and trait combinations. For comparison, studies that have documented anthropogenic effects on trait composition of benthic invertebrate communities have included where effects of anthropogenic disturbance on trait distribution is documented have included more than 100 species (e.g. Usseglio-Polatera et al. 2000, Oug et al. 2012). In the open, high-salinity parts of the Baltic Sea proper, as well as on the Swedish west coast, a more promising approach is to look specifically at the distribution and abundance of *Zostera marina*, and possibly the relative abundance of this species compared to the abundance of opportunistic macroalgal species. Such seagrass indicators are already in use for the WFD in several European countries, including areas in the Baltic Sea (Marbà et al. 2013).



## 8. Species richness of macroalgae

### 8.1 Introduction

A high species diversity of marine biota in a given habitat is often associated with a good environmental status. High biodiversity is, therefore, a common target in marine management as exemplified by the Water Framework Directive and the Marine Strategy Framework Directive. Accordingly, the species richness / diversity of macroalgae and other biota are commonly used indicators of ecological quality and ecosystem status. However, variables which are not directly related to environmental quality also affect species richness and contribute to define its upper boundary and, therefore, must be taken into account when attempting to apply species richness as a quality indicator. These variables include salinity, physical exposure, seafloor characteristics, habitat size as well as dispersal potential of the benthic marine biota (Middelboe et al. 1998, Josefson & Hansen 2004).

The number of macroalgal species decreases markedly from the Skagerrak through the Kattegat and Öresund to the inner Baltic Sea (Figure 4, Nielsen et al. 1995, Middelboe et al. 1997), and declines in the species number also typically occur from outer to inner parts of the coast (Klavestad 1978, Middelboe et al. 1998 and 2004). Reduced salinity is a main driver of these reductions in macroalgal species richness along the Baltic gradient, a relationship which reflects that macroalgae arose and evolved in marine waters and from there have spread to brackish environments. But the large-scale reduction in salinity across the Baltic Sea is also accompanied by increasing distance to the mother populations of macroalgae in the Skagerrak and given the relatively young age of the Baltic Sea it is likely that dispersal limitation contributes to the low species richness in the inner Baltic Sea (Middelboe et al. 1997). Reductions in salinity from outer to inner parts of fjords and archipelagos are also typically associated with reduced physical exposure, softer sediments, nutrient enrichment and reduced water clarity which directly and also indirectly, by reducing the area available for colonization, can affect the species number. Such combined effects of eutrophication-related variables and inherent habitat characteristics on macroalgal species richness have been explored at the entrance of the Baltic Sea in the Skagerrak, Kattegat and Öresund region (Littler and Murray 1975, Klavestad 1978, Middelboe et al. 1998, Pedersen & Snoeijs 2001) but no information of this type is available at the larger scale along the gradient from the entrance to the inner part of the Baltic Sea.

Based on a large monitoring dataset covering the entire Swedish coastline this study aims to identify how the number of macroalgal species on hard substrata relates to habitat characteristics reflecting eutrophication and inherent habitat characteristics from the entrance to the inner part of the Baltic Sea.

### 8.2 Methods

#### Data and study area

Overall information on the dataset and study area is provided in Ch. 3. The dataset extracted for analysis is basically the same as for analysis of cumulative cover of macroalgae (Ch. 5). Note that some taxa were grouped be-

fore analysis in order to reduce differences between different datasets. This means that real species richness probably is higher than the values we have used.

### Analysis

Analysis is conducted as described for the cumulative cover of macroalgae (Ch 5) with slight modifications as described below. The depth relationship is categorical instead of linear (dividing depths into classes of 2 m, i.e. 0-2 m, 2-4 m, etc.) because the nature of the relationship is unknown and therefore has to be estimated for specific depth intervals separately. The response variable is ‘taxon richness of macroalgae’ defined as the number of macroalgae taxa identified. The common base for assessing the number of taxa is ‘segments’ along the transect line. The counted number of taxa in each segment of the transect was assumed Poisson distributed.

Moreover, an extra term,  $\log(\text{segment}_{length})$ , was added to the model (Ch. 5, Eq. 1) for macroalgae taxon richness to account for an expected increase in diversity with increasing length of transect segment i.e. increasing area surveyed (monitoring effort). For each region marginal means for areas, years and months were computed from the parameter estimates of Eq. (1) by averaging over the other factors in the equation and choosing a standard segment length of 5 m. Since maximum depths varied from 10 m in inner coastal areas of the Bothnian Bay to 30 m in other regions, the area-specific marginal means for the number of macroalgal taxa were computed for depths up to 10 m only.

Since the taxon richness model was complex (Poisson distribution and with segment length as covariate) the full model did not converge for all regions and the number of factors had to be reduced. Diver-specific variation was excluded as it was not possible to estimate the diver-specific variation for any of the regions. The seasonal variation was excluded for analysis of the Bothnian Bay as well as for Bothnian Sea inner where it could not be estimated; however, this variation was unlikely to be significant given the few months spanned by the monitoring data. Finally, the random variation between transects within areas was excluded from analysis of Bothnian Bay inner and Bothnian Sea inner. Overall, it was difficult to get the full model to converge in the two regions in the Gulf of Bothnia because the low number of macroalgal species in these regions results in less variation for estimating the many parameters.

## 8.3 Results

The random variation between transects in given areas was significant except for the Southern coast (Table 15) but was still consistently lower than the residual variation (Table 16) suggesting a considerable small-scale patchiness of macroalgal taxon richness. Spatial differences between areas were also significant with the exception of Bothnian Bay outer. Segment length had a highly significantly positive effect (except in the Bothnian Bay where the species number was extremely low), reflecting that the number of identified species is strongly dependent on the monitoring effort/the area examined.

All regions, except Bothnian Bay inner, showed a consistent depth-relationship (Table 15) with decreasing taxon richness from the surface or just below the surface (Figure 19). These depth-patterns were most pronounced for the Baltic Proper and West coast, where monitoring data spanned over 20 m. By contrast, in the inner Bothnian Bay the overall number of macroalgal taxa was so low that it was difficult to observe any differences at all.

The macroalgae taxon richness was consistently higher in outer coastal regions than inner coastal regions (Figure 19). A distinct geographical pattern was also observed from the low diversity regions in the Bothnian Bay (~1-2 species observed per segment), increasing up to 3-5 taxa in the Bothnian Sea and Baltic Proper, followed by a slight increase at the Southern coast (~6-8 taxa) and a further doubling on the West coast. This distinct geographical pattern suggests that salinity is a major driver of macroalgal taxon richness.

TABLE 15

Test of fixed and random factors for modelling the number of macroalgal taxa. P-values less than 0.05 are highlighted in bold. The diver-specific random variations could not be estimated with the generalized linear mixed model for any of the regions, and the model has to be reduced for Bothnian Bay and Bothnian Sea inner to ensure converge. Note that depth is a categorical factor in this model.

Region	Number of obser- vations	Fixed factors					Random factor Tran- sect
		Area	Year	Month	Depth	Segment length	
Bothnian Bay inner	104	<b>0.0079</b>	0.2078	N/A	0.5548	0.0941	N/A
Bothnian Bay outer	269	0.6720	<b>&lt;0.0001</b>	N/A	<b>0.0049</b>	0.6279	<b>0.0196</b>
Bothnian Sea inner	1040	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	N/A	<b>&lt;0.0001</b>	0.4635	N/A
Bothnian Sea outer	951	<b>0.0127</b>	<b>&lt;0.0001</b>	0.0868	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Baltic Proper inner	4037	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Baltic Proper outer	3775	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>
Southern coast	106	<b>0.0343</b>	0.1753	0.3046	<b>0.0024</b>	0.1720	0.2646
West coast inner	606	<b>&lt;0.0001</b>	<b>0.0013</b>	0.7695	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0005</b>
West coast outer	1331	<b>0.0037</b>	<b>&lt;0.0001</b>	<b>0.0292</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>0.0002</b>

TABLE 16

Variance estimates for the random factors and their relative contribution to the uncertainty associated with individual segment observations of taxon richness.

Region	Number of obser- vations	Variance estimates		Relative uncertainty	
		Transect	Residual	Transect	Residual
Bothnian Bay inner	104	N/A	0.6577	N/A	125%
Bothnian Bay outer	269	0.2406	0.2790	63%	70%
Bothnian Sea inner	104	N/A	0.7193	N/A	134%
Bothnian Sea outer	951	0.0996	0.4909	37%	102%
Baltic Proper inner	4037	0.1077	0.4878	39%	101%
Baltic Proper outer	3775	0.0574	0.4922	27%	102%
Southern coast	106	0.0054	0.2754	8%	69%
West coast inner	606	0.0710	0.8485	31%	151%
West coast outer	1331	0.0334	0.4732	20%	99%

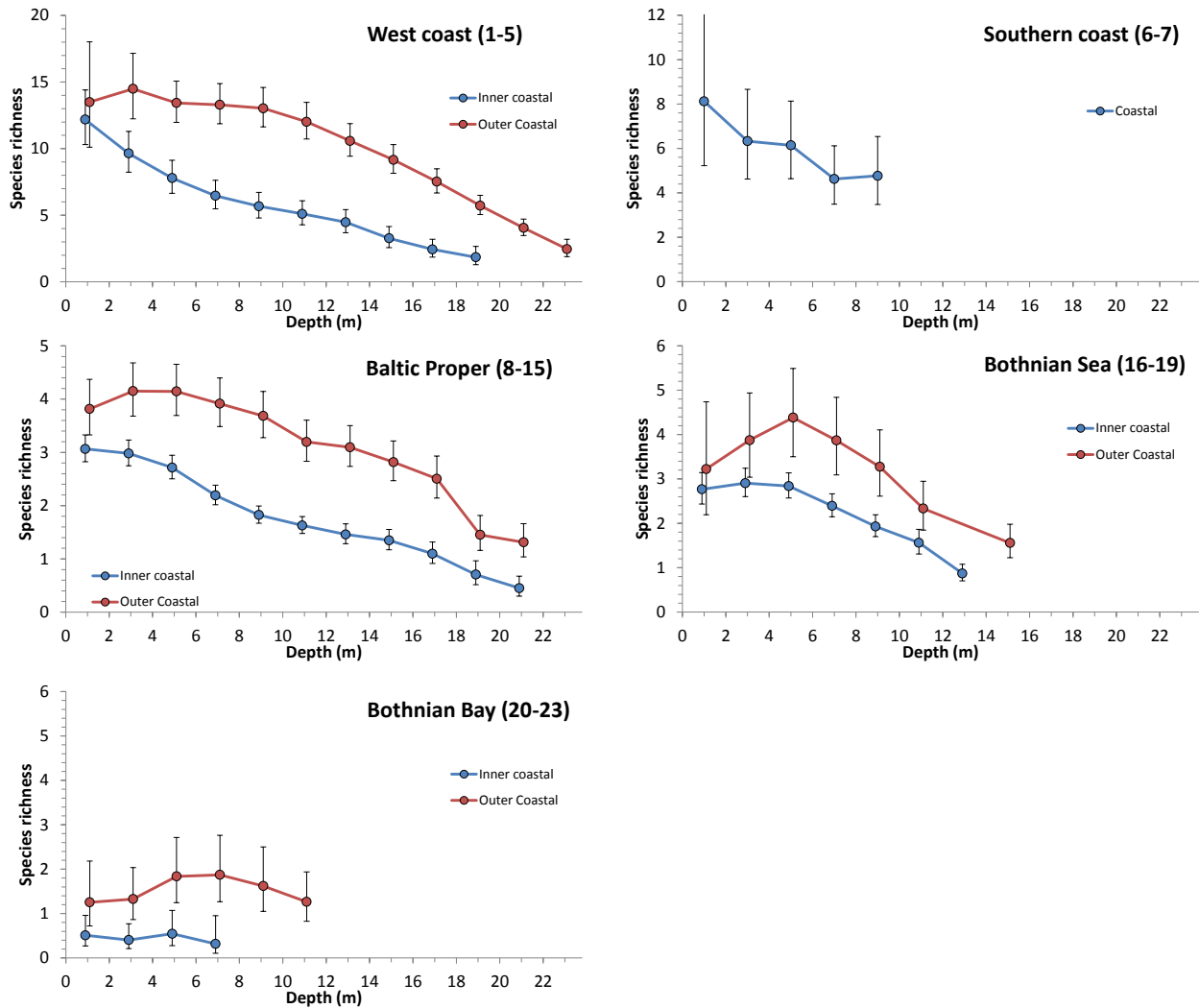


Figure 19. Estimated depth relationships for macroalgal taxon richness for the nine regions. Numbers after the inserted regional name refer to the Swedish WFD typology. Error bars mark the 95% confidence interval for the geometric means.

The interannual variation in taxon richness was significant in seven of the nine regions (Table 15, Figure 20). For most of these regions there was no consistent pattern, but the Baltic Proper had a significant increase in taxon richness, both in the inner (linear regression,  $P=0.0005$ ) and outer (linear regression,  $P=0.0119$ ) coastal regions over the monitoring period 2000-2013. The inner coastal region of the West coast also showed a general increasing tendency, albeit it was borderline significant (linear regression,  $P=0.0541$ ). Although there was a general significant trend in the Baltic Proper outer region, the taxon richness peaked in 2009 and decreased in the following years. The most significant seasonal patterns were found in the Baltic Proper that covered more months of the year than the remaining areas; significant seasonal patterns were also identified for the West coast outer (Table 15, Figure 20).

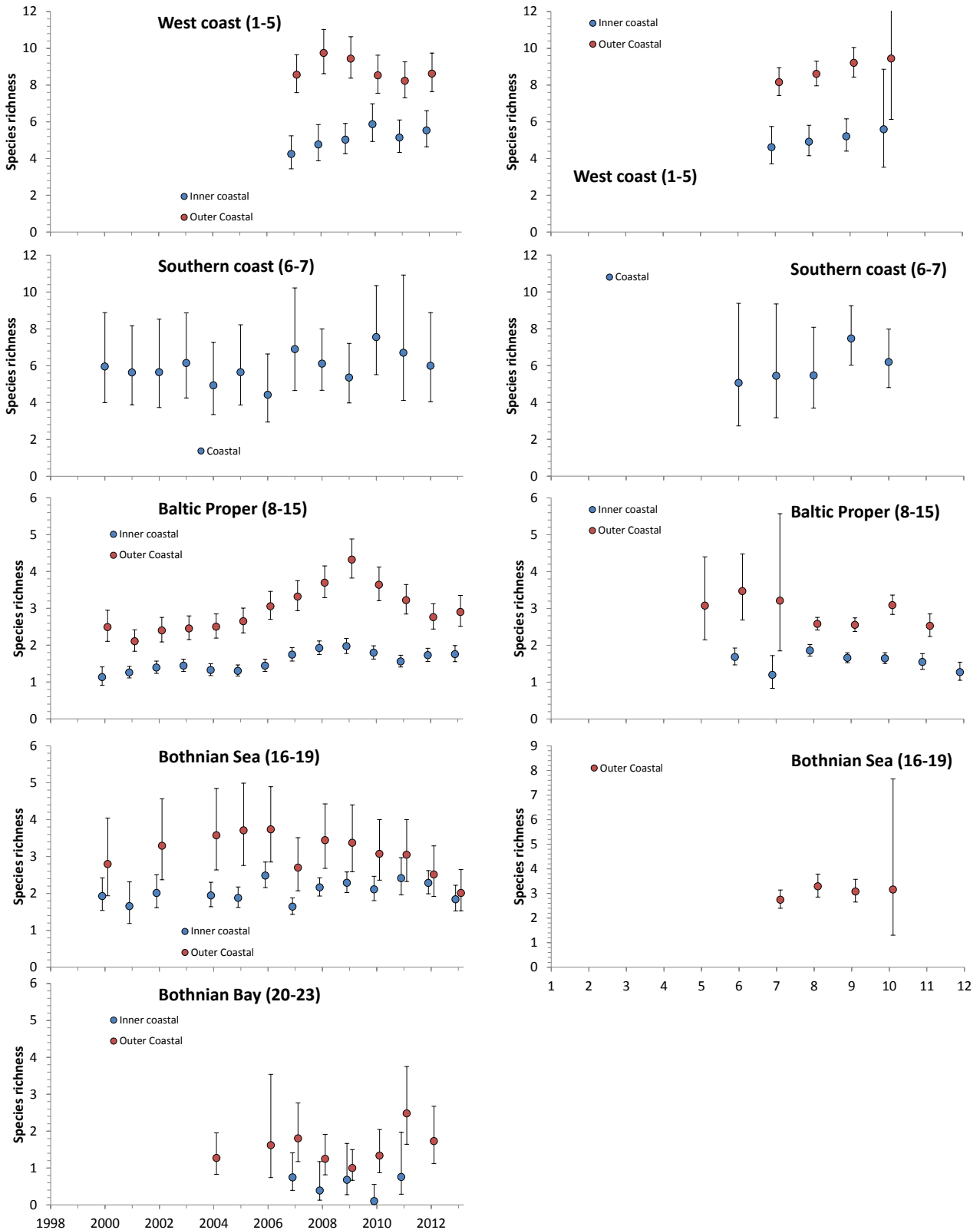


Figure 20. Estimated interannual (left panel) and seasonal variation (right panel) for macroalgae species richness in nine regions. Seasonal variation was not modelled for Bothnian Bay and Bothnian Sea inner. Numbers after the inserted regional name refer to the Swedish WFD typology. Error bars mark the 95% confidence interval for the geometric means.

The area-specific marginal means for macroalgae species richness were significantly related to a combination of four environmental variables (Figure 21); a positive, non-linear relationship with salinity ( $P < 0.0001$  for linear component and  $P < 0.0001$  for smoother) and positive, linear relationships with Secchi depth (slope=0.126;  $P < 0.0001$ ), log(SWM) (slope=0.088;  $P = 0.0004$ ), and log(TN) (slope=-0.493;  $P = 0.0190$ ). The descriptive geographical pattern suggesting salinity as a driver was confirmed with the GAM approach. The expected median number of species, for average values of log(SWM), Secchi depth and TN, increased from 1 to 6 over the entire salinity range. Observed species richness at the West coast were higher, but this area is also characterized by high physical exposure, good light conditions and low nutrient levels. Thus, the combination of these factors suggests an expected even higher number of macroalgae species on the West coast. Physical exposure promoted macroalgae diversity by a factor 2 from sheltered towards exposed areas. Secchi depth had a positive effect on species richness by doubling the number of species over the range from 1 to 8 m. Finally, nutrient enrichment reduced species richness slightly, suggesting that eutrophic areas have a poorer macroalgae community. Similar results were obtained using modelled environmental variables with chlorophyll substituting for Secchi depth and TN (Figure A4). The relationship with modelled chlorophyll was negative, as expected, consistent with the positive relationship for Secchi depth and the negative relationship for TN obtained with monitoring data.

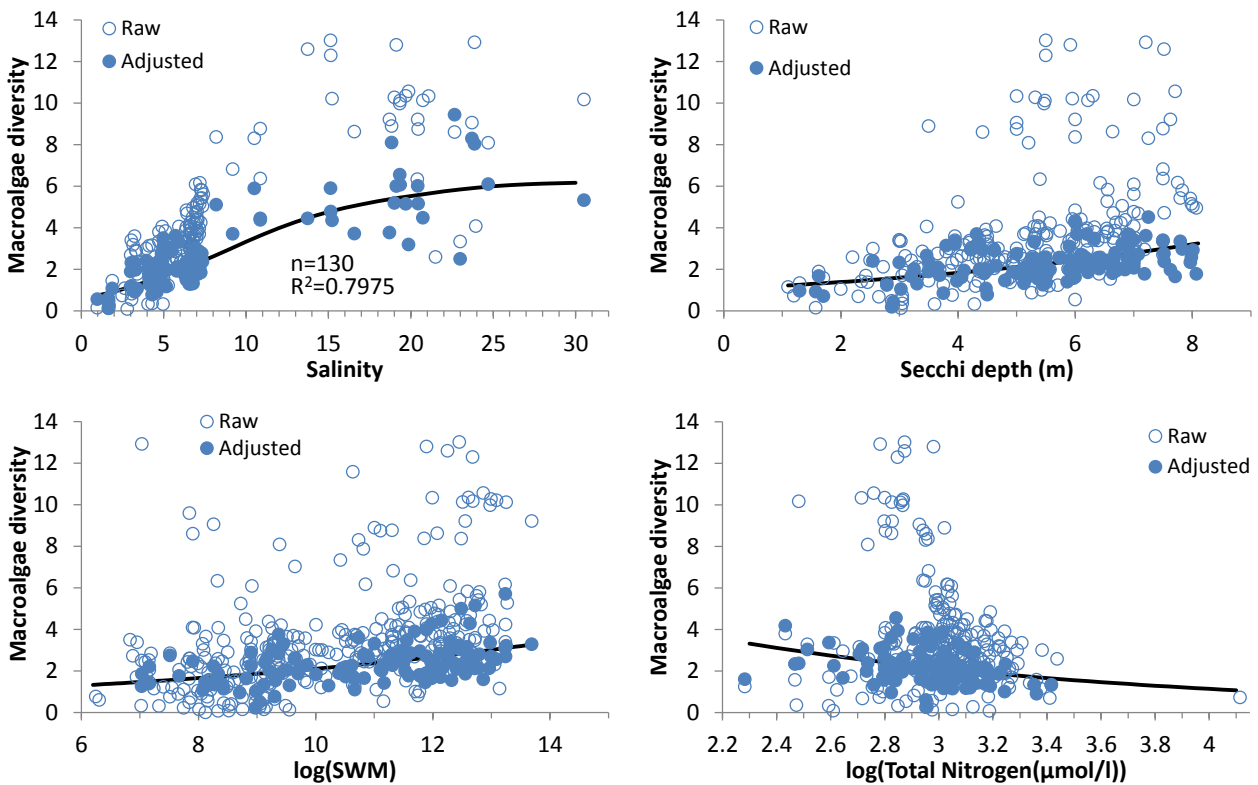


Figure 21. GAM relationships between area-specific means of macroalgae species richness (Poisson distributed with log-link) and environmental variables obtained from monitoring data. Open symbols show the area-specific means (raw) and filled symbols show the means adjusted for variations explained by the other three factors in the GAM model. Expected mean taxon richness was adjusted to average salinity of 6.5, Secchi depth of 5.1 m, log(SWM) of 10.1, and log(TN) of 3. Adjusted means could only be calculated for areas where data on all environmental variables were available. Statistics for the GAM are inserted in the salinity plot.

## 8.4 Discussion

The long salinity gradient in Swedish coastal waters makes it challenging to use diversity as indicator of ecological quality. As expected, the species richness in transects paralleled the large differences in the number of macroalgal species occurring in different coastal areas (Nielsen et al 1995, Middelboe et al. 1997). For instance, the number of species found in transect sections at a certain depth was three to four times larger in the West coast compared to the Bothnian Sea, which can be compared with the decrease from more than 300 species recorded in Kattegat to less than 100 recorded in the Bothnian Sea. This reflects that the number of species that occurs in a region (the regional species pool) is one important determinant of small-scale (within-transect) diversity (e.g. Ricklefs 1987). Salinity is likely the most important driver of the difference in species richness between regions, although other factors such as dispersal limitation from the source populations in Skagerrak may also contribute (Middelboe et al. 1997).

However, apart from salinity we could show that a number of other factors contributed to determine macroalgal richness in transect sections. Firstly, species richness increased with physical exposure. This may be connected to disturbance from waves and ice that remove dominant species and allow colonization of less competitive species (e.g. Connell 1978). An alternative but not exclusive explanation is that wave exposure increase the amount of hard substrate in an area, by washing away fine sediment from the sea floor. All transects included in our analyses were dominated by hard bottom, but the species richness may also be affected by the amount of suitable habitat for macroalgae in the surrounding area that can support the local community with colonists.

Secondly, macroalgal species richness decreased with increasing TN and chlorophyll concentration and decreasing Secchi depth. A similar correlation between macroalgal richness and water quality variables has previously been shown for Danish fjords (Middelboe et al. 1998, Middelboe & Sand-Jensen 2004), but we show that the same relationship holds also for the entire Baltic Sea when accounting for the gradient in salinity. The decrease in species richness may be due to loss of species that are sensitive to eutrophication, i.e. slow-growing species that are over-shadowed and outcompeted by fast-growing species that are favoured by high nutrient availability.

However, the decrease in species number with increased eutrophication may also be explained by a reduction of light energy reaching the sea floor, which is a crucial resource for benthic seaweeds. Our analyses showed that macroalgal richness was strongly related to depth. In the outer, more exposed regions there was a tendency of peak richness at 2-6 m depth, which could be explained by strong exposure and ice restricting survival of many species in the shallowest depth interval. But overall there was a decrease in richness with depth, which we interpret as the effect of decreasing light availability with depth. In shallow areas, the high light levels allow formation of multi-layered seaweed communities where many species can coexist, while deeper areas can only house a restricted number of shade-tolerant species. Thus, changes in water quality that decreases the width of the depth interval with optimal growth conditions and high macroalgal diversity can be expected to decrease the mean diversity of vegetation transects.

The fact that species richness responded to differences in water quality across the Baltic Sea, when accounting for differences in salinity and wave exposure between areas, shows that this vegetation variable could possibly be used as indicator for ecological quality of coastal vegetation. However, the strong effect of salinity on species richness means that the use of such indicator will require high-quality salinity data on relevant temporal and spatial scales. If such data is not available, there is a risk that inter- and intra-annual variation in salinity, as well as small-scale salinity gradients within water bodies, gets a large influence on the indicator value.

The Bothnian Bay stood out compared to the other regions with less than two species per transect segment and small differences between depth intervals and water bodies. Very few macroalgal species can grow and reproduce in the very low salinity (<4 psu) of this region and the vegetation is dominated by a few species with similar depth distribution (Bergström & Bergström 1999, Johansson et al 2012). It is therefore unlikely that changes in water quality will affect macroalgal species richness in this region. It is possible that species richness of soft-

bottom macrophytes (vascular plants and charophytes) could instead be used to indicate ecological quality in coastal areas with very low salinity. In Danish fjords, eutrophication in combination with reduced salinity has been associated with reduced species richness of vascular plants (Mathiesen and Nielsen 1956, Nielsen et al. 2003) and eutrophication has been suggested as a reason for decline in species richness of charophytes in Swedish coastal areas (Blindow 2000). It would, therefore, be interesting to go further by exploring which factors regulate species diversity of soft-bottom macrophytes in coastal areas of the Baltic Sea.

An interesting result that we have not explored further is the large temporal variation in species richness, both within and among years. In some of the regions we could document temporal trends in macroalgal richness, for instance in the Baltic proper where there was a general increase up to a peak in 2009, but there were also seemingly erratic differences between years in several regions. It would be interesting to see to what extent this variance can be explained by environmental drivers, for instance salinity, and to what extent it reflects random variation or methodological differences. Taxonomic richness is very sensitive to differences in the area that is surveyed, as was clearly shown by the significant positive effect of segment length in species richness, as well as on the methods used for identification (e.g. if microscopic characters are examined or not) and taxonomic expertise. If the long-term trends in species richness are due to changes in monitoring methods or taxonomic training of divers, this is important to acknowledge when establishing reference conditions for a species richness indicator. Another important implication is that monitoring for a species richness indicator requires a fixed effort, e.g. by using a fixed size of the investigated surface area, defining a set of species that should be looked for in a certain region and which taxa have to be identified under microscope.

In conclusion, species richness of macroalgae responded to anthropogenic pressures when accounting for natural gradients in salinity and physical exposure and normalising for sampling effort (area surveyed). This implies that macroalgal richness could be used as indicator of ecological status, except in the Bothnian Bay with constantly very low richness, but this requires careful consideration of how to handle the strong effect of salinity on the indicator and the development of a suitable monitoring method.



## 9. Conclusions

All the candidate indicators responded to eutrophication gradients, characterized by nutrient concentrations, chlorophyll concentrations and/or Secchi depth, when accounting for natural gradients in salinity, latitude and physical exposure. Cumulative cover of macroalgae on hard substrate was the indicator that showed the strongest response to eutrophication-related variables and therefore seems a promising indicator of ecological quality. Also species richness of macroalgae could be predicted with high confidence based on natural and anthropogenic gradients, but was most strongly affected by salinity. This means that macroalgal species richness could be used as indicator of ecological quality, but only if the strong effect of salinity is carefully accounted for.

The remaining candidate indicators showed a weaker pattern to the natural and anthropogenic gradients and a large, unexplained variability. The failure of functional composition and trait-based indicators is likely at least in part due to the interacting effect of salinity and eutrophication on species composition in the long salinity gradient of the Swedish coastline. A possible way forward is therefore to explore this interaction further, by testing the candidate indicators in more restricted salinity intervals. This might enable us to find a stronger response of these indicators to eutrophication.

None of the tested candidate indicators for soft-bottom vegetation were identified as promising. This is disappointing, given that soft-bottom vegetation is an important component of coastal vegetation. We therefore suggest further studies testing whether distribution and abundance of *Zostera marina* in moderate-high salinity and diversity and/or composition of soft-bottom macrophytes in low salinity can be used as indicators for ecological quality.

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## 11. Appendices

Appendix A: Depth limits of selected species. [\*Link to the file at the WATERS webpage.\*](#)

Appendix B: GAM results using modelled environmental variables. [\*Link to the file at the WATERS webpage.\*](#)

Appendix C: Morphology and longevity classification of macroalgae, with confidence values. [Link to the file at the WATERS webpage.](#)

Appendix D: Traits of soft bottom vegetation. [\*Link to the file at the WATERS webpage.\*](#)

## Response of coastal macrophytes to pressures

This study tested a number of candidate vegetation indicators, including ‘distribution’, ‘abundance’ and ‘diversity and composition’ indicators, for their responsiveness to eutrophication and natural environmental gradients. The analyses were based on the large monitoring data set on benthic vegetation collected along the extended Swedish coastline. The clearest response of vegetation indicators to eutrophication was identified for the cover of macroalgae and the species richness of macroalgae, when accounting for the effect of salinity. The results will provide a basis for development of refined macrophyte indicators.

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